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SHOSHONI BROWNWARE FROM GRASS VALLEY, NEVADA

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ABSTRACT

A survey of 56 archaeological sites produces evidence that Shoshoni Brownware ceramics are common below the pinyon-juniper ecozone in Grass Valley, Nevada. Analysis of the large ceramic collection from these sites provides additional information about Shoshoni ceramic technology and style.

INTRODUCTION

The three pottery wares of the Shoshonean tradition, as defined by Tuohy (1965) and Coale (1963), that were manufactured in the Great Basin during prehistoric and protohistoric times are Shoshoni Brownware, Southern Paiute Utility Ware, and Owens Valley Brownware. Shoshoni Brownware has been found in central and eastern Nevada, Utah, Idaho, Wyoming, and Montana (Fowler, 1968*b*:11). Southern Paiute Utility Ware is known from southeastern Nevada, southern Utah, and northwestern Arizona (Fowler, 1968*b*:12). Owens Valley Brownware was made east of the Sierra Mountain Range in the Owens Valley and adjacent regions (Riddell, 1951:20–23; Elsasser, 1960:30). All three of these wares share common features such as "a dull brown finish, obliterated coils, and wiping marks" (Tuohy, 1965:62). Variations between the wares occur in the vessel shapes and decoration.

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Fig. 1.—Map of Nevada showing location of Grass Valley.

Unfortunately most finds of the Shoshonean tradition ceramics consist of only a handful of sherds. Large collections are rare because the pottery does not preserve well. Besides fracturing easily, some pieces are so low fired, if fired at all, that they decompose in the rains. A further complication is the color of the ceramics. The brown, unpainted surface blends into the color of many soils and cannot be seen. Because most archaeological sites in the Great Basin are surface scatters, only rarely is the pottery recovered during the excavation of a stratified midden deposit.

A direct result of this situation is a fragmentary understanding of the age, exact distribution of the different Shoshonean tradition ceramics, the types of vessels, and the nature of their manufacture and use. In fact the discovery of Shoshoni Brownware in Grass Valley, Nevada, by Molly Magee Knudtsen, was the first find of Shoshoni ceramics in central Nevada (Magee, 1964). In order to preserve the data, Molly Knudtsen systematically recorded the archaeological sites and collected the artifacts that were exposed on the surface of the sites.

During the summer field seasons of 1972 and 1973, the author joined the multi-faceted archaeological research program, directed by C. W. Clewlow, Jr., and Richard D. Ambro, which has been conducting archaeological investigations in Grass Valley since 1969 (Clewlow and Rusco, 1972; Clewlow et al., 1978). The valley has merited continuous investigation because: 1) it had a long, continuous, aboriginal occupation from prehistoric into historic times; and 2) most of the archaeological sites are very well preserved and have not been disturbed due to the vigilance of M. M. Knudtsen. The data presented in this paper are the result of research which focused on recording the pottery sites and analyzing the associated ceramics.

Setting

Grass Valley is located in Lander and Eureka counties, 26 mi northeast of Austin in central Nevada (Fig. 1). The valley, which runs slightly northeast-southwest, is about 40 mi long and reaches a maximum width of 10 mi. It is bounded on the north by the Cortez Mountains, on the east by the Simpson Park Range and on the west by the Toiyabe Range which has a maximum elevation slightly over 10,000 ft (Fig. 2).

As its name implies, Grass Valley is one of the richer biotic regions in the Great Basin. Mountain streams bring large amounts of perennial water to the valley floor; cold springs are common in the lower foothills; and hot springs dot the valley floor. The diversity of flora and fauna must have created a hospitable environment for aboriginal habitation. On the west side of the valley the pinyon-juniper zone does not extend below 6800 ft except at the northern end near Cortez. On the east side, however, the pinyon-juniper zone extends as low as 6200 ft in areas such as McClusky Creek and Wood Canyon. In the lower foothills of the mountains where pinyon and juniper trees are absent, service berries, aspens and willows parallel perennial streams, such as Skull Creek.

The valley floor ranges in elevation between 5600 and 6200 ft. The northern end of the valley is covered by a large, dry lake bed called a playa lake. Most of the southern end of the valley is either under cultivation or used to graze cattle and horses. Formerly, the entire region, both the valley floor and mountains, was used by Basque herders to graze their sheep. Today the uncultivated plants in this zone are sagebrush, rabbitbrush, greasewood, Great Basin rye, hologeton, and salt brush. Along the creeks grow various grasses and tule reeds.

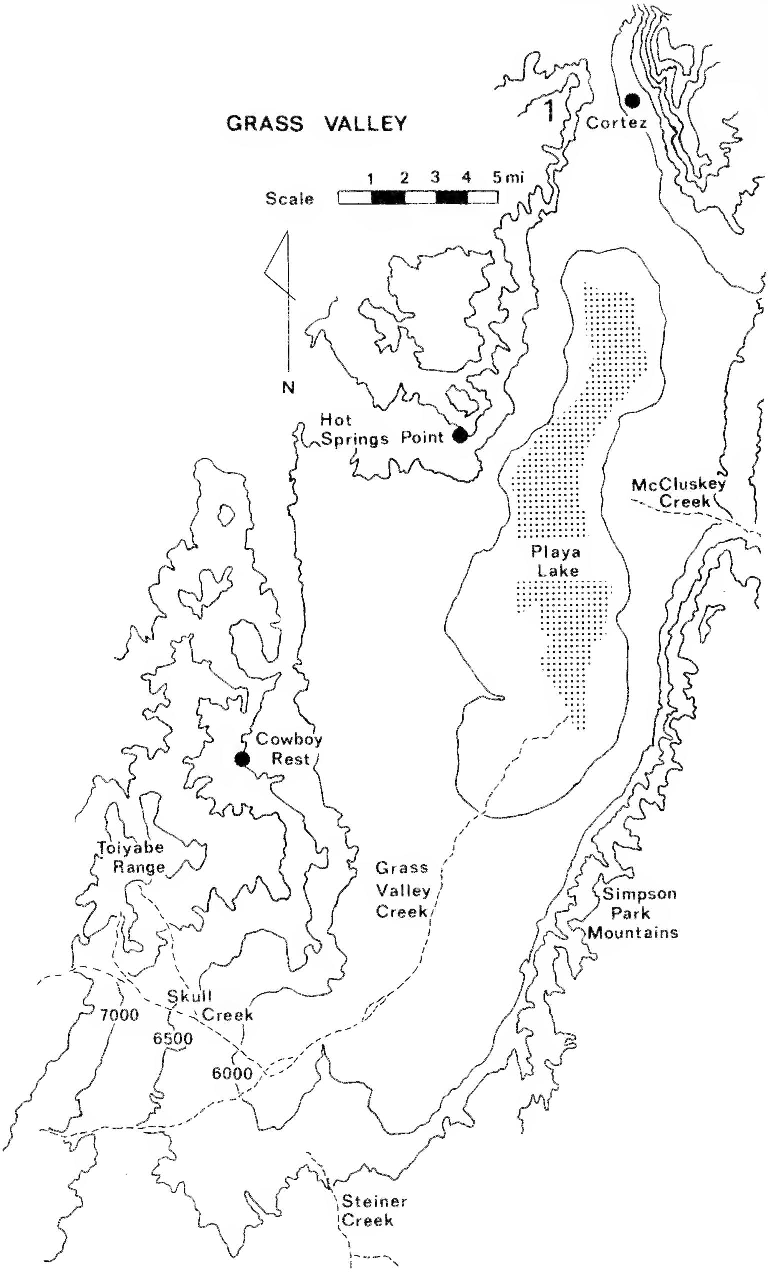

Fig. 2.—Map of Grass Valley, Nevada.

SITE SURVEY

Fifty-seven archaeological sites with Shoshoni Brownware were surveyed in 1972 and 1973. Fifty-six of the sites were located in Grass Valley and one site was at the northern end of the Great Smokey Valley. Fifty-five of the sites had been previously recorded and collected by Molly Magee Knudtsen. The two remaining sites were discovered by the Grass Valley Archaeological Project.

The purpose of the survey was to record the ecozone location and to determine the cultural components of each site. Therefore, the sample was limited to known pottery bearing sites and is not the result of a stratified, sampling procedure. Instead, the sample reflects the areas visited by Molly Knudtsen and the zones surveyed by the Grass Valley Archaeological Project.

Site Types

The classification of the sites is a modified version of the site categories proposed by Fowler (1968*a*:9) for the Great Basin. He divided sites into seven categories: 1) chipping stations, 2) gathering sites, 3) campsites, 4) quarry sites, 5) village sites, 6) rockshelters, and 7) petroglyph panels. Quarry, rockshelter, and petroglyph panel were not applicable to the sites in this survey. Fowler defines three of the other four as follows: 1) chipping station—a site with no cultural deposit, only flakes and chipped stone implements; 2) gathering site—a site in the pinyon-juniper zone where seeds and roots could be procured, or a site near grasses; 3) campsite—a site with hearths and cultural deposit. Fowler does not present a definition of a village site. Certain problems arise between the application of chipping station and gathering site to the Grass Valley situation. Following the divisions above, the presence of pottery would immediately place a site in the gathering category because a chipping station has only flakes and chipped stone implements. In many instances, however, sherds were associated only with debitage and it is possible that the vessels do not reflect gathering activities at the site. When all other cultural remains point to a chipping station, the site is categorized as a chipping-gathering station. Sites without hearths but with ground stone implements, manos and metates, are considered to be gathering sites. When hearths and other cultural debris are present, the site is a camp. A village is a site with several permanent dwellings, hearths and assorted cultural remains. An isolated site refers to a location where the sherds are not associated with any other cultural remains.

Description of the Sites

A brief description of the location, components and previously published information on each site is presented below. The location of site #1 is shown in Fig. 2, sites #2–56 are on Fig. 3, and site #57 is located south of Grass Valley. Table 1 summarizes this information as well as categorizing the type of artifacts at each site. Most of the artifacts are self-explanatory. However, trade goods refer to items, such as beads, in a situation where contact with the migrating, non-aboriginal population probably was still indirect; house rings refer to the foundations of permanent structures; and historic artifacts include horseshoes, harmonicas, and metal implements indicative of the historic period.

1. *Cortez Canyon.*—The site is a prehistoric camp, situated near a spring at the lower limits of the pinyon-juniper zone.

2. *Hot Springs Point.*—This isolated sherd scatter is near a group of hot springs, west of the playa lake on the valley floor.

3–7. *McCluskey Creek* A, B, C, D, E.—All five sites are prehistoric camps or gathering sites on the McCluskey Creek drainage and the Sage Hen Canyon tributary in the pinyon-juniper zone. McCluskey Creek D was described by Magee (1967:226) and incorrectly located in Wood Canyon instead of Sage Hen Canyon. McCluskey Creek E

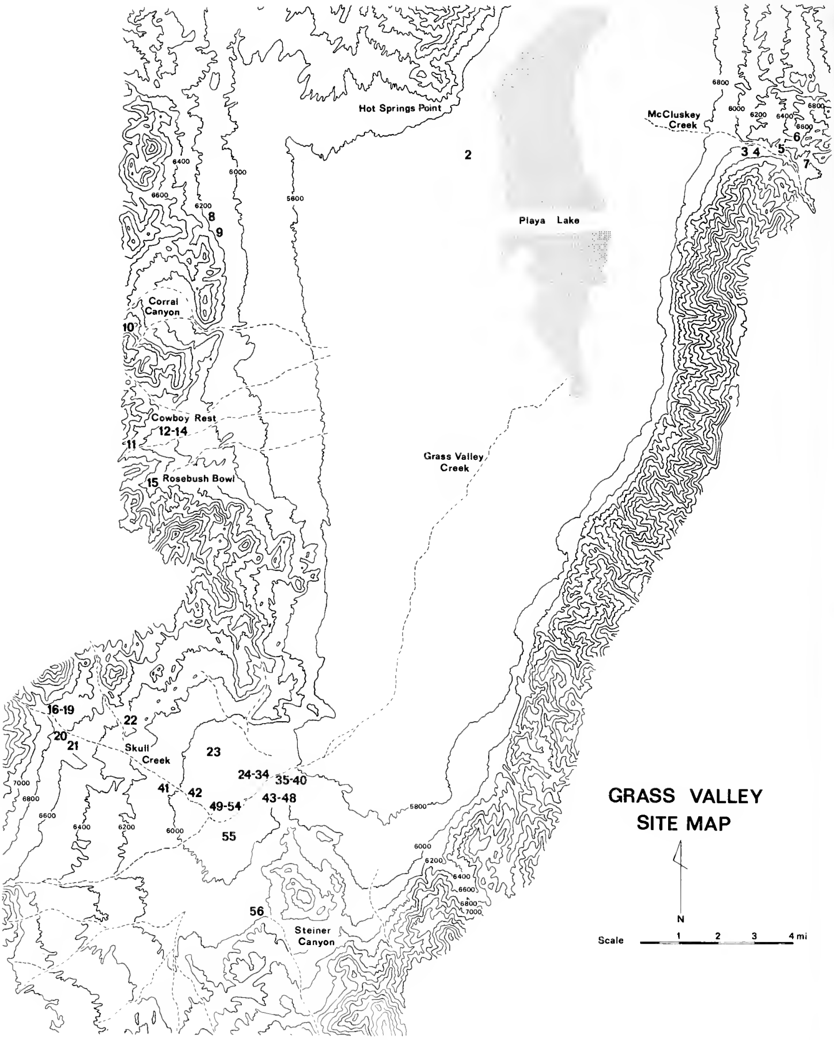

Fig. 3.—Map of southern two-thirds of Grass Valley, Nevada, showing the locations of the archeological sites.

also was discussed in the same article and was referred to as Baummann Pottery Site 2 (1967:226).

8–9. *Stink Hole* A, B.—The Stink Hole sites are north of Corral Canyon on the valley floor, adjacent to the foothills. At both of these sites the sherds were associated with hearths and flaked, stone tools, indicating a camp site.

10. *Corral Canyon.*—This isolated surface scatter of sherds is in the pinyon-juniper zone near a spring and annual stream.

11–14. *Cowboy Rest* A, B, C, D.—These four sites are prehistoric chipping-gathering stations along Cowboy Rest Creek. Only Cowboy Rest A (#11) is in the pinyon-juniper zone. Several other prehistoric hunting and gathering sites are known along Cowboy Rest Creek and Canyon (Clewlow and Pastron, 1972:23, Fig. 3; 25, Fig. 5).

15. *Rosebush Bowl Canyon*.—This is an isolated surface scatter of sherds in the pinyon-juniper zone. In the vicinity are several prehistoric hunting and gathering sites (Clewlow and Pastron, 1972:23, Fig. 3; 25, Fig. 5).

16–19. *Skull Creek* A, B, C, D.—All four sites are prehistoric chipping-gathering stations, located along the north side of Skull Creek in the vicinity of a spring. Also in the area are a prehistoric gathering site (Clewlow and Pastron, 1972:25, Fig. 5) and a rockshelter investigated by Pastron (1972).

20–21. *Skull Creek* E, F.—These two prehistoric chipping stations are on the south side of Skull Creek, near prehistoric hunting and gathering sites (Clewlow and Pastron, 1972:23, Fig. 3; 25, Fig. 5).

22. *Skull Creek* G.—The site is a chipping-gathering station on the North Fork of Skull Creek, near a rockshelter occupied in prehistoric times (Pastron, 1972).

23. *Pottery Hill* B.—Pottery Hill is a three component occupation site (prehistoric, protohistoric, and historic) on the valley floor. Various aspects of the occupation have been discussed by Payen (1978) and Rosen (1978). In the literature Pottery Hill is divided into Pottery Hill 1 and 2 which correlate with Pottery Hill A and B in this paper. Sherds from Pottery Hill A were sent to the Smithsonian Institution over a decade ago. Because these sherds were not available for analysis, they are not included in this report.

24–34. *Grass Valley Creek* A, B, C, D, E, F, G, H, I, J, K.—All of these sites are scattered along the north side of Grass Valley Creek in areas disturbed by cultivation or used to pasture horses. Except for G, which is an isolated sherd scatter, evidence of prehistoric activity is in the form of chipping-gathering stations or gathering sites; the sites' locations near the Horse Pasture Village (Clewlow et al., 1972) support a prehistoric date for the remains.

35–40. *Grass Valley Creek* L, M, N, O, P, Q.—These six sites are south of Grass Valley Creek and have been disturbed by cultivation and herding. Only site P was an isolated sherd scatter. Site N was associated with chippage and trade goods and probably is protohistoric. L, M, O, and Q are prehistoric surface scatters with chippage; M, in addition, had an occupation with flaked stone tools, ground stone tools and a hearth.

41. *Old Skull Creek Village*.—Old Skull Creek Village is a prehistoric occupation site, south of Skull Creek. Artifacts at the site include chippage, flaked and ground stone tools, and house foundations.

42. *Dead Pile Village*.—Dead Pile Village is north of Skull Creek and is a multicomponent site with a prehistoric, protohistoric and historic occupation comprised of chippage, flaked and ground stone tools, hearths, trade goods, house foundations, and historic artifacts (Bouey, 1979; Wallof, 1978).

43–48. *Rocky Point* A, B, C, D, E, F.—Rocky Point, as its name indicates, is a rocky hill which projects onto the valley floor and is littered with prehistoric remains that suggest hunting activities in the area (Clewlow and Pastron, 1972:23, Fig. 3). These six sites vary between chipping-gathering stations, gathering sites, and camps.

49–54. *Grass Valley Tom* A, B, C, D, E, F.—The Grass Valley Tom sites are on the valley floor east of Dead Pile Village, between Skull Creek and Grass Valley Creek. Grass Valley Tom A is also known as Grass Valley Tom's Village and has been discussed by Magee (1964:97), Hector (1978), and Rosen (1978). Grass Valley Tom's Village A is a three component site with a prehistoric, protohistoric, and historic occupation which produced a wide range of artifacts—chippage, ground stone tools, hearths, house foundations, and trade goods. Grass Valley Tom B, E, and F are associated with chippage; and Grass Valley Tom C and D are isolated sherd scatters.

57. *Cahill Canyon*.—The Cahill Canyon site is south of Grass Valley at the north end of the Great Smokey Valley. The site is located in the pinyon-juniper zone. Chippage

Table 1.—*Site description: number, type, cultural remains, and age. Abbreviations: Jp—juniper-pinyon zone; Cg—chipping and gathering station; Ga—gathering site; Ca—campsite; Vi—village; Is—isolated site; c—chippage; f—flaked stone tools; g—ground stone tools; h—hearth; t—trade goods; r—house rings; hi—historic artifacts.*

Site no. and name	Type	Prehistoric	Historic
1. Cortez Canyon (Jp)	Ca	c, f, h	—
2. Hot Springs Point	Is	—	—
3. McCluskey Creek A (Jp)	Ca	c, f, g, h	—
4. McCluskey Creek B (Jp)	Cg	c, f	—
5. McCluskey Creek C (Jp)	Ga	c, f, g	—
6. McCluskey Creek D (Jp)	Ca	c, f, g, h	—
7. McCluskey Creek E (Jp)	Cg	c	—
8. Stink Hole A	Ca	c, f, h	—
9. Stink Hole B	Ca	c, f, h	—
10. Corral Canyon (Jp)	Is	—	—
11. Cowboy Rest A (Jp)	Cg	c, f	—
12. Cowboy Rest B	Cg	c	—
13. Cowboy Rest C	Cg	c	—
14. Cowboy Rest D	Ga	c, f, g	—
15. Rosebush Bowl (Jp)	Is	—	—
16. Skull Creek A	Cg	c, f	—
17. Skull Creek B	Cg	c, f	—
18. Skull Creek C	Cg	c, f	—
19. Skull Creek D	Cg	c, f	—
20. Skull Creek E	Cg	c, f	—
21. Skull Creek F	Cg	c, f	—
22. Skull Creek G	Cg	c, f	—
23. Pottery Hill B	Vi	c, f	r, t, hi
24. Grass Valley Creek A	Cg	c, f	—
25. Grass Valley Creek B	Ga	c, f, g	—
26. Grass Valley Creek C	Cg	c	—
27. Grass Valley Creek D	Ga	c, f, g	—
28. Grass Valley Creek E	Cg	c	—
29. Grass Valley Creek F	Ga	c, g	—
30. Grass Valley Creek G	Is	—	—
31. Grass Valley Creek H	Cg	c, f	—
32. Grass Valley Creek I	Cg	c	—
33. Grass Valley Creek J	Ga	c, f, g	—
34. Grass Valley Creek K	Cg	c	—
35. Grass Valley Creek L	Cg	c	—
36. Grass Valley Creek M	Ca	c, f, g, h	—
37. Grass Valley Creek N	Cg	c	t
38. Grass Valley Creek O	Cg	c	—
39. Grass Valley Creek P	Is	—	—
40. Grass Valley Creek Q	Cg	—	—
41. Old Skull Creek Village	Vi	c, f, g, h, r	—
42. Dead Pile Village	Vi	c, f, g, r	g, r, t
43. Rocky Point A	Ca	c, g, h	—
44. Rocky Point B	Cg	c, f	—
45. Rocky Point C	Ga	c, g	—
46. Rocky Point D	Ca	c, f, g	—

Table 1.—*Continued.*

Site no. and name	Type	Prehistoric	Historic
47. Rocky Point E	Cg	c	—
48. Rocky Point F	Cg	c	—
49. Grass Valley Tom A	Vi	c, f, g, h, r	g, r, t, hi
50. Grass Valley Tom B	Cg	c	—
51. Grass Valley Tom C	Is	—	—
52. Grass Valley Tom D	Is	—	—
53. Grass Valley Tom E	Cg	c	—
54. Grass Valley Tom F	Cg	c	—
55. Ridge Village South	Vi	c, f, g	g, r, t, hi
56. Steiner Canyon	Cg	c	—
57. Cahill Canyon (Jp)	Cg	c, f	—

and flaked stone tools accompanied the sherds. Although this site is outside of Grass Valley, it has been included in the ceramic analysis in this report because the sherds comprise part of Molly Knudtsen's collection.

Since the survey of these sites, another pottery site in Grass Valley was discovered and subsequently described by Deatrick (1978). This site is located somewhere along Skull Creek. The data indicate that the site was a gathering site or a camp, but it is not included in this discussion as primary data because the author has not seen the site or the sherds.

Site Distribution

In spite of the limitations of the sample which were mentioned earlier, the distribution of the pottery sites by ecozone location and type raises interesting questions.

In terms of ecozone location, 47 (84%) of the sites in Grass Valley are below the pinyon-juniper zone. Only nine sites (16%) are in the pinyon-juniper zone. These sites are as follows: 1) Cortez Canyon (#1); 2) McCluskey Creek A (#3); 3) McCluskey Creek B (#4); 4) McCluskey Creek C (#5); 5) McCluskey Creek D (#6); 6) McCluskey Creek E (#7); 7) Corral Canyon (#10); 8) Cowboy Rest A (#13); 9) Rosebush Bowl (#15). The McCluskey Creek sites are near a perennial stream and the other sites are in the vicinity of cold water springs. All of these sites were prehistoric and the pottery was associated with chippage, flaked stone tools, ground stone tools, and in certain cases, hearths.

The most frequent type of site in Grass Valley is a chipping-gathering station. The 29 sites in this category comprise slightly over half the sample (57%). The chipping-gathering station is a locality where an activity related to hunting occurred, possibly repeatedly over a long period of time. The gathering aspect of the site is based solely upon the presence of pottery. However, it would have been much easier to place seeds, roots and nuts in a lighter more portable container made of hide or reeds. Lack of ground stone tools negates processing as a major activity at these sites. This frequent association of pottery with chippage and flaked stone tools suggests the possibility that the vessels contained water and food and may not indicate gathering activities. Nevertheless, such an endeavor cannot be entirely ignored, but a sherd should not always equal gathering activities when found outside a camp or village context. It, first and foremost, is a food container and it is possible that pots were left at such stations for use when the people returned.

As far as ecozone location, three chipping-gathering stations (10%) were in the pinyon-

Table 2.—*Distribution of sherds per site in Grass Valley, Nevada. Surface area given in square cm and weight in g.*

Site name and no.	Surface area	Weight	Rims	Bases	Body	Total
1. Cortez Canyon	420	524.7	—	—	32	32
2. Hot Springs Point	252	202.0	—	—	103	103
3. McCluskey Creek A	64	84.7	1	2	5	8
4. McCluskey Creek B	300	325.9	5	—	41	46
5. McCluskey Creek C	90	83.2	—	—	17	17
6. McCluskey Creek D	600	634.4	12	—	41	53
7. McCluskey Creek E	483	566.0	5	3	49	57
8. Stink Hole A	48	41.9	—	—	1	1
9. Stink Hole B	48	43.7	2	—	7	9
10. Corral Canyon	30	26.9	—	—	5	5
11. Cowboy Rest A	160	127.3	11	—	12	23
12. Cowboy Rest B	90	68.8	2	—	10	12
13. Cowboy Rest C	351	144.4	7	—	61	68
14. Cowboy Rest D	12	17.4	—	—	1	1
15. Rosebush Bowl	15	75.4	—	1	1	2
16. Skull Creek A	48	29.0	—	—	11	11
17. Skull Creek B	44	18.5	—	—	6	6
18. Skull Creek C	52	43.2	—	—	3	3
19. Skull Creek D	24	22.7	—	—	6	6
20. Skull Creek E	338	220.15	—	—	28	28
21. Skull Creek F	400	276.2	4	2	80	86
22. Skull Creek G	4	2.9	—	—	1	1
23. Pottery Hill B	121	78.0	1	3	13	17
24. Grass Valley Creek A	90	134.1	16	—	20	36
25. Grass Valley Creek B	72	73.4	—	—	19	19
26. Grass Valley Creek C	342	209.3	2	—	79	81
27. Grass Valley Creek D	10	17.6	—	—	12	12
28. Grass Valley Creek E	49	48.1	3	—	12	15
29. Grass Valley Creek F	10	12.9	1	—	1	2
30. Grass Valley Creek G	740	694.1	—	3	153	156
31. Grass Valley Creek H	270	170.8	5	—	48	53
32. Grass Valley Creek I	64	74.1	2	1	13	16
33. Grass Valley Creek J	100	69.5	4	—	23	27
34. Grass Valley Creek K	540	483.3	—	—	233	233
35. Grass Valley Creek L	45	35.4	—	—	9	9
36. Grass Valley Creek M	195	154.0	—	—	46	46
37. Grass Valley Creek N	120	89.1	—	—	46	46
38. Grass Valley Creek O	684	702.4	13	4	97	114
39. Grass Valley Creek P	990	869.7	3	—	228	231
40. Grass Valley Creek Q	6	12.3	—	—	4	4
41. Old Skull Creek Village	976	825.2	23	—	256	279
42. Dead Pile Village	864	585.8	5	5	291	301
43. Rocky Point A	1474	1229.1	2	—	197	199
44. Rocky Point B	195	181.3	1	—	18	19
45. Rocky Point C	195	147.2	—	—	23	23
46. Rocky Point D	72	66.5	—	—	8	8
47. Rocky Point E	40	22.1	1	—	6	7
48. Rocky Point F	90	69.7	—	—	8	8

Table 2.—*Continued.*

Site name and no.	Surface area	Weight	Rims	Bases	Body	Total
49. Grass Valley Tom A	1240	1510.3	8	15	510	533
50. Grass Valley Tom B	420	308.6	—	—	186	186
51. Grass Valley Tom C	255	203.7	3	—	53	56
52. Grass Valley Tom D	132	76.5	2	—	38	40
53. Grass Valley Tom E	238	142.5	2	—	63	65
54. Grass Valley Tom F	24	19.5	—	—	3	3
55. Ridge Village South	28	25.3	—	—	4	4
56. Steiner Canyon	25	46.2	—	—	48	48
57. Cahill Canyon	420	524.7	7	—	32	39
Total	15,009	13,646.05	153	39	3321	3513

juniper zone and 26 (90%) were below the pinyon-juniper zone. These statistics indicate three things. First, the region probably has suffered defoliation. Second, the number of sites near or on the valley floor suggest hunting along streams where animals could feed on grasses and drink water. Third, preparation for hunting activities frequently occurred in these zones, near the permanent settlements on the valley floor.

The eight gathering sites comprise 14% of the sample. Because metates are not easily portable items, the presence of the tools indicates the locality was used to process food. Only one (13%) gathering site was in the pinyon-juniper zone and seven (87%) were on the valley floor. It is logical that the processing would take place near the permanent or semipermanent settlements and a water source.

Camp sites are 12.5% of the sample. Only one of the seven camp sites, Grass Valley Creek M (#36), had ground stone tools in addition to the chippage, flaked stone tools, and hearths. Because a camp indicates temporary residence, it is interesting that five of the camps (63%) occurred below the pinyon-juniper zone and three (37%) of the camps were in the pinyon-juniper zone. This situation suggests small, mobile groups moving throughout the region. The pottery in a camp could have been used for cooking, storage of food, and possibly gathering.

Village sites comprise 9% of the pottery bearing sites. Four (80%) of the five village sites had prehistoric, protohistoric, and historic occupations. The other one, Old Skull Creek Village, was a single component prehistoric site. These five villages were built on the valley floor. This is not surprising because the zone provides a large, clear area for numerous structures near a permanent water source. The historic occupations also benefitted from their proximity to the ranch house. The vessels in a village could have been used for any number of activities.

There were only seven isolated sherd scatters (12.5% of the sites). Usually an isolated sherd scatter marks the place where a vessel broke beyond repair.

In summary, eight of the sites in the pinyon-juniper zone were prehistoric and two were isolated scatters. In the lower foothills and on the valley floor, 42 sites had a prehistoric component, four had an historic component and five were isolated.

It is difficult, if not impossible, to generalize on site distribution trends with a biased sample. When a summary of the locations of all the sites in Grass Valley is available, it will be possible to present a clear idea of the indigenous population's activities.

Nevertheless, the data from the survey do demonstrate that Shoshoni pottery often was used at chipping-gathering stations, gathering sites, camps, and villages. The repeated incidence of fragile, ceramic vessels at sites with seasonal or temporary occu-

Table 3.—*Distribution of the types of temper in pottery from Grass Valley, Nevada. Type 0 = no temper present; Type 1 = mica; Type 2 = small sand particles; Type 3 = coarse sand particles; Type 4 = mica, quartzite; Type 5 = mica, quartzite, coarse sand; Type 6 = small granitic particles; Type 7 = medium granitic particles; Type 8 = coarse granitic particles.*

	Types								
Site name and no.	0	1	2	3	4	5	6	7	8
1. Cortez Canyon									x
2. Hot Springs Point									x
3. McCluskey Creek A							x		
4. McCluskey Creek B								x	
5. McCluskey Creek C								x	
6. McCluskey Creek D	x								
7. McCluskey Creek E									x
8. Stink Hole A									x
9. Stink Hole B	x								
10. Corral Canyon			x						
11. Cowboy Rest A									x
12. Cowboy Rest B	x								
13. Cowboy Rest C			x						
14. Cowboy Rest D	x								
15. Rosebush Bowl	x								
16. Skull Creek A							x		
17. Skull Creek B					x				
18. Skull Creek C							x		
19. Skull Creek D							x		
20. Skull Creek E							x		
21. Skull Creek F							x		
22. Skull Creek G							x		
23. Pottery Hill B							x		
24. Grass Valley Creek A	x								
25. Grass Valley Creek B							x		
26. Grass Valley Creek C					x				
27. Grass Valley Creek D	x								
28. Grass Valley Creek E									x
29. Grass Valley Creek F									x
30. Grass Valley Creek G							x		
31. Grass Valley Creek H			x						
32. Grass Valley Creek I							x		
33. Grass Valley Creek J		x							
34. Grass Valley Creek K			II						I
35. Grass Valley Creek L							x		
36. Grass Valley Creek M	x								
37. Grass Valley Creek N					x				
38. Grass Valley Creek O	x								
39. Grass Valley Creek P	x								
40. Grass Valley Creek Q	x								
41. Old Skull Creek Village			I						II–III
42. Dead Pile Village							x		
43. Rocky Point A			x						
44. Rocky Point B			x						

Table 3.—*Continued.*

Site name and no.	Types 0	1	2	3	4	5	6	7	8
45. Rocky Point C						x			
46. Rocky Point D				x					
47. Rocky Point E								x	
48. Rocky Point F							x		
49. Grass Valley Tom A							x		
50. Grass Valley Tom B							x		
51. Grass Valley Tom C	x								
52. Grass Valley Tom D		x							
53. Grass Valley Tom E		x							
54. Grass Valley Tom F			x						
55. Ridge Village South			x						
56. Steiner Canyon		x							
57. Cahill Canyon									x
Total	12	4	9	1	3	1	16	3	10

pations suggests that the Shoshoni may have left the pottery at these locales as they did metates, for later use. It should always be kept in mind that the presence of sherds and vessels represents the breaking of the pot or abandonment. Therefore, pottery may have been used frequently at sites, such as chipping-gathering stations, but may only rarely show up in the archaeological record.

Of greater importance is the number of pottery sites below the pinyon-juniper ecozone. Although further survey in the forested areas may reveal more pottery sites, the large number of sites in the lower foothills and on the valley floor raise the possibility that the settlement patterns in Grass Valley may be very different from the patterns in the Reese River Valley, where the majority of sites with pottery were located in the pinyon-juniper ecozone (Thomas 1970:697).

CERAMIC ANALYSIS

The 57 archaeological sites produced 3513 sherds. Of this total, 153 are rim sherds, 39 are base sherds, and 3321 are body sherds. The number of sherds per site varies from one to 533. This statistic is only a general gauge of the sample because sherd size in this collection ranged from 1 cm^2 to 81 cm^2. In order to present a clearer idea of the sample, the surface area and weight of the sherds from each site are shown in Table 2, as well as the number of rim sherds, base sherds and body sherds. Total surface area of the 3513 sherds is 15,009 cm^2 and total weight is 13,646.05 g. By comparing the surface area to weight it is possible to see that the pottery falls into two categories—light and heavy sherds. When the surface area is smaller than the weight, the pottery is heavy; when the surface area is greater than the weight the pottery is light. This correlates with the varying thickness

Table 4.—*Coils in pottery from Grass Valley, Nevada.*

Site	Cracks	Coil size
7. McCluskey Creek E	x	1.1–1.8 cm
15. Rosebush Bowl	x	1.2–2.1 cm
20. Skull Creek E	x	1.0–1.5 cm
21. Skull Creek F	x	—
31. Grass Valley Creek H	x	—
32. Grass Valley Creek I	x	—
38. Grass Valley Creek O	x	1.2 cm
39. Grass Valley Creek P	x	1.2–2.5 cm
41. Old Skull Creek Village	x	—
42. Dead Pile Village	x	.8–1.3 cm
44. Rocky Point B	x	—
57. Cahill Canyon	x	—

of the sherds, particularly the bases which are the heaviest part of a vessel.

Due to the large size of the sample, construction features will be discussed in general terms with tables showing the variations among the sites. The division by site is not arbitrary. The sherds from each of the sites showed a remarkable lack of internal variation with the exception of two sites. The pottery at Grass Valley Creek K (#34) was divided into Type I and Type II on the basis of temper; and the pottery at Old Skull Creek Village (#41) was divided into Types I, II, and III due to variations in temper, color, and thickness.

Over the years Molly Magee Knudtsen donated sherds to the Smithsonian Institution and allowed other archaeologists to remove sherds from the collection for comparative analysis. As a result there are discrepancies between the number of sherds Magee (1964, 1967) reported at sites and the number of sherds at the same sites in this report.

Clay

The clay used to construct the pots was obtained at local sources. Clay deposits are common in the vicinity of the cold springs, hot springs, and the streams, which are scattered along the land across the valley floor. Cursory analysis of clay from six deposits did not allow for determination of the exact clay source for each of the sherds, but it did reveal that mica, sand, and quartzite particles were present in varying amounts in the clay at four of the deposits. These elements were absent from the clay at the other two deposits.

This situation, if true for all of the clay sources, indicates that Coale's (1963:1–2) assertion that many of the Shoshoni Brownware pots are devoid of added temper is correct. In other words, the Shoshoni Indians used the clay as it came from the ground and did not feel the need to add elements in order to strengthen or alter the consistency of the clay.

Grasses are quite common at the clay deposits which frequently occur near water. When removing the clay, I discovered that it is very difficult to avoid collecting these grasses with the clay. The Shoshoni must have encountered the same problem because the sherds from seven sites contained carbonized and uncarbonized plant remains—1) Cortez Canyon (#1), 2) McCluskey Creek B (#4), 3) McCluskey Creek D (#6), 4) Cowboy Rest B (#12), 5) Skull Creek A (#16), 6) Grass Valley Creek B (#25), and 7) Grass Valley Creek E (#28). Therefore the presence of these plant remains indicates that the clay was not systematically cleaned, after it was removed from the ground.

Temper

Temper in this discussion refers to any particles in the clay. As the previous discussion pointed out, temper may not have been purposefully added to the clay. The analysis of the temper in the sherds was done by magnification, not thin sections. Eight types of temper were identified. Table 3 presents the temper types and their distribution by site.

Type 6, small granitic particles, is the most common temper, present at 16 sites. Surprisingly, at 12 sites temper is completely absent in the sherds (Type 0). Coarse granitic particles (Type 8) appeared in the sherds from 10 sites. The next most frequent type was Type 2, small sand particles, which is present at nine sites. Type 4, mica and quartzite, and Type 7, medium granitic particles, are evident in the sherds from three sites. Type 3, coarse sand particles, and Type 5, mica, quartzite and coarse sand, each occur at only one site.

The consistency of temper types at the sites indicates that the people at each site were utilizing specific clay sources, probably the deposits nearest to the site. Type 0 through 5 are clays that did not require the addition of temper. Types 6 through 8 contain granitic particles and represent the purposeful addition of the ground rocks.

The distribution of the temper types is interesting. The sherds from all but one of the sites, 1 through 7 in the north end of the valley and all of the Skull Creek sites (16 through 22), contain temper that was added to the clay. Only one of these sites is located on the valley floor. Possibly the clay sources in the lower foothills and the pinyon-juniper zone have a clay that requires additional particles when it is used to make vessels. Looking at the data another way, eight of the 10 sites in the pinyon-juniper zone had purposeful temper. If the pinyon-juniper zone used to be lower, the Skull Creek sites would fit into this pattern. On the other hand, the distribution of temper types on the valley floor is mixed with no apparent pattern and the situation in the pinyon-juniper zone may change after more of the area is surveyed.

Construction

In terms of construction, the Grass Valley pottery was shaped by hand and there is strong evidence that coil construction was predominant in the region. Sherds from twelve of the sites showed visible evidence of this technique (Table 4). At six of the 12 sites the pottery had cracks where the coils had not been completely smoothed away. However, the coils on the sherds from the other six sites could be measured and they range from .8 cm to 2.5 cm in width (Fig. 4a, b). Variation in the size of a coil on a single sherd was .5 cm.

The sherds from the other sites also appeared to be coiled rather than modeled. Frequently on the exterior or interior ripples appear where the coils had been obliterated but not completely flattened. A paddle and anvil technique may have been used to smooth the coils and shape some of the vessels but this cannot be documented. In certain cases the coils were smoothed irregularly and look to have been done by hand. Because most of the coils are visible on the interior of a sherd, the appearance of the exterior was more important to the pottery. However, it should be noted that most sherds had been smoothed completely.

None of the sherds in the sample had basketry impressions. Because the collection is quite large, it seems safe to assume that the pots were not shaped and smoothed in baskets.

Finish

After the pot was shaped it was finished by smoothing and wiping the surface by hand. At this time a light wash was applied to some of the vessels. As Table 5 demonstrates most of the sherds were well smoothed on the exterior and interior. However, in some cases one side was given preferential treatment. Sherds from eight sites were poorly finished with both surfaces left very uneven.

Wiping marks are frequent and are visible on the sherds from 35 sites (Table 5). The wiping marks were produced by the potter wiping the clay either with a hand or with grass, which left striations on the clay. Wiping direction was quite variable. At three sites, Cowboy Rest A (#11), Grass Valley Creek F (#29), and Rocky Point B (#44), the vessel was wiped diagonal to the rim on the interior and exterior. Wiping marks were parallel to the rim on the inside and perpendicular to the rim on the outside at nine sites—McCluskey Creek A (#3), McCluskey Creek E (#7), Cowboy Rest C (#13), Grass Valley Creek

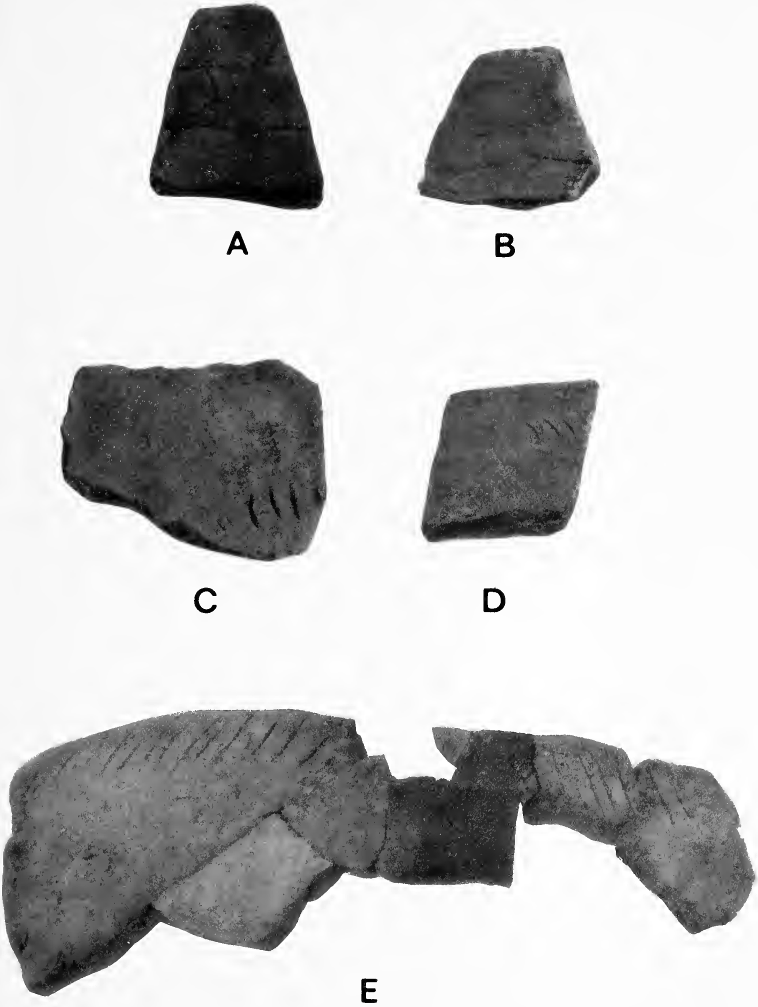

Fig. 4.—A and B are examples of coils still visible on the sherds (actual size). C and D are examples of indented decoration (actual size). E is an example of incision decoration (actual size).

sites A (#24), H (#31), K (#34) and P (#39), Old Skull Creek Village (#41), Dead Pile Village (#42) and Grass Valley Tom A (#49). At Skull Creek D (#19), one sherd had been wiped in several different directions.

Table 5.—*Surface finish and wiping marks on pottery from Grass Valley, Nevada.*

	Inside			Outside		
Site name and no.	Smooth	Uneven	Wiping marks	Smooth	Uneven	Wiping marks
1. Cortez Canyon	x	—	—	x	—	—
2. Hot Springs Point	x	—	—	x	—	x
3. McCluskey Creek A	x	—	x	x	—	x
4. McCluskey Creek B	x	—	—	x	—	—
5. McCluskey Creek C	x	—	—	x	—	—
6. McCluskey Creek D	x	—	—	x	—	—
7. McCluskey Creek E	x	—	—	x	—	—
8. Stink Hole A	—	x	—	x	—	—
9. Stink Hole B	x	—	x	x	—	—
10. Corral Canyon	x	—	—	x	—	—
11. Cowboy Rest A	x	—	x	x	—	x
12. Cowboy Rest B	x	—	x	—	x	x
13. Cowboy Rest C	—	x	x	x	—	x
14. Cowboy Rest D	x	—	x	x	—	x
15. Rosebush Bowl	x	—	—	x	—	—
16. Skull Creek A	x	—	x	x	—	x
17. Skull Creek B	x	—	—	x	—	—
18. Skull Creek C	x	—	x	x	—	x
19. Skull Creek D	—	x	—	x	—	—
20. Skull Creek E	—	x	x	—	x	x
21. Skull Creek F	—	x	x	—	x	x
22. Skull Creek G	x	—	—	x	—	—
23. Pottery Hill B	x	—	x	x	—	x
24. Grass Valley Creek A	—	x	x	—	x	x
25. Grass Valley Creek B	x	—	x	—	x	—
26. Grass Valley Creek C	x	—	—	x	—	—
27. Grass Valley Creek D	x	—	x	—	x	x
28. Grass Valley Creek E	x	—	—	x	—	x
29. Grass Valley Creek F	—	x	—	x	—	x
30. Grass Valley Creek G	—	x	—	—	x	—
31. Grass Valley Creek H	—	x	x	—	x	x
32. Grass Valley Creek I	x	—	—	x	—	—
33. Grass Valley Creek J	x	—	x	—	x	—
34. Grass Valley Creek K	x	—	x	—	x	x
35. Grass Valley Creek L	x	—	—	x	—	—
36. Grass Valley Creek M	x	—	—	x	—	—
37. Grass Valley Creek N	—	x	—	x	—	—
38. Grass Valley Creek O	—	x	—	x	—	—
39. Grass Valley Creek P	x	—	x	x	—	x
40. Grass Valley Creek Q	x	—	—	x	—	—
41. Old Skull Creek Village	x	—	—	x	—	—
42. Dead Pile Village	x	—	x	—	x	x
43. Rocky Point A	x	—	x	—	x	x
44. Rocky Point B	—	x	x	x	—	x
45. Rocky Point C	x	—	x	x	—	x
46. Rocky Point D	—	x	x	—	x	x
47. Rocky Point E	—	x	—	—	x	—

Table 5.—*Continued.*

	Inside			Outside		
Site name and no.	Smooth	Uneven	Wiping marks	Smooth	Uneven	Wiping marks
48. Rocky Point F	—	x	x	—	x	x
49. Grass Valley Tom A	x	—	x	—	x	x
50. Grass Valley Tom B	x	—	x	—	x	x
51. Grass Valley Tom C	x	—	x	—	x	—
52. Grass Valley Tom D	x	—	x	x	—	x
53. Grass Valley Tom E	x	—	x	x	—	x
54. Grass Valley Tom F	—	x	—	x	—	—
55. Ridge Valley South	x	—	x	—	x	—
56. Steiner Canyon	x	—	x	—	x	x
57. Cahill Canyon	x	—	x	x	—	x

Decoration

Decoration was applied to the vessels before firing. The only decorative elements on the Grass Valley sherds are indentations and incisions. Paint was not used. Decorated sherds came from four sites—Cowboy Rest B (#12), Cowboy Rest D (#14), Grass Valley Creek A (#24) and Rocky Point A (#43).

The sherd from Cowboy Rest B is a body sherd. It has four fingernail indentations, 4 mm apart and 5 mm long (Fig. 4c). Cowboy Rest D produced two decorated rim sherds from two different vessels, both flat-bottomed, truncated cones. One sherd has three fingernail indentations, 2 to 3 mm apart, 3 to 4 mm long. These indentations are 8 mm below the rim (Fig. 4d). The other sherd is similar. It has five fingernail incisions which are 2 mm apart. They begin 4 mm below the rim and then arc towards the rim. These indentations are slightly smaller than the previous example.

The six decorated sherds from Grass Valley Creek A are from the same vessel, another flat-bottomed truncated cone (Fig. 4e). Twenty-six incisions extend down from the rim and vary between 4 mm and 7 mm in length. These lines were produced by using an implement such as a small piece of wood.

The sherd from Rocky Point A is a decorated rim sherd. The 12 incisions are adjacent to the rim for a distance of 3.8 cm. They are 3 to 4 mm long, and are 1 to 7 mm apart, perpendicular to the rim.

Firing

One of the distinctive characteristics of Shoshonean tradition ceramics is that they were fired at a low temperature. The variability of color which can frequently be seen on one pot or sherd indicates that

Table 6.—*Perforated sherds from Grass Valley, Nevada. Diameters given in mm.*

Site	Inside diameter	Outside diameter	Complete hole
6. McCluskey Creek D	45	90	X
	41	90	X
	40	90	—
	40	90	—
39. Grass Valley Creek P	40	68	X
	40	75	X
57. Cahill Canyon	60	68	—

the open firing was not controlled, resulting in the uneven coloration. The effects of later use over a fire as a cooking vessel are sometimes difficult to distinguish from the initial firing.

The colors of the sherds from the sites are so inconsistent that it is not feasible to present a breakdown of the colors by site. In general terms the sherd colors varied from buff to light and dark brown with or without reddish hues, to light and dark grey, and black. Most of the sherds had a greyish cast, the result of a reduced atmosphere during firing. Carbon streaks were visible on some of the sherds at Grass Valley Creek L (#35) and Dead Pile Village (#42).

Polishing

The ceramics from six sites were polished after the firing—McCluskey Creek D (#6), Skull Creek B (#17), Skull Creek C (#18), Skull Creek E (#20), Grass Valley Creek L (#35), and Rocky Point B (#44). The polishing was very distinct and probably done with a small stone.

Perforations

The seven perforated sherds in the collection came from three sites—McCluskey Creek D (#6), Grass Valley Creek P (#39), and Cahill Canyon (#57). The holes were made after the vessel was fired. The inside diameter of the holes is always smaller than the outside diameter which means the holes were drilled from the outside towards the inside (Table 6).

Two of the sherds from McCluskey Creek D and the sherd from Cahill Canyon are interesting because the drilling was stopped before completing the hole. Incomplete drill holes reflect that the project was abandoned or that the incomplete holes were designed for a specific purpose. If they are the result of abandonment they may indicate that the vessel broke or was about to break during the drilling process and

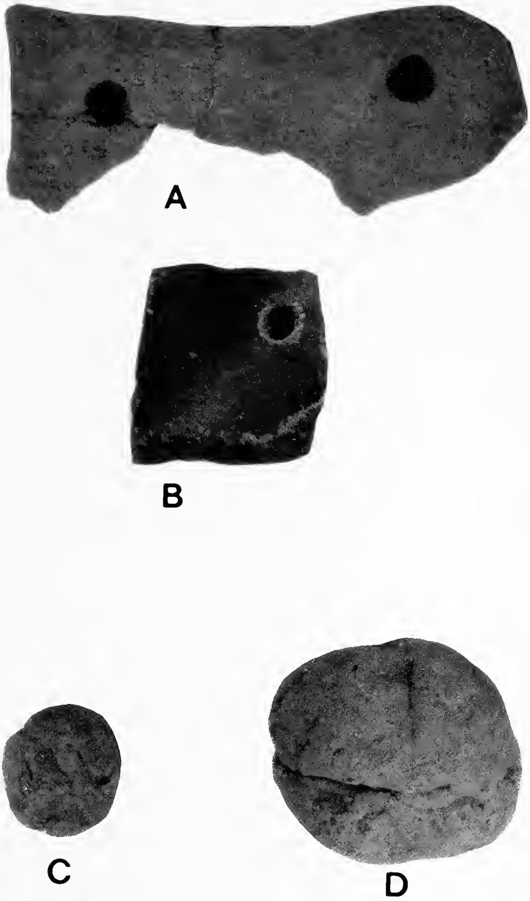

Fig. 5.—A and B are examples of conical perforations (actual size). C and D are mud balls (actual size).

could not be repaired. However, they may be purposeful constructions because they comprise 43% of the sample. The only explanation this author can suggest is that the holes could have served as receptacles for sticks which were then used to lift the vessel when it was hot.

The purpose of the completed holes has been disputed. Magee (1967) suggested that the perforated sherds were fragments of a colander. In support of Magee's interpretation is the fact that five of the seven perforated sherds are body sherds. On the other hand, the practice of

Table 7.—*Distribution of sherds in Grass Valley, Nevada, according to thickness.*

Site	Number
1 mm	
22. Skull Creek G	1
Total	1
4 mm	
2. Hot Springs Point	103
29. Grass Valley Creek F	2
45. Rocky Point C	23
47. Rocky Point E	3
56. Steiner Canyon	48
Total	179
5 mm	
8. Stink Hole A	1
9. Stink Hole B	9
16. Skull Creek A	11
21. Skull Creek D	86
27. Grass Valley Creek D	12
34. Grass Valley Creek K	233
41. Old Skull Creek II	76
43. Rocky Point A	199
47. Rocky Point E	2
Total	629
6 mm	
3. McCluskey Creek A	8
5. McCluskey Creek C	17
10. Corral Canyon	5
11. Cowboy Rest A	23
12. Cowboy Rest B	12
13. Cowboy Rest C	68
14. Cowboy Rest D	1
15. Rosebush Bowl	2
17. Skull Creek B	6
18. Skull Creek C	6
19. Skull Creek D	28
23. Pottery Hill B	4
26. Grass Valley Creek C	81
30. Grass Valley Creek G	156
31. Grass Valley Creek H	53
32. Grass Valley Creek I	16
33. Grass Valley Creek J	27
35. Grass Valley Creek L	9
36. Grass Valley Creek M	46
40. Grass Valley Creek Q	4
41. Old Skull Creek I	41
42. Dead Pile Village	107
47. Rocky Point E	2

Table 7.—*Continued.*

Site	Number
48. Rocky Point F	8
50. Grass Valley Tom B	131
51. Grass Valley Tom C	56
52. Grass Valley Tom D	40
53. Grass Valley Tom E	65
54. Grass Valley Tom F	53
55. Ridge Village South	4
Total	1035
7 mm	
4. McCluskey Creek B	46
6. McCluskey Creek D	53
7. McCluskey Creek E	57
18. Skull Creek C	3
23. Pottery Hill B	6
41. Old Skull Creek III	58
42. Dead Pile Village	178
46. Rocky Point D	8
49. Grass Valley Tom A	202
50. Grass Valley Tom B	55
57. Cahill Canyon	39
Total	705
8 mm	
1. Cortez Canyon	32
23. Pottery Hill B	6
25. Grass Valley Creek B	19
28. Grss Valley Creek E	15
37. Grass Valley Creek N	46
38. Grass Valley Creek O	65
39. Grass Valley Creek P	231
42. Dead Pile Village	104
44. Rocky Point B	19
49. Grass Valley Tom A	331
Total	868
9 mm	
24. Grass Valley Creek A	36
38. Grass Valley Creek O	49
42. Dead Pile Village	16
Total	101
10 mm	
23. Pottery Hill B	1
Total	1

Table 8.—*Distribution of rim types of pottery from Grass Valley, Nevada.*

	Types																
Site no.	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
3.	1																
4.	4	1															
6.	12																
7.	2		1	2													
9.							1								1		
11.	8			2													1
12.								1	1								
13.				2	3	1										1	
21.	1	1			2												
23.	1																
24.	9	4	3														
26.		2															
28.							2					1					
29.													1				
31.	1					4											
32.	2																
33.	4																
38.		8	4	1													
39.	3																
41. (I)	21																
(II)	2																
42.	5																
43.	1		1														
44.	1																
47.	1																
49.	5		3														
51.*	2																
52.	2																
53.	2																
57.	4				1					1				1			
Total	94	16	8	7	6	5	3	1	1	1	1	1	1	1	1	1	1

* Rim sherd too small to categorize.

mending pottery and other artifacts by perforating an object and sewing the holes together is well known among North American Indians.

Thickness

The sherds in the collection ranged in thickness from 1 mm to 10 mm; the majority were between 5 and 8 mm (Table 7).

VESSEL SHAPES

The vessel shapes known for the Shoshonean tradition are 1) flat bottomed vessels with straight, oval and flaring profiles; 2) bowls with

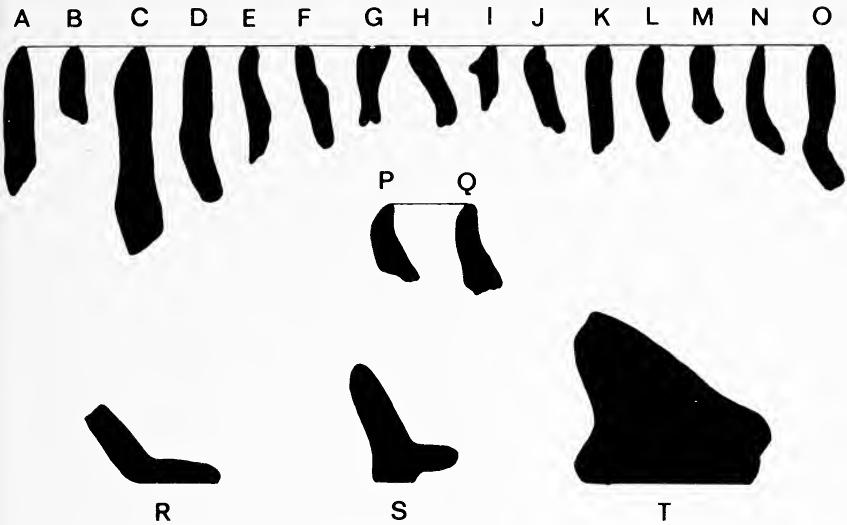

Fig. 6.—A through Q are rim sherds (actual size). R through T are base sherds (actual size).

round bottoms; and 3) pointed bottom vessels with an oval profile. Flat bottom and round bottom vessels from Grass Valley have already been published. Magee (1964) illustrated the flat bottom, flaring sided vessel from Grass Valley Tom A (#49). Deatrick (1978) described a round base vessel from the area near Skull Creek.

Rim Sherds

The 153 rim sherds were divided into 17 rim types (Fig. 6a through q; Table 8). Reconstruction of a vessel shape solely on a rim sherd is difficult because few whole Shoshoni pots have ever been illustrated and the actual range of variation is unknown. However, the two most frequent rim types, A and B, and rim type I should be fragments of a straight sided, flat bottom vessel. Their diameters range from 18 to 26 cm. Types C, E, and K are from vessels which had neither very straight nor flaring sides but were somewhere in between. The diameters on these pots vary between 22 and 26 cm. The flaring sided, flat bottom vessels with diameters between 24 and 26 cm, are types F, H, and J. Types D and L through Q are from round sided vessels with diameters between 18 and 26 cm. Type G could not be assigned to a specific category. In terms of frequency, straight sided vessels were by far the most common (121 rim sherds). The almost straight sided vessels were the next most frequent type (15 rim sherds). Thirteen rim

Table 9.—*Distribution of base types in Grass Valley, Nevada—Type 1 is Fig. 6r; Type 2 is Fig. 6s; Type 3 is Fig. 6t; and Type 4 is a rounded base (not illustrated).*

	Base types			
Site	1	2	3	4
3. McCluskey Creek A	1	1		
7. McCluskey Creek E	2		1	
15. Rosebush Bowl	1			
21. Skull Creek F	1		1	
23. Pottery Hill	3			
30. Grass Valley Creek G				3
32. Grass Valley Creek I				1
38. Grass Valley Creek O	4			
42. Dead Pile Village	5			
49. Grass Valley Tom A	12			3
Total	29	1	2	7

sherds belonged to round sided vessels and seven came from flaring sided pots.

Base Sherds

The 39 base sherds were divided into four types of bases (Table 9). Type 1 (Fig. 6r) is the most frequent in the sample. It is a flat bottom with sides that flair at the base. Type 1 have diameters between 10 and 12 cm. Only one base of type 2 (Fig. 6s) was found. This is a ring base with flaring sides that had a 6 cm diameter. Type 3 (Fig. 6t) is an angular, flat bottom base with flaring sides. The two examples of this type are 6 and 7 cm in diameter. Type 4, a round base, is the second most common type of base sherd.

Vessel Use

Determining the use of a vessel is a difficult endeavor unless a pot is discovered filled with remains or shows evidence of exposure to a cooking fire. The first situation was not encountered in Grass Valley. However, sherds from thirteen sites contained carbonized remains adhering to their interior; and sherds from five sites showed fire-blackening which was not related to their initial firing. This evidence demonstrates that the primary function of many of the pots was as a cooking utensil.

OTHER ARTIFACTS

Two other types of artifacts were collected at the sites, projectile points and mud balls. Twenty-four projectile points were found at the Shoshoni pottery sites (Table 10). Direct association between the pro-

Table 10.—*Projectile point types from Grass Valley, Nevada.*

Site	Type
1. Cortez Canyon	1 Elko Eared
2. Hot Springs Point	1 Desert Side-Notched
8. Stink Hole A	2 Rose Spring Corner-Notched
12. Cowboy Rest B	1 Elko Eared
	1 Desert Side-Notched
21. Skull Creek E	1 Rose Spring Corner-Notched
24. Grass Valley Creek A	1 Elko Eared
31. Grass Valley Creek H	1 Cottonwood Triangle
32. Grass Valley Creek I	2 Eastgate Expanding Stem
41. Old Skull Creek Village	5 Rose Spring Corner-Notched
	1 Desert Side-Notched
44. Rocky Point B	1 Rose Spring Corner-Notched
52. Grass Valley Tom D	2 Elko Eared
	1 Rose Spring Corner-Notched
56. Steiner Canyon	2 Elko Eared
	1 Desert Side-Notched
Total	24

jectile points and the pottery cannot be established because these artifacts were recovered from surface scatters. Nevertheless, it is important to note the occurrence of the projectile point types in case future researchers find a similar pattern between the projectile points and the pottery.

There are five different types of projectile points from eleven sites (Table 10)—seven, Elko Eared; two, Eastgate Expanding Stem; 10, Rose Spring Corner-Notched; four, Desert Side-Notched; one, Cottonwood Triangle. The chronological ordering of the point types, presented below, is based upon Clewlow's (1967:144), O'Connell's (1967:133–134), Fowler's (1968*b*:30), and Hester's (1973) work. The Elko series is generally thought to end around 600 A.D., about 400 to 600 years before the presently accepted date of the initial manufacture of Shoshoni Brownware in the Great Basin. The association of seven points of the Elko series with pottery may be accidental but it also raises the possibility that Shoshoni Brownware might have been introduced into the region at an earlier time.

The transition between the Eastgate and Rose Spring points (600–1000 A.D.) and the Desert Side-Notched and Cottonwood points (1000–1700 A.D.) is presumed to correlate with the migration of Numic speakers into the Great Basin, who are credited with the introduction of ceramics to the area. Therefore, the association of Eastgate and Rose Spring points with Shoshoni pottery is not controversial because such a replacement was probably a long process. Four Desert Side-Notched and one Cottonwood Triangle were associated with the ceramics. This correlates with the accepted pattern of the association of Shoshoni Brownware with these point types (Thomas, 1970:696).

Three fired mud balls were found in Grass Valley and all are slightly irregular. One mud ball which was found at Grass Valley Tom B (#50), weights 8.7 g and has a diameter that ranges between 1.8 cm and 2.1 cm (Fig. 5c). The remaining two examples are from the McCluskey Creek drainage. The ball from McCluskey Creek B (#4) weighs 52.5 g and is 3.5 cm in diameter (Fig. 5d). The other mud ball is from McCluskey Creek D (#6) and weighs 54 g and has a diameter of 3.9 cm.

Fired mud balls are generally thought to have been used as cooking stones. However, none of these balls showed evidence of carbonized remains. Rocks are common in Grass Valley and would have functioned better in this capacity. Most likely, the mud balls were used as gaming pieces.

CONCLUSIONS

Grass Valley, Nevada, has produced a large sample of Shoshoni archaeological sites with ceramic remains. These sites indicate that Shoshoni occupation of the region was extensive and possibly focused, to a greater extent than in other valleys, below the pinyon-juniper ecozone.

The analysis of the ceramics reveals that Shoshoni ceramic technology in Grass Valley is comparable to other regions of the Great Basin. The clays utilized for vessel production were extracted from local deposits. Coil construction was dominant in the area but the potters executed the finishing touches in their own fashion.

The diversity in the location and the types of archaeological sites with Shoshoni pottery in Grass Valley, as well as the large quantity of ceramics they contained, substantially increase our understanding of Shoshoni settlement patterns and the integral role ceramics played in their society.

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EVALUATION OF SWIMMING ABILITY AS A MEANS OF ISLAND INVASION BY SMALL MAMMALS IN COASTAL VIRGINIA

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Abstract

Small mammals were live-trapped on the mainland and on an island located in the southeast corner of Virginia. White-footed mice (*Peromyscus leucopus*) were trapped on the mainland, but not on the island, whereas meadow voles (*Microtus pennsylvanicus*) inhabited both the island and mainland areas located to the south and west of the island. A series of swimming tests was performed on both of these species in both field and laboratory to determine if swimming abilities could be a factor preventing *P. leucopus* from invading the island. Both species of small mammals showed good swimming endurance in water of 30°C, but meadow voles had significantly better swimming endurance in water of 20 and 10°C than did white-footed mice. The pelage of *M. pennsylvanicus* repelled water better in water of 30 and 20°C than did that of *P. leucopus*. The repellent properties of the fur of meadow voles may be due in part to their grooming habits. After being removed from water, meadow voles began grooming more quickly than did white-footed mice. Ninety-five % of *M. pennsylvanicus* tested voluntarily crossed an artificial water barrier, whereas only 50% of *P. leucopus* crossed the barrier of their own volition. When released 200 m from shore, meadow voles swam directly to land; however, only a few white-footed mice could orient toward land from a minimal distance of 50 m from shore. The comparatively poor swimming ability of *P. leucopus* is thought to be an important factor accounting for its meager representation on islands in North America.

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INTRODUCTION

Studies examining the dynamics of small mammals inhabiting islands in North America are relatively common, focusing primarily on species composition. In Canada, most available work on insular populations of small mammals is from eastern provinces (Sutton and Hamilton, 1932; Cameron, 1958; Sheppe, 1965). In the conterminous United States, Marshall (1940) surveyed mammals occupying islands in the Great Salt Lake, Utah, and Daugherty et al. (1978) evaluated mammalian distribution on many islands in Flathead Lake, Montana. Many studies of island populations have been conducted in the Midwest (Dice, 1925; Manville, 1950, 1951; Pruitt, 1951; Beer et al., 1954). More recently, Ozoga and Phillips (1964) and Fall et al. (1968) investigated mammalian population dynamics and distributional patterns on islands in Lake Michigan and western Lake Erie, respectively. Farther east, studies have detailed distribution and abundance of mammals residing on islands in New York state (Hatt, 1928; Werner, 1956; Webb, 1965). Small islands along the coast of eastern United States have served well for investigations of experimental zoogeography (Crowell, 1973; Crowell and Pimm, 1976; Grant, 1970, 1971; Mehlhop and Lynch, 1978).

Surveys of the mammalian constituents of islands located along the coast of Maryland and Virginia are sparse. Paradiso and Handley (1965) provided a checklist of mammals occupying Assateague Island and Dueser et al. (1979) provided information on local distribution and relative abundance of mammals inhabiting nine barrier islands along the Delmarva Peninsula. No published work is available to account for mammals inhabiting the islands of the Back Bay region of coastal Virginia. However, reconnaissance trapping for the present study and trapping conducted by Handley (personal communication) in 1956 revealed that mainland areas had populations of *P. leucopus* and *M. pennsylvanicus,* whereas the largest island in the region (Long Island) supported only *M. pennsylvanicus* and *Oryzomys palustris. Peromyscus leucopus* was not found to occupy Long Island although seemingly suitable habitat existed.

The white-footed mouse and meadow vole are broadly sympatric and widespread in North America. However, the former is absent from most islands throughout its range, whereas the latter is common on islands. This fact suggests that there has been little movement of *P. leucopus* from mainland populations onto islands. Some exceptions include the work of Paradiso and Handley (1965) who found *P. leucopus* to be common on Assateague Island in Virginia. However, this island has been isolated from the mainland for only 50 years, having been formed when hurricane activity created an inlet, separating it from the mainland. Recent connection with the mainland may account for the high number of *P. leucopus* on the island. Other investigators have reported the presence of *P. leucopus* on islands in the Midwest and in Canada (Werner, 1956; Sheppe, 1965; Fall et al., 1968). Water in these areas froze during winter months, providing an avenue for dispersal.

In order to understand more fully a given insular fauna, investigators have evaluated the swimming ability of selected species. To this end, most reports tend to be anecdotal, based on brief encounters with individuals in the field (Orr, 1933; Blair, 1939; Davis, 1942; Teeters, 1945; Fisler, 1961). The swimming ability of cricetid rodents also has been evaluated by employing controlled laboratory studies. Behavioral comparisons, which included swimming within the genus *Peromyscus,* were carried out by King (1961) and King et al. (1968). Getz (1967) measured swimming ability of four species of small mammals and correlated their abilities with habitat selection. A thorough laboratory investigation of swimming of small mammals was conducted by Dagg and Windsor (1972). They observed and filmed swimming of 31 species, and measured gait pattern, speeds, and position in the water. More recently, Evans et al. (1978) performed a comparative study of swimming behavior in eight species of muroid rodents. Esher et al. (1978) recently compared the swimming behavior of rice rats (*O. palustris*) and cotton rats (*Sigmodon hispidus*) and correlated swimming ability with habitat utilization. In the present study, our objective was to test swimming ability both in the field and laboratory of two common species of rodents inhabiting an estuarine embayment region of southeastern Virginia, in order to understand why one species (*M. pennsylvanicus*) has successfully invaded an island and the other (*P. leucopus*) has been unable to do so. An understanding of this local phenomenon may aid in explaining the distribution patterns of these species on islands in North America.

METHODS

This study was conducted in Back Bay National Wildlife Refuge, Virginia Beach, Virginia, located at 36°40′ and 75°55′ on the east coast of Virginia, and is comprised of 1861 ha. The Refuge consists of a shallow bay with two large islands and many smaller ones. In addition, it includes part of the mainland which is a narrow strip of land that separates Sand and Shipps bays (both part of Back Bay proper) from the Atlantic Ocean (Fig. 1). The Refuge was established in 1938 and at that time was largely a salt water estuarine embayment, with abundant eel grass (*Zostera marina*) growing in the bay waters. With the advent of dune management practices a large dune system was established along the coastal line. This dune system caused the bay areas to support a relatively freshwater situation resulting in a profuse growth of milfoil (*Myriophyllum* sp.) during summer months.

The mainland of Back Bay consisted of four distinctive habitat types—sand dunes with adjoining beach area, scrub-brush thickets, marsh, and pine woodland. The principal plant of the dune area was sea oats (*Uniola paniculata*), whereas bayberry (*Myrica

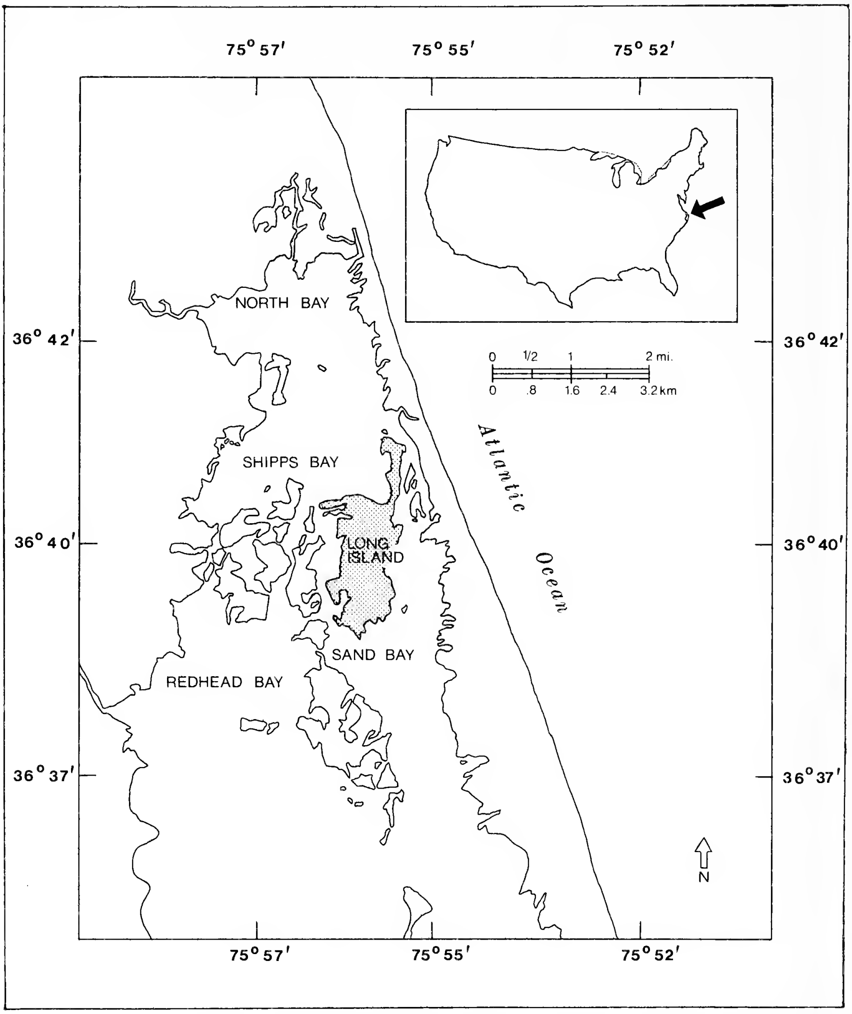

Fig. 1.—Map of Back Bay National Wildlife Refuge showing position of Long Island and surrounding mainland. Inset signifies approximate position of study region along the Atlantic Coast of the United States.

cerifera) and live oak (*Quercus virginiana*) were common in the scrub-brush thickets. Members of the cordgrass family (principally *Spartina* spp.) were abundant in the marsh habitat. Periodic stands of *Juncus roemerianus* and cat-tail (*Typha latifolia*) also contributed to the marsh habitat. Loblolly pine (*Pinus taeda*) was dominant in the pine woodland with intermingling of live oak (*Q. virginiana*). Long Island showed a generally similar floral composition to the mainland. This island (7.6 ha in area) possessed a shrub-brush area, marsh area, and pine woodland community, but instead of a sand dune-beach habitat, it possessed a grass-field community. Also, the pine woodland habitat showed infiltration of hardwood species. Three fields of tall fescue (*Festuca arundinacea*) were present on the island. Prior to 1938, these fields were farmed commercially but currently are managed by the Refuge to provide food for wintering waterfowl. A detailed account of flora of the mainland and Long Island was provided by Carter (1979). The eastern side of Long Island is isolated from the mainland by a channel of 520 to 960 m of water, whereas the western side averaged a distance of 2.73 km from the mainland. Numerous small islands surround Long Island, making the longest uninterrupted water expanse about 160 m. These smaller islands are cordgrass marshes unsuitable for colonization by small mammals. Small mammals were collected for swimming trials from the Back Bay area by employing live-trapping methods. Sherman traps were set along 100 m line transects with two traps per station with a station to station interval of 10 m. Traps were baited with sunflower seeds.

Field Procedures

To determine if swimming abilities may account for the presence of *M. pennsylvanicus* on Long Island and the absence of *P. leucopus* from this island, 10 meadow voles and 10 white-footed mice were tested in the waters of Back Bay. *Oryzomys palustris* (an inhabitant of Long Island) was not tested for it has been demonstrated clearly to be a proficient swimmer (Esher et al., 1978). As a means of measuring swimming distance and orientation, a 200 m line was established radiating from the shoreline of Long Island with markers positioned at 50 m intervals. Animals were introduced into the water initially at 50 m from shore and followed in a boat as they swam. If the animal began to submerge involuntarily or if it successfully reached the shore, it was removed from the water by use of a net. The animal was then released where it was originally captured. If the animal was unsuccessful at reaching land from 50 m, another member of the same species was tested from 25 m and if unsuccessful the trial was conducted at 10 m from shore. If the animal successfully reached shore from 50 m, another member of the same species was tested from 100 m and this sequence was continued until a given animal was unable to orient to land or could not successfully complete the distance. Two members of each species were required to complete a given distance before that species was considered "acceptable" at a specified distance. During field trials, the following information was taken: water temperature; water condition (choppy, slightly choppy, calm); position of body in water; type of locomotion employed; pelage condition; distance attempted and completed; length of time in water. Carter (1979) provided a thorough description of each criterion used to evaluate swimming ability.

Laboratory Procedures

Twenty meadow voles and 20 white-footed mice were collected during January 1979 through April 1979 from the Back Bay region. Animals were housed in the laboratory and maintained on a diet of Purina laboratory chow, sunflower seeds, oranges, and water *ad libitum* for the duration of the study.

To determine if animals exhibited the endurance to swim the distance between the mainland and Long Island and how seasonal variation in water temperature affected their performance, swimming bouts were conducted in a 60 by 58 by 30 cm tank for 30 min at three different temperatures (10, 20, 30°C). These temperatures were selected in that they corresponded to the typical temperature regime encountered year-round in the waters of Back Bay. During each test, swimming ability was analyzed by recording the following information: weight before and after swimming; time of swimming bout; grooming characteristics; type of locomotion employed; posture; pelage condition. When possible, the above data were analyzed for significance at the 0.05 confidence level by the Student's *t*-test.

Table 1.—*Mean swimming times (minutes) for* Microtus pennsylvanicus *and* Peromyscus leucopus *in water temperatures of 30°C, 20°C, and 10°C. Sample size was 20 individuals of each species per trial (±S.E.).*

	Microtus pennsylvanicus			*Peromyscus leucopus*		
Sex	30°C	20°C	10°C	30°C	20°C	10°C
Sexes combined	30 (0)	29.5 (0.47)	16.1 (1.61)	30 (0)	26.6 (1.03)	9.5 (0.58)
Males	30 (0)	30 (0.11)	16.6 (1.95)	30 (0)	27.5 (0.85)	10.4 (0.76)
Females	30 (0)	29 (0.67)	16.0 (0.76)	30 (0)	25.8 (1.16)	8.5 (0.36)

In order to assess the degree in which mice and voles voluntarily enter water a wooden test chamber equipped with a water barrier was employed. The test chamber consisted of a plastic-lined trough (260 by 56 by 16 cm) with a platform at each end. A water barrier 200 cm in length and 9 cm deep was located between the platforms. This water barrier made it necessary for small mammals to swim to reach the other platform. The entire apparatus was covered with hardware cloth. The test chamber was modified from that employed by Esher et al. (1978). Testing consisted of removing an animal from its holding cage and placing it into a large Sherman trap (supplied with sunflower seeds and cotton nesting material) which was placed on a platform with the door secured open. On the opposite platform was set another large Sherman trap equipped with the same amount of sunflower seeds and cotton nesting material. Each animal tested was allowed to remain in the chamber no more than 18 h. If the animal was able to swim the water barrier it was trapped on the opposite platform and if not, it was secured from the same platform and returned to the laboratory holding cage. No animals were tested more than once. Results were tested for significance with the Chi-square test.

RESULTS

Directional Orientation

Directional orientation of *M. pennsylvanicus* and *P. leucopus* was tested in the field. In three different sessions, ten individuals of each species were tested. The distances that animals were released from shoreline ranged from 10 to 200 m. With the exception of one meadow vole, all individuals completed swimming trials when tested at varying distances from shore. As expected, both choppy water and lower water temperatures produced slower swimming times and many variables associated with field circumstances complicated exact quantitative analyses. Individual variation made inter- and intraspecific comparisons difficult and therefore only general trends are reported.

Nine out of 10 voles tested swam directly for land as soon as released into the water. At variance to this strong orientation ability was a single individual female that did not reach shore. When released, it initially swam in small circles for 30 sec, then began swimming with the wind, parallel to the island shoreline. Meadow voles were able to reach land from 200 m with little difficulty. Moreover, the route of travel to land was straight with no directional changes.

Table 2.—*The mean weight gain (g) due to water retention in pelage of* Microtus pennsylvanicus *and* Peromyscus leucopus *in water temperatures of 30°C, 20°C, and 10°C. Sample size was 20 individuals of each species per trial (±S.E.). Figures represent the per cent weight gained of the initial body weight.*

	Microtus pennsylvanicus			*Peromyscus leucopus*		
Sex	30°C	20°C	10°C	30°C	20°C	10°C
Sexes combined	7.1 (0.94)	8.0 (1.16)	14.1 (1.79)	17.5 (1.45)	12.7 (1.43)	13.4 (0.89)
Males	8.0 (0.96)	9.9 (1.16)	13.2 (0.89)	17.1 (1.36)	10.4 (1.30)	15.9 (2.06)
Females	6.2 (0.92)	6.1 (1.16)	13.6 (0.92)	17.9 (1.54)	14.9 (1.54)	11.8 (1.43)

Results of the field swimming tests for *P. leucopus* contrasted sharply with those of meadow voles. White-footed mice did not perform well in this test as demonstrated by the fact that only two of the 10 mice tested showed positive signs of actually swimming for shore as a means of escape or orientation in the water. Only four mice reached shore from 50 m. However, two of these mice swam in very irregular patterns characterized by swimming in circuitous patterns accompanied by almost fortuitous straight-line orientations toward land. The other two individuals that reached shore from a distance of 50 m did swim continuously on a straight line toward the nearest land mass. Six of the 10 mice tested appeared disoriented, changing their course many times and often swimming in circles. When the first white-footed mouse was tested from 50 m and it was noted that they may only swim in circles, the distance attempted was reduced in order to delimit a particular distance at which all could orient toward land. One individual was released as close as 10 m from land, swam within 7 m of this land mass, and then radically changed direction away from land.

Although field tests lacked rigid quantitative comparisons, work clearly demonstrated the superior ability of meadow voles to orient to land and to endure travel in water of low temperatures characterized by turbulence. In contrast, white-footed mice demonstrated inferior ability to orient and to endure water conditions found naturally in the Back Bay region. In order to refine the field investigation, swimming ability of white-footed mice and meadow voles also was analyzed in the laboratory.

Swimming Endurance

Swimming endurance was tested in the laboratory for meadow voles and white-footed mice at three different temperatures. Testing entailed 30-min swimming trials for 20 animals of each species at temperatures of 30, 20, and 10°C (Table 1).

Microtus pennsylvanicus.—When tested at 30°C all meadow voles swam well for the duration of the testing period. During the trial, voles maintained the dorsal half of their body well above the surface of the water while swimming and floating, and comparatively little energy was expended to maintain this posture in the water. During testing, voles explored the tank by diving beneath the water. As a result of submersion, the pelage took on a glistening appearance due to a layer of air being trapped within the fur. Their eyes were kept open at all times and upon surfacing the pelage was quite dry. A decrease of 10°C in water temperature did not greatly affect swimming endurance of *M. pennsylvanicus*. Only one vole was unable to swim for the 30-min trial period at 20°C. In general, their behavior in water of 20°C was similar to that seen in 30°C. No significant difference was found between mean endurance time for males and females. When tested at 10°C, a greatly reduced swimming ability (endurance) was noted in voles. Only 10% of the animals tested in water of 10°C could withstand immersion for the full 30-min period. Mean swimming time for sexes combined was shorter by about one half in water 10°C than 30°C. Body flotation was similar to that seen in higher water temperatures, however, muscular activity declined resulting in locomotor ataxia. Floating rather than active swimming occurred about 6 min after initiation of trial. As fatigue developed, dipping of the head became common, eventually causing death due to excessive aspiration of water. When symptoms of drowning appeared, animals were removed from water.

Peromyscus leucopus.—Swimming endurance of white-footed mice was good in water of 30°C, all animals completing the 30-min swimming duration (Table 1). White-footed mice commonly floated high in the water although not to the degree seen in voles. Diving was not observed in *P. leucopus* at any time during this study. Swimming duration in water of 20°C was depressed compared to that for trials conducted in water of 30°C. Thirty-five % of animals could not complete the swimming period of 30 min. The mean time for combined sexes was about 3 min less than that for meadow voles at the same temperature. Those mice that completed the entire 30-min swim showed partial paralysis of the hind limbs and moved in jerky, labored actions. As was the case with voles at 10°C, white-footed mice exhibited ataxia resulting in the inability to maintain their noses above the surface of the water. No significant difference was found between mean swimming endurance of male and female mice as compared by Student's *t*-tests. A very low tolerance was seen in white-footed mice when subjected to water of 10°C. Here, the mean endurance time was about 6.5 min shorter than that exhibited by meadow voles at the same temperature. Physical reactions of mice at 10°C were similar to those at 20°C although symptoms occurred earlier in the trial. Once again, mice began imbibing water during final stages of the test. At times during the swim, mice appeared to fall asleep, at which time their noses dipped below the surface of the water. This startled the animals and precipitated increased locomotor activity for a short time.

Comparison between the swimming endurance of meadow voles and white-footed mice revealed that the former exhibited greater endurance. At water of 30°C no significant difference was found on the interspecific level. However, a significant difference ($P \leqslant 0.05$) was found in mean swimming times between the two species in water of 20 and 10°C—*M. pennsylvanicus* showing a longer endurance time than *P. leucopus*.

Weight Dynamics

The weight gained by meadow voles and white-footed mice due to water retention in the fur while in the water for a 30-min trial was measured in the laboratory. Twenty individuals of each species were weighed prior to and following swimming bouts in water of 30, 20, and 10°C (Table 2).

Microtus pennsylvanicus.—The weight of voles before and after 30-min swimming trials was determined and the resulting weight gain due to water retention in the pelage was expressed as a percent gain of the initial body weight. When tested in water of 30°C, voles gained an average of 7.1% of their original body weight due to water retention. The percent of body weight gained ranged from 0.3 to 22%; the two greatest percentage gains were by the two largest voles. One vole weighing 68.6 g gained 16.8% of its original body weight due to water. The second largest vole (60.9 g), gained 22% of its original body weight in water during a 30-min swimming trial. When tested in water of 20°C, voles gained a mean of 8% of their body weight due to water. However, the largest voles did not gain the most weight in water of 20°C. Rather, largest gain was 17.8% of original body weight by a small vole of only 28 g. Percentage of body weight gained due to water retention in water of 10°C ranged from 5.8 to 40% with a mean of 14.1%. In water of 10°C, the mean percentage of weight gained by voles was significantly greater than in water of higher temperatures. This was twice the retention measured for voles in water of 30°C and animals were in water for less than half as long. The largest individual (65.3 g) gained the most weight (40% of initial body weight) from water maintained in the pelage.

Peromyscus leucopus.—As shown in Table 2, white-footed mice gained a mean of 17.5% of their original body weight due to water retention after swimming in water of 30°C for a 30-min trial. Unlike *M. pennsylvanicus,* the largest individuals tested did not gain the most weight during swimming. The percent of weight gained ranged from

6.6 to 28.6%. *Peromyscus leucopus* retained a significantly larger amount of water in its pelage than did *M. pennsylvanicus* during endurance trials in water of 30°C. Swimming trials in water of 20°C resulted in an average of 12.7% gain in weight by white-footed mice during a swimming bout of about 26.5 min. As was the case in water of 30°C, the largest individuals tested did not gain the most weight due to water. The per cent weight gain ranged from 3.6 to 26%, and *P. leucopus* was found to retain a significantly larger amount of water in its pelage than *M. pennsylvanicus* during endurance trials in water of 20°C. Swimming trials for endurance of *P. leucopus* were comparatively short as detailed in Table 1. During a swimming bout in water of 10°C for 9.5 min, mice gained 13.4% of their original body weight due to water—a mean rate of about 0.3 g water/min retained in the pelage during swimming. The percentage of body weight gained due to water ranged from 8.5 to 24.3%. In water of 10°C, *P. leucopus* gained significantly less weight than *M. pennsylvanicus* due to water retention. This difference was due to the fact that *P. leucopus* spent less time in the water (average, 9.5 min) than *M. pennsylvanicus* (average, 16.3 min) giving less time for water retention in the pelage.

Latency before Grooming

The amount of time that passed before an animal began grooming once it was removed from the swimming tank at the conclusion of a trial was referred to as grooming latency time. This experiment dealt only with animals tested in water of 30°C. Latency before grooming was not recorded from swimming trials in water of 20 and 10°C because animals were generally too cold and immobile to groom when removed. Latency times were recorded for 20 *M. pennsylvanicus* and 20 *P. leucopus*.

Microtus pennsylvanicus.—All meadow voles tested began grooming before 3 min following removal from swimming chamber. Grooming latency time ranged from 3 sec to 2 min post-removal. Three individuals initiated grooming 3 sec following removal. The mean time elapsed before grooming occurred was 23.2 sec after removal from the tank following a 30-min swim in water of 30°C.

Peromyscus leucopus.—Only five of the 20 white-footed mice tested began grooming before 3 min post-removal. Others began grooming at various intervals following the 3-min mark. The earliest at which a mouse began to groom was 3 sec post-removal. A mean of about 2.5 min represented the latency before grooming for *P. leucopus*. White-footed mice averaged about 2 min slower than meadow voles with respect to time elapsed before grooming.

Voluntary Crossing of a Water Barrier

To determine whether *M. pennsylvanicus* and *P. leucopus* would voluntarily cross a water barrier to reach an artificial "island," 20 individuals of each species were tested in the laboratory. Ninety-five % of voles tested (19/20) entered the water and swam 200 cm across the water barrier—one female did not complete this trial. Ten females and 10 male meadow voles were tested and no significant difference was found between sexes by employing the Chi-square test. Unlike meadow voles, only 50% of the white-footed mice successfully crossed the water barrier. Eleven males and nine females were tested resulting in successful crossing by seven males and three females. A significantly greater number of males crossed the barrier than did females (χ^2, $P \leqslant 0.05$).

In addition to those behaviors discussed above, Carter (1979) analyzed and compared the following swimming behaviors in *M. pennsylvanicus* and *P. leucopus*: swimming gait; body position in the water; influence of water on pelage condition; diving and swimming beneath the water. Although no discussion will be undertaken at this time, in each test, *M. pennsylvanicus* showed greater refinement of characters adaptive for colonization of insular environments than did *P. leucopus*.

DISCUSSION

Insular mammalian faunas may be established in different ways such as swimming, transport on ice bridges, rafting on pieces of terrestrial debris originating from mainland areas, and transportation by man. In the present study, we have concentrated on detailing the swimming ability of two small mammals as a mode of island invasion. One may visualize an animal's chance of invading an island as being largely determined by its ability to cross a water barrier to reach that island. In order to elucidate the potential for small mammals actively to invade islands completely surrounded by water on a year-round basis, knowledge of their swimming ability is essential.

In order to invade an island other than by chance, it is assumed that an animal must first perceive an offshore land mass and be able to swim toward it, thereby exhibiting directional orientation. Sheppe (1965) reported that *P. leucopus* released 59 m offshore swam toward the shore, and if driven off course soon returned to the original course. White-footed mice released 305 m offshore tended to swim irregularly, frequently changing direction. Sheppe (1965) concluded that mice tested oriented toward shore primarily by visual means. In the present study, *P. leucopus* showed considerable difficulty orienting to land while in the water at distances ranging from 10 to 50 m from land.

No published work is available to document orientation ability in water of *M. pennsylvanicus*; however, its presence on islands in North America is well known (see Grant, 1971, for review). Jackson (1920) found *M. pennsylvanicus* on islands in Lake Superior that were not more than 2.4 km from the mainland. Crissey and Darrow (1949) found meadow voles on Valcour Island in Lake Champlain located about 2 km from shore. More recently, Mehlhop and Lynch (1978) and Dueser et al. (1979) reported *M. pennsylvanicus* from islands in the eastern Chesapeake Bay and Virginia barrier islands, respectively. In the above studies the means employed by meadow voles to invade these islands generally were not known. In the present study, experimental results from field tests indicated that meadow voles showed superior directional orientation in the water with several voles swimming a straight line toward shore from a distance of 200 m. This ability would allow this small mammal the potential to invade islands in the Back Bay region.

Water temperatures of the Back Bay region during summer months averaged approximately 30°C. Laboratory tests of the present study run at this temperature indicated that voles and mice had no difficulty swimming for the 30-min test period. Sheppe (1965), working during summer in Lake Opinicon, Ontario, found channels separating islands from the mainland to be covered by floating mats of algae. *Peromysus leucopus* was found to employ these mats to travel to islands from the mainland. During summer months, the waters of Back Bay were largely covered with a mat of milfoil (except for a 75 to 100 m expanse across the middle of the Bay). Tests conducted in our study confirm that the weight of either *P. leucopus* or *M. pennsylvanicus* could be supported by this mat of vegetation, thus providing a partial route for island invasion. However, the appeal of this route was somewhat compromised by the increased number of predators present in the waters of Back Bay during summer months (that is, large mouth bass, snapping turtles, water snakes, and the cottonmouth).

During spring and autumn water temperatures of Back Bay averaged about 20°C. Laboratory and field tests revealed that voles and mice were stable in their swimming ability at these temperatures; however, the density of milfoil growth was greatly reduced at this time of year thus eliminating the possible utilization of this invasion route to the island.

Water temperature frequently fell below 10°C during winter months in the Back Bay region and for short periods of time ice sheets would develop except in those more central, open waters of the Bay. During this time (generally not more than one month in duration) small mammals could walk out on the ice and swim across an expanse of open water to another land-connected sheet of ice. However, our laboratory experiments showed that small mammals demonstrated lowered survival when tested in water approximating winter conditions. Esher et al. (1978) reported that most individuals of *S. hispidus* and *O. palustris* showed effects of cold exposure when tested in water baths of 15°C for 40 min—many cotton rats were incapacitated upon removal. Getz (1967) tested *P. leucopus* and *M. pennsylvanicus* in water of 15°C and noted that they swam an average of only 2.4 and 2.8 min, respectively, before exhaustion. Results of our study indicate that survival time of *P. leucopus* and *M. pennsylvanicus* was longer in water of 10°C than those reported by Getz (1967). Attempts by small mammals to traverse bodies of water in Back Bay during mid-winter surely would result in high mortality.

The superior swimming ability exhibited by meadow voles in the present study was due partially to the water repellent and insulative qualities of their fur. Small mammals are known to lose heat rapidly in cold water due to neuromuscular depression which adversely affects swimming capacity (Wilber, 1959; Wilber and Hunn, 1960; Wilber and Weidenbacher, 1961; Sealander and Guess, 1970; Esher et al., 1978). Dry fur possesses superior insulative qualities and conducts heat at a slower rate than does wet fur (Scholander et al., 1950). A dry pelage also increases the buoyancy of an animal, by more readily trapping air between the hairs (Dagg and Windsor, 1972). Esher et al. (1978) indicated that the superior endurance of *O. palustris* over that of *S. hispidus* was due partially to the greater ability of the fur of the former to repel water, thus increasing buoyancy. In the present study, *M. pennyslvanicus* was a more accomplished swimmer than *P. leucopus,* in part due to its ability to maintain a comparatively dry pelage causing the animal to float easily in the water. The pelage of *M. pennsylvanicus* was very dense and well-groomed (grooming was initiated about 20 sec following removal from water). In contrast, the pelage of *P. leucopus* was not as dense as that of *M. pennsylvanicus,* and the former did not initiate grooming as quickly following removal from water as the latter.

The ability to dive and swim underwater has been observed in *O. palustris* (Esher et al., 1978), *Microtus californicus* (Fisler, 1961), and to a lesser degree in *M. pennsylvanicus* (Blair, 1939). Because these species occupy marshy habitats, this aquatic behavior may be adaptive in habitat utilization and colonization. In our study meadow voles commonly dove and swam underwater in both laboratory and field. During the period of submersion, eyes were kept open facilitating orientation. In sharp contrast, when tested under similar circumstances, the white-footed mouse was never observed to dive or swim underwater.

If small mammals were to invade an island actively they normally would enter the water of their own volition. Blair (1939) reported that

M. pennsylvanicus entered and successfully swam across a stream in Michigan and Sheppe (1965) found *P. leucopus* voluntarily to cross water barriers in order to return to their "home" islands when released on "foreign" islands nearby. The distance crossed by mice was small (average 38 m). Experiments with *S. hispidus* and *O. palustris* (Esher et al., 1978) showed that 74% of cotton rats tested voluntarily swam a 200 cm water barrier and all rice rats tested crossed this barrier. Getz (1967) reported that when *P. leucopus* was forced to swim to a feeding station which it previously had been able to walk to, the mice made an average of 31.1% fewer visits to the station, indicating a reluctance to swim. However, under the same circumstances, *M. pennsylvanicus* averaged only a 3.4% reduction in visits to the station. In the present study, we found that *M. pennsylvanicus* successfully crossed a water barrier in 95% of the trials, whereas *P. leucopus* successfully crossed the barrier in only 50% of the trials. These results are in agreement with the trend of voluntary crossing of a water barrier by *P. leucopus* and *M. pennsylvanicus* reported above.

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COLLECTIONS OF RECENT MAMMALS OF THE WORLD, EXCLUSIVE OF CANADA AND THE UNITED STATES

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Abstract

A survey of the Recent mammal collections outside of Canada and the United States revealed the existence of 321 collections with more than 50 specimens. These collections are located in 76 countries and hold 2,358,356 specimens. Fifty collections holding more than 10,000 specimens were located. These 50 collections hold 81.3% of the specimens of Recent mammals in collections outside of Canada and the United States.

Introduction

Recently, Choate and Genoways (1975) completed the fourth survey of the collections of Recent mammals in North America (Howell, 1923; Doutt et al., 1945; Anderson et al., 1963). These surveys have proven to be useful in locating specimen-based research resources and have documented the development of these resources. Because no survey has ever been made on a worldwide basis, we believed that it would be useful to attempt such a survey. Our main concern was to learn what and where are the specimen-based systematic resources of mammalogy around the world. Because of the very recent survey for Canada and the United States, we did not feel that it was necessary for us to include them in our work.

Submitted 26 September 1980.

Table 1.—*Collections from outside Canada and the United States containing 10,000 or more specimens of Recent mammals.*

Institution	Number of specimens
British Museum (Natural History), London, England	300,000
Zoological Museum of Moscow University, Moscow, USSR	150,000
Mammal Research Institute, Polish Academy of Sciences, Białowieza, Poland	145,000
Zoological Institute, Leningrad, USSR	100,000
Zoologische Staatssammlung München, München, Federal Republic of Germany	100,000
Museu Nacional, Rio de Janeiro, Brazil	85,000
Rijksmuseum van Natuurlijke Histoire, Leiden, The Netherlands	80,000
National Museum of Zimbabwe, Bulawayo, Zimbabwe	67,000
Forschungsinstitut und Natur-Museum Senckenberg, Frankfurt am Main, Federal Republic of Germany	55,000
Zoology Museum of the Institute of Plant and Animal Ecology, Sverdlovsk, USSR	48,404
Koninklijk Museum voor Midden-Afrika, Tervuren, Belgium	47,500
Naturhistorisches Museum Wien, Vienna, Austria	40,000
Zoological Museum of the University, Copenhagen, Denmark	35,000
Institute of Vertebrate Zoology, Czechoslovak Academy of Sciences, Brno, Czechoslovakia	30,000
Staatliches Museum für Naturkunde Stuttgart, Stuttgart Federal Republic of Germany	30,000
Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Federal Republic of Germany	30,000
Transvaal Museum, Pretoria, Republic of South Africa	28,000
Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium	26,000
Kaffrarian Museum, King William's Town, Republic of South Africa	25,000
Muséum d'Histoire Naturelle, Geneve, Switzerland	25,000
National Museum, Praha, Czechoslovakia	24,500
Zoological Museum, Amsterdam, The Netherlands	21,000
National Science Museum, Tokyo, Japan	20,214
Australian National Wildlife Collection, Lyneham, Australia	20,000
National Museum of Victoria, Melbourne, Australia	20,000
National Zoological Collection of India, Calcutta, India	20,000
Staatliches Museum für Tierkunde, Dresden, Democratic Republic of Germany	20,000
Zoological Museum, Oulu, Finland	20,000
Lunds Universitets Zoologiska Museum, Lund, Sweden	18,700
Bombay Natural History Society, Bombay, India	18,000
Western Australia Museum, Perth, Australia	18,000
Universidad Nacional Autónoma de México, México, México	18,000
Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina	17,100
Institute of Systematic Zoology, Praha, Czechoslovakia	16,000
Laboratoire d'Anatomie Comparée, Museum National d'Histoire Naturelle, Paris, France	16,000

Table 1.—*Continued.*

Institution	Number of specimens
Museu de Zoologia, São Paulo, Brazil	15,764
Department of Vertebrate Taxonomy and Faunology, Peking Institute of Zoology, Peking, People's Republic of China	15,000
The Australian Museum, Sydney, Australia	14,000
Queensland Museum, Fortitude Valley, Australia	13,600
Escuela Nacional de Ciencias Biologicas, México, México	13,500
Museum Zoologicum Bogoriense, Bogor, Indonesia	13,000
Zoological Museum, Helsinki, Finland	13,000
Zoological Museum, Oslo, Norway	12,000
Zoological Reference Collection, Singapore, Singapore	12,000
Laboratoire de Zoologie, Muséum National d'Histoire Naturelle, Paris, France	10,000
Landessammlungen für Naturkunde, Karlsruhe, Federal Republic of Germany	10,000
Museo Zoologico de "La Specola," Firenze, Italy	10,000
Naturhistorisches Museum, Bern, Switzerland	10,000
South Australian Museum, Adelaide, Australia	10,000
Zoologisches Institut und Zoologisches Museum, Hamburg, Federal Republic of Germany	10,000
Total	1,916,282

In order to assess the location and holdings of collections of mammals, we prepared the following questionnaire:

1. What is the formal name (if any), address, and standard abbreviation (if any) of your private or institutional collection?
2. What is the name and address of the person directly responsible for the collection?
3. Approximately how many specimens of Recent (not fossil) mammals were in the collection as of 1 January 1978?
4. How many holotypes are in the collection? Has a catalogue or list of those types been published? If so, please give citation.
5. What geographic areas are best represented in the collection?
6. What systematic groups are best represented in the collection?
7. Does the collection include specimens formerly included in other major private or institutional collections which have been merged with your collection? If so, please indicate the name of these collections.

Copies of the questionnaire were mailed to curators or directors of all known or suspected collections based upon our own experience and listings in such books as *Directory of the Natural Sciences Museums of the World* (Muzeelor, 1971) and *Museums of the World* (1975). A total of 740 questionnaires was mailed and second questionnaires were sent when no reply was received within six months. We received 413 replies, indicating the existence of 321 collections of 50 or more mammals and 26 of fewer than 50 mammals outside of Canada and the United States. Replies were received from collections in 76 countries. We are well aware that the results of our survey do not give a total representation of the collections from around the world. Our efforts suffer from the same problem as any survey in that we can record only the information that is returned to us. However, we believe that the current survey is a significant step in locating the specimen-based resources of mammalogy. Rather than being an end to this effort we hope that similar surveys will be conducted in the future.

Data compiled from returned questionnaires indicated that 2,358,356 specimens of mammals are held by collections outside of Canada and the United States (specimens from owl pellets not included). These, together with the 2,521,342 specimens held by collections in Canada and the United States (Choate and Genoways, 1975) give a total of 4,879,698 specimens of mammals held by the research collections of the world. Of the specimens of mammals outside of Canada and the United States, 81.3 percent are held in 50 collections of 10,000 or more specimens (Table 1). These collections together with the 37 from Canada and the United States gives a total of 87 collections of mammals that hold more than 10,000 specimens. These 87 collections are located in 29 countries.

In the list below, data are listed as follows: name of collection (including self assigned acronym); address of collection; number of specimens in collection; number of holotypes represented; geographic areas best represented; systematic groups best represented; if the collection includes material held previously by another collection; name of person in charge of the collection. The following list only includes those collections of 50 or more specimens.

ARGENTINA

Centro Nacional Patagonico (CNP), 28 de Julio 28, 9120 Puerto Madryn, Chubut. 127 specimens; Patagonia; Rodentia, Carnivora, Pinnipedia, Camelidae. Persons in charge are José Luis Garrido and José Alejandro Scolaro.

Colección de Mamíferos de Elio Massoia y Flia, Teniente 1° Fernandez 3405, 1712 Castelar, Pcia. Buenos Aires. 6000 specimens; 6 holotypes; Argentina; Marsupialia, Chiroptera, Rodentia, Carnivora. Person in charge is Elio Massoia.

Fundación Miguel Lillo (FML), Miguel Lillo 205, 4000 Tucumán. 2500 specimens; northeastern Argentina; Marsupialia, Chiroptera, Edentata, Rodentia, Mustelidae. In addition, includes the "Rusconi" collection of 2500 skulls. Person in charge is C. C. Olrog.

Instituto Argentino de Investigaciones de las Zonas Aridas (IADIZA), Casilla de Correo 507, 5500 Mendoza. 3660 specimens; 3 holotypes;

central and western Argentina; Rodentia. Person in charge is Prof. Julio R. Contreras.

Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Av. Angel Gallardo 470, 1405—Buenos Aires. 17,100 specimens; 12 holotypes; Argentina, Bolivia, Paraguay; Chiroptera, Rodentia, Edentata, Cetacea. Person in charge is Dr. Jorge A. Crespo.

Museo de Ciencias Naturales y Antropológicas "Juan Cornelio Moyano," Subsuelo Plaza Independencia, Ciudad, 5500—Mendoza. 597 specimens; 42 holotypes; South America; general species representation. Person in charge is Profesora Ketty Böhm de Saurina, Aristóbulo del Valle 499.

Museo de Ciencias Naturales y Centro de Investigación, Instituto Superior del Profesorado Antonio R. de Montoya, San Luis 384, 3300 Posadas, Misiones. 50 specimens; subtropical Argentina. Person in charge is Profesora Nélida M. Hienrich.

Museo de Entre Ríos de Ciencias Naturales y Antropológicas, Casilla de Correo No. 71, 3100 Paraná, Entre Ríos. 100 specimens; Argentina. Person in charge is Prof. Juana María Barzanti.

Museo de Historia Natural de San Rafael, Mendoza. 150 specimens; Mendoza and Chaco, Argentina; Rodentia, Felidae. Person in charge is Dr. Humberto A. Lagiglia.

Museo Municipal de Ciencias Naturales "Lorenzo Scaglia" (MMP), CC 1207, Correo Central, 7600 Mar de Plata. 1500 specimens; southeastern portion of the Province of Buenos Aires, Argentina; Marsupialia, Rodentia. Person in charge is Lic. Carlos Alberto Velázquez.

Museo Provincial, Calle Pellegrini 180, 6300 Santa Rosa, La Pampa. 60 specimens; Patagonia; Felidae. Person in charge is Reynaldo Orrego Aravena.

Museo Provincial de Ciencias Naturales "Florentino Ameghino," Moreno 2557, 3000 Santa Fe. 260 specimens; Argentina; Primates, Edentata, Rodentia, Carnivora, Artiodactyla. Person in charge is Lic. Carlos A. Virasoro.

AUSTRALIA

Arthur Rylah Institute for Environmental Research, Fisheries and Wildlife Division, Ministry for Conservation, P.O. Box 137, Heidelberg, Victoria 3087. 700 specimens; Victoria and adjacent waters; Pinnipedia. Person in charge is Mr. Robert M. Warneke.

Australian National Wildlife Collection (ANWC), C.S.I.R.O., Division of Wildlife Research, P.O. Box 84, Lyneham, A.C.T. 2602. 20,000 specimens; 4 holotypes; Australia, New Guinea; Monotremata, Marsupiala, Chiroptera, Rodentia. Person in charge is Dr. J. H. Calaby.

Central Australian Museum (CAM), Territory Parks and Wildlife

Commission, P.O. Box 1046, Alice Springs, Northern Territory 5750. 750 specimens; 1 holotype; arid zone of central Australia; Marsupialia, Chiroptera, Rodentia. Person in charge is Dr. K. A. Johnson.

D. C. D. Happold Collection of Mammals, Department of Zoology, Australian National University, Canberra, A.C.T. 2000. 1000 specimens; Nigeria; Chiroptera, Rodentia. Person in charge is Dr. D. C. D. Happold.

Monash University, Museum, Department of Zoology, Clayton, Victoria. 750 specimens; southeastern Australia; Monotremata, Marsupialia, Rodentia. Person in charge is A. K. Lee.

National Museum of Victoria, 285-321 Russell Street, Melbourne, Victoria 3000. 20,000 specimens; 25 holotypes; Australia; Monotremata, Marsupialia, Chiroptera, Rodentia. Includes material formerly held in the following collections: Arthur Rylah Research Institute, Fisheries and Wildlife Division, Ministry for Conservation; Monash University; Melbourne University. Person in charge is Miss Joan M. Dixon.

Queensland Museum (QM), Gregory Terrace, Fortitude Valley, Queensland 4006. 13,600 specimens; 20 holotypes; Queensland; Marsupialia. Person in charge is R. E. Molnar.

Queen Victoria Museum and Art Gallery, Wellington Street, Launceston, Tasmania 7250. 2300 specimens; Tasmania; Dasyuridae, Vespertilionidae, Muridae. Person in charge is Mr. Robert G. H. Green.

South Australian Museum, North Terrace, Adelaide, South Australia 5000. 10,000 specimens; 15 holotypes; southern and central Australia; Marsupialia, Chiroptera, Rodentia. Person in charge is Peter F. Aitkens.

Taronga Zoo, Zoological Parks Board of New South Wales, P.O. Box 20, Mosman, New South Wales 2088. 810 specimens; Australasia; Monotremata, Marsupialia. Person in charge is Mr. J. L. Throp.

Tasmanian Museum and Art Gallery, GPO Box 1164 M, Hobart, Tasmania 7001. 1200 specimens; Tasmania; Phalangeriidae, Macropodidae. Person in charge is A. P. Andrews.

The Australian Museum, 6-8, College Street, Sydney, New South Wales 2000. 14,000 specimens; 118 holotypes; Australia, New Guinea; Monotremata, Marsupialia, Chiroptera, Rodentia, Pinnipedia. Person in charge is Basil J. Marlow.

The MacLeay Museum, The University of Sydney, Sydney, New South Wales 2006. 1000 specimens; 8 holotypes; Australia, New Guinea; Marsupialia, Pteropodidae. Includes the MacLeay Collections. Person in charge is Dr. P. J. Stanbury.

Western Australia Museum (WAM), Francis Street, Perth, Western Australia 6000. 18,000 specimens; 7 holotypes; Western Australia; Marsupialia, Chiroptera, Rodentia. Person in charge is Dr. D. J. Kitchener.

AUSTRIA

Landesmuseum Joanneum, Raubergasse 10, A-8010 Graz. 1000 specimens (plus about 1000 fragmentary skulls); Rodentia, Carnivora. Person in charge is Dr. Erich Kreissl.

Landesmuseum für Kärnten, Museumgasse 2, A-9010 Klagenfurt. 100 specimens; Austria; Carnivora. Person in charge is Dr. Hans Sampl.

Naturhistorisches Museum der Benediktiner-Abtei Admont, A-8911 Admont. 94 species and subspecies are represented in collection; Europe, India, Africa; general taxonomic representation. Includes material formerly belonging to Schlüter, Baron Brenner, Dr. Holub, and Hofmuseum Dresden. Person in charge is Prof. Dr. rer. silv. habil. Günter Morges.

Naturhistorisches Museum Wien (NMW), Postfach 417, A-1014 Wien. 40,000 specimens; 200 holotypes; central and southeastern Europe, Turkey and Near East, eastern Zaire, Indonesia, Brazil (Natterer's historic collection); general taxonomic representation. Includes the former private collections of L. Adametz (primitive breeds of domestic ungulates), K. Bauer, F. Spitzenberger, and O. Wettstein. Person in charge is Dr. Friederike Spitzenberger.

Oberösterreichisches Landesmuseum, Abteilung Zoologie, Museumstrasse 14, A-4001 Linz. 2600 specimens; Austria; Insectivora, Rodentia, Carnivora. Person in charge is Dr. Gertrud Mayer.

Sternwarte Kremsmünster Naturhistorische Sammlungen, A-4550 Kremsmünster. 200 specimens; Middle Europe; Rodentia, Carnivora. Person in charge is Dr. P. Jakob Krinzinger.

Vorarlberger Naturschau, Marktstrasse 33, A-6850 Dornbirn. 157 specimens; Austrian Vorarlberg. Person in charge is Dir. Dr. Walter Krieg.

BELGIUM

Institut Royal des Sciences Naturelles de Belgique (IRSB), 31 rue Vautier, B-1040 Brussels. 26,000 specimens; 11 holotypes; Africa; general taxonomic representation. Includes the collection of de Selys Longchamps. Person in charge is Xavier Misonne.

Koninklijk Museum voor Midden-Afrika (KMMA), Steenweg op Leuven, B-1980 Tervuren. 47,500 specimens; Africa south of Sahara; general taxonomic representation for geographic area covered. Includes material formerly in the collections of the National Parcs of Zaire and Ruanda. Persons in charge are D. Meirte and D. Thys van den Audenaerde.

Koninklijke Maatschappij voor Dierkunde van Antwerpen, Koningin Astridplein 26, B-2000 Antwerpen. 350 specimens; Europe. Person in charge is G. Van Steenbergen.

Laboratorium voor Algemende Dierkunde, R.U.C., Groenenborgerlaan 171, B-2020 Antwerpen. 6000 specimens (plus 35,000 skulls from owl pellets); Belgium; Insectivora, Rodentia. Person in charge is Dr. Erik van der Straeten.

Musee Provincial de la Foret, 9 Route Merveilleuse, B-5000 Namur. 80 specimens; southern Belgium; Cervidae. Person in charge is Ir. Roger L. A. Damoiseau.

Musée de Zoologie de l'Université de Liège, quai Ed. Van Beneden 22, B-4020 Liège. 1000 specimens; 1 holotype; Holoarctic; Cetacea. Person in charge is Dr. Noël Magis.

BRAZIL

Coleção Adriano L. Peracchi, Instituto de Biologia, Universidade Rural, 23460 Seropédica, RJ. 3312 specimens; Brazil; Chiroptera. Person in charge is Adriano L. Peracchi.

Coleção Deoclécio Guerra (DG), Dept. Biologia, Universidade Federal de Pernambuco, Cidade Universitario, 50000 Recife, PE. 100 specimens; Brazil; Chiroptera, Rodentia. Person in charge is Deoclécio de Queiroz Guerra Filho.

Coleção Privado de Estanislau Kostka Pinto da Silveira, % Maria Consuelo P. da Silveira, Rua Evaristo da Veiga, 45/302, Cinelândia, 20,000 Rio de Janeiro. Count of specimens not given; Brazil; Primates, Rodentia, Carnivora. Person in charge is Estanislau Kostka Pinto da Silveira.

Departamento dos Mamiferos Aquaticas, Instituto Nacional de Pesquisas da Amazônia, C.P. 478, 69000 Manaus, AM. 190 specimens; Brazil; *Trichechus, Inia, Sotalia.* Person in charge is Robin C. Best.

Museu "Ângelo Moreira da Costa Lima," Av. Feliciano Coelho 1509, 68900 Macapá, AP. 72 specimens; Brazil; Edentata, Primates. Person in charge is Antonio Carlos da Silva Farias.

Museu de Ciências Naturais, Fundação Zoobotânica, Rua Coronel Vicente, 281 6° andar., 90000 Porto Alegre, RS. 710 specimens; Brazil; Chiroptera, Rodentia. Person in charge is Flavio Silva.

Museu Nacional (MN), Universidade Federal do Rio de Janeiro, Quinta da Boa Vista, São Cristovão, 20942 Rio de Janeiro, RJ. 85,000 specimens; 60 holotypes; Brazil; Marsupialia, Edentata, Primates, Rodentia. Person in charge is José Francisco da Cruz and João Moojen.

Museu Oceanográfico do Rio Grande, Fundação Universidade do Rio Grande, C.C. 474, 96200 Rio Grande, RS. 100 specimens; Brazil; Cetacea, Pinnipedia. Persons in charge are Hugo P. Castello and Maria Cristina Pinedo.

Museu Paraense "Emílio Goeldi" (MPEG), Caixa Postal 399, 66000 Belém, Pará. 8864 specimens; 5 holotypes; Brazil; Chiroptera, Primates, Carnivora, Artiodactyla. Person in charge is Dr. Fernando C. Novaes.

Museu de Zoologia, Universidade de São Paulo, Caixa Postal 7172, São Paulo. 15,764 specimens; 19 holotypes; Brazil; Marsupialia, Chiroptera, Primates, Rodentia. Includes material formerly in the Museu Paulista. Persons in charge are Helio Ferraz de Almeida Camargo and Dr. Paulo E. Vanzolini.

Universidade Estadual Paulista (UNESP), Departamento de Zoologia, Instituto de Biociências, 15100 São José do Rio Preto, SP. 4500 specimens; 1 holotype; Brazil; Chiroptera. Person in charge is Valdir Antonio Taddei.

Zoologia—Universidade Estadual de Campinas (ZUEC), Caixa Postal 1170, Campinas 13100, São Paulo, SP. 1000 specimens; Brazil; Marsupialia, Rodentia. Person in charge is Prof. Fernando Dias de Avila-Pires.

BRUNEI

Muzium Brunei, Kota Batu. 63 specimens; Brunei; Carnivora. Person in charge is P. M. Dato Shariffuddin.

BULGARIA

Institute of Zoology, Bulgarian Academy of Sciences, Boul. Ruski 1, 1000 Sofia. 5900 specimens; 2 holotypes; Bulgaria; Insectivora, Rodentia, Artiodactyla. Person in charge is Dr. S. Gerasimov.

Institute of Zoology, Bulgarian Academy of Sciences, Boul. Ruski 1, 1000 Sofia. 2500 specimens; Mediterranean; Insectivora, Rodentia, Artiodactyla. Person in charge is Georgi Markov.

National Natural History Museum, Bulgarian Academy of Sciences, Boul. Ruski 1, 1000 Sofia. 1010 specimens; Bulgaria; Lagomorpha, Carnivora, Artiodactyla. Person in charge is N. B. Spassov.

Natural History Museum, 34 Gen. Zaimov, Plovdiv. 150 specimens; Bulgaria; Carnivora. Person in charge is Tzeno Hristov Petrov.

University of Plovdiv, Biological Faculty, Zar Asen 24, 4000 Plovdiv. 1500 specimens; Bulgaria; Insectivora, Rodentia. Person in charge is Dr. D. Mitev.

University of Sofia, Biological Faculty, Dragan Zankov 6, 1421 Sofia. 600 specimens; Bulgaria; Insectivora, Rodentia. Person in charge is Prof. Z. Peshev.

CHILE

Colección Particular de Fabian Jaksić y José Yañez, Laboratorio de Ecología, Universidad Católica de Chile, Santiago. 250 specimens (skulls only); Chile; Rodentia. Person in charge is Fabian M. Jaksić.

Colección Zoológica, Instituto de la Patagonia, Casilla 102-D, Punta Arenas. 1000 specimens; 1 holotype; southern Chile; Rodentia, Carnivora, Pinnipedia, Delphinidae, Cervidae. Person in charge is Walter H. Sielfeld K.

Instituto de Ecología y Evolución (IEEUA), Universidad Austral de Chile, Casilla 567, Valdivia. 800 specimens; central and southern Chile; Marsupialia, Rodentia. Person in charge is Milton Gallardo Narcisi.

Laboratorio de Citogenética (LCM), Departamento de Biología Celular y Genética, Fac. de Medicina, Universidad de Chile, Casilla 6556, Santiago 7. 800 specimens; northern and central Chile; Rodentia. Person in charge is Prof. Angel Spotorno O.

Museo Nacional de Historia Natural, Casilla 787, Santiago. 560 specimens; 18 holotypes; central Chile; Rodentia. Person in charge is Lic. José Yañez.

Museo de Zoologia de la Universidad de Concepción (MZUC), Instituto de Biología "Ottmar Wilhelm G.," Casilla 1367, Concepción. 574 specimens; Chile; Chiroptera, Rodentia, Mustelidae. Includes part of the former collection of Dr. Guillermo Mann F. Person in charge is Tomás Cekalovic K.

COLOMBIA

Instituto de Ciencias Naturales (ICN), Museo de Historia Natural, Universidad Nacional de Colombia, Apartado Aéreo 7495, Bogotá. 8300 specimens; 6 holotypes; Colombia; Marsupialia, Chiroptera, Lagomorpha, Edentata, Primates, Carnivora, Artiodactyla. Includes some specimens from the Parque Catios del INDERENA and the bats from the collection of the Universidad del Valle. Person in charge is Dr. Alberto Cadena.

Instituto de Recursos Naturales Renovables (INDERENA), Calle 26 #13-B-47, Bogotá. 3000 specimens; eastern plains and Amazonian Colombia; Chiroptera, Rodentia. Person in charge is Dr. Hernando Chiriví.

Museo de Historia Natural del Colegio de San José, Apartado Aéreo 11-80, Medellín. 300 specimens; Departamento de Antioquia, Colombia; Marsupialia, Chiroptera. Person in charge is Hno. Marco A. Serna D.

Museo del Instituto de la Salle, Calle 11 No. 1-69, Apartado Aéreo 27389, Bogotá, D.E. 2500 specimens; Colombia; Chiroptera. Persons in charge are Hno. Nicéforo María and Hno. Daniel Julain González P.

CUBA

Instituto de Zoología, Academia de Ciencias de Cuba, La Habana 2. 5000 specimens; 5 holotypes (sub-Recent fossils); Cuba; Chiroptera. Person in charge is Gilberto Silva.

Instituto de Zoología, Dept. de Vertebrados, Capitolio Nacional, La Habana 2. No count of specimens given; 4 holotypes; Cuba; Chiroptera, Rodentia. Person in charge is Lic. Lourdes Rodriguez.

CZECHOSLOVAKIA

Department of Anatomy, Faculty of Medicine, U nemocnice 3, Charles University, Praha 2. 2000 specimens; Palearctic; Primates. Person in charge is Prof. R. Čihák.

Institute of Systematic Zoology, Charles University, Viničná 7, Praha 2. 16,000 specimens; Czechoslovakia, Balkans, Middle Asia; Insectivora, Chiroptera, Rodentia. Person in charge is Dr. Vladimír Hanák.

Institute of Vertebrate Zoology, Czechoslovak Academy of Sciences, Květná 8, 66365 Brno. 30,000 specimens; 2 holotypes; Czechoslovakia; Insectivora, Chiroptera, Rodentia, Carnivora. Person in charge is Dr. Oldřich Stěrba.

Ivan Horáček Private Collection, S. Michelská 1182, 14500 Praha 4. 150 specimens; Europe; Insectivora, Chiroptera, Rodentia. Person in charge is Ivan Horáček.

Krajské Múzeum, Přírodověd. odd., Husovo nám. 124, 50002 Hradec Králové. 300 specimens; Czechoslovakia; Chiroptera, Rodentia. Person in charge is Dr. Karel Lohniský.

Museum of the South Bohemian Peat-bogs, Soběslav. 1050 specimens; Czechoslovakia; Insectivora, Rodentia. Person in charge is Petr Zbytovský.

National Museum (NH), Václavské ném. 68, CS 11579 Praha 1. 19,000 specimens in mammalogy and 5500 specimens in osteology; 2 holotypes; central and southern Europe; Insectivora, Primates, Rodentia. Persons in charge are Dr. Vratislav Mazák (mammalogy) and Dr. Ivan Heráň (osteology).

Okresní Múzeum Orlických Hor, 51611 Rychnov nad Kněžnou. 600 specimens; Czechoslovakia; Rodentia. Person in charge is Zdeněk Nespěchal.

Polabské Múzeum, Palackého třida 68/III, CS 29001 Poděbrady. 387 specimens; Czechoslovakia; Insectivora, Rodentia, Carnivora. Person in charge is Dr. Václav Ziegler.

Považské Múzeum, Budatínsky Zámok, 01003 Zilina-Budatín. 1000 specimens (plus about 10,000 pieces from owl pellets); Czechoslovakia; Insectivora, Rodentia, Carnivora. Person in charge is Ing. Ján Obuch.

Slezské Múzeum, 74646 Opava. 5500 specimens; Czechoslovakia; Insectivora, Rodentia, Carnivora. Person in charge is Bohuslav Beneš.

Slovenské Národné Múzeum, Prírodovedný ústav, Vertebratologické odd., Vajanského nábr. 2, 88536 Bratislava. 1500 specimens; Czechoslovakia; Insectivora, Chiroptera, Rodentia. Persons in charge are Dr. Alojz Habovštiak, Dr. Štefan Juriš, and Dr. Branislav Matoušek.

Východoceské Múzeum, Zámek 1, 53134 Pardubice. 700 specimens; Czechoslovakia; Chiroptera, Rodentia. Person in charge is Jan Sklenář.

Západočeské Múzeum v Plzni, Kopeckého sady 2, Plzeň. 5000 specimens; Czechoslovakia; Insectivora, Chiroptera, Rodentia. Person in charge is Dr. Luděk Hůrka.

Zbierka Liptovského Múzea, 03450 Ružomberok. 50 specimens; Czechoslovakia; Carnivora, Artiodactyla. Person in charge is Ing. Pavol Karč.

Zoologické Sbírky, Severočeského Musea, Liberec. 1000 specimens; Czechoslovakia; Chiroptera, Rodentia. Person in charge is Dr. Miloslav Nevrlý.

DENMARK

Natural History Museum, Building 210, Universitetsparken, 8000 Aarhus C. 3000 specimens; Europe, Africa. Person in charge is Birger Jensen.

Zoological Museum of the University (ZMUC), Universitetsparken 15, 2100 Copenhagen Ø. 35,000 specimens; 40 holotypes; Europe, Greenland, Brazil, West Pacific, Africa; general taxonomic representation. Person in charge is Dr. Hans J. Baagøe.

EGYPT

Wassif's Collection, Department of Zoology, Faculty of Science, Ain Shams University, Abbasia, Cairo. 1300 specimens (plus many alcoholic specimens of bats and insectivores); Egypt including Sinai; Insectivora, Chiroptera, Rodentia. Person in charge is Mr. Soheil S. Soliman.

Zoological Museum, Giza Zoological Garden, Giza, Orman. No count of specimens given; Egypt; Chiroptera, Rodentia. Includes the Flower's Collection. Person in charge is Dr. Mervat Morcos.

EL SALVADOR

Museo de Historia Natural de El Salvador, Parque Saburo Hirao, San Salvador. 306 specimens; El Salvador; Chiroptera, Rodentia. Persons in charge are Victor Hellebuyck and Salvador Gómez.

ENGLAND

Birmingham Museums and Art Gallery (BIRMG), Chamberlain Square, Birmingham B3 3DH. 400 specimens; Great Britain, Ireland; Chiroptera, Rodentia, Mustelidae. Includes material from J. L. Auden collection. Person in charge is Dr. B. Abell Seddon.

Booth Museum of Natural History, 194 Dyke Rd., Brighton, Sussex. 1800 specimens; 5 holotypes; worldwide; Primates, Rodentia, Carnivora. Persons in charge are Dr. G. Legg and Mr. J. M. Adams.

Borough of Ipswich Museums, The Museum, High Street, Ipswich IP1 3QH. 500 specimens. Person in charge is H. Mendel.

British Museum (Natural History), Cromwell Road, London SW7 5BD. 300,000 specimens; approximately 9000 holotypes; cosmopolitan; all taxonomic groups represented. Includes material of Lidthdejeude, Tomes, Forsyth Major, Lataste, Selous, Rothchild, Robinson, Zoological Society of London, Gould, and many other historical collections. Person in charge is Ian R. Bishop.

Buckinghamshire County Museum (BCM), Church Street, Aylesbury, Buckinghamshire. 100 specimens; Buckinghamshire, England. Person in charge is Miss J. Raystan.

City of Bradford Metropolitan Council Art Galleries and Museums (BRFMS), Cliffe Castle Museum, Spring Gardens Lane, Keighley, West Yorkshire BD20 6LH. 515 specimens; Yorkshire, England; Insectivora, Chiroptera, Rodentia. Person in charge is Miss M. M. Hartley.

City of Bristol Museum and Art Gallery (BRSMG), Queen's Road, Bristol, Avon BS8 1RL. 3500 specimens; Great Britain, Africa, Australasia; Marsupialia, Insectivora, Chiroptera, Rodentia. Includes material formerly held by The Bristol Philosphical and Literary Institution. Persons in charge are Mrs. A. F. Hollowell and Mr. C. J. T. Copp.

Clifton Park Museum (ROTMG), Clifton Lane, Rotherham, South Yorkshire. 150 specimens; Yorkshire, England; Insectivora, Rodentia, Carnivora. Person in charge is W. A. Ely.

Harrison Zoological Museum (HZM), Bowerwood House, St. Botolph's Road, Sevenoaks, Kent. 9500 specimens; South West Asia, Africa, Europe, South America; Insectivora, Chiroptera, Rodentia. Person in charge is Dr. David L. Harrison.

Horniman Museum, London Road, Forest Hill, London SE23 3PQ. 1000 specimens; worldwide. Person in charge is Gordon E. Williams.

Kendal Museum, Station Road, Kendal, Cambria. 160 specimens (mainly trophy heads). Person in charge is W. M. Grange.

Leicestershire Museums, Art Gallery and Records Service (LEICS), 96 New Walk, Leicester LE1 6TD. 2640 specimens; British Isles; Insectivora, Chiroptera, Rodentia, Carnivora. Includes part of the F. Nisbet private collection. Person in charge is Dr. John H. Mathias.

Museum and Art Gallery, Civic Centre, Bolton, Lancs BL1 1SA. 450 specimens; British Isles; Insectivora, Rodentia. Person in charge is Miss K. M. Berry.

North Hertfordshire Museums Service, Natural History Department, Paynes Park, Hitchin, Hertfordshire SG5 1EQ. 253 specimens; Britain. Address inquiries to Keeper of Natural History.

Passmore Edwards Museum, Romford Road, Stratford, London E15 4LZ. 175 specimens; Essex, England. Person in charge is Ian G. Robertson.

Powell-Cotton Museum, Quex Park, Birchington, Kent. 6000 specimens; approximately 40 holotypes; Africa, Asia; Primates, Rodentia, Carnivora, Proboscidea, Perissodactyla, Artiodactyla. Person in charge is L. R. Barton.

Private Collection of D. M. Stoddart, Department of Zoology, University of London King's College, Strand, London WC2R 2LS. 261 specimens; England, Europe; Rodentia. Person in charge is Dr. D. M. Stoddart.

Sunderland Museum, Tyne & Wear County Council Museums, Borough Rd., Sunderland, Tyne & Wear SR1 1PP. 300 specimens; northeastern England; Insectivora, Carnivora. Includes specimens formerly in South Shields Museum & Art Gallery, Tyne & Wear, and Saltwell Towers Museum, Gateshead, Tyne & Wear. Person in charge is Mr. P. S. Davis.

University College Museum of Zoology and Comparative Anatomy (LDUCZ), Gower Street, London WCIE 6BT. 827 specimens; Africa, Asia, Australasia, Europe, South America; Marsupialia, Insectivora, Primates, Rodentia, Carnivora. Person in charge is Mrs. R. M. Downs.

FEDERAL REPUBLIC OF GERMANY

Anatomisches Institut der Georg-August-Universität, Kreuzbergring 36, D-3400 Göettingen. 3000 specimens; Liberia; Primates. Person in charge is Hans-Jürg Kuhn.

Coll. Helversen, Zoologisches Institut, Albert-Ludwigs-Universität, Albertstrasse 21, D-7800 Freiburg im Breisgau. 100 specimens; Europe. Person in charge is Dr. O. V. Helversen. .

Coll. Pieper/Kiel, Geologisch-Paläontologisches Institut und Museum, Universität Kiel, Olshausenstrasse 40/60, D-2300 Kiel. 30,000 to 40,000 specimens from owl pellets; Germany; Insectivora, Chiroptera, Rodentia. Person in charge is Dr. Harald Pieper.

Forschungsinstitut und Natur-Museum Senckenberg (SMF), Senckenberg-Anlage 25, D-6000 Frankfurt am Main. 55,000 specimens; approximately 190 holotypes; worldwide; Chiroptera, Primates, Rodentia, Ungulata. Person in charge is Dr. Heinz Felten.

Landessammlungen für Naturkunde (LNK), Erbprinzenstrasse 13, P.O. Box 4045, D-7500 Karlsruhe 1. 10,000 specimens; 1 holotype; Liberia, Tanzania; Primates, Rodentia, Carnivora, Artiodactyla. Includes the collection of the ethnologist Dr. H. Himmelheber, Heidelberg. Person in charge is Dr. Ralf Angst.

Privatsammlung Prof. Dr. Jochen Niethammer, Zoologisches Institut der Universität, Poppelsdorfer Schloss, D-5300 Bonn. 6000 specimens; southern and central Europe, Afghanistan; Insectivora, Rodentia. Person in charge is Prof. Dr. Jochen Niethammer.

Staatliches Museum für Naturkunde Stuttgart (SMNS), Säugetier-

Abteilung, Schloss Rosenstein, D-7000 Stuttgart 1. 30,000 specimens; 30 holotypes; Africa, Europe, Australia; Marsupialia, Insectivora, Chiroptera, Rodentia, Carnivora. Person in charge is Dr. Fritz Dieterlen.

Zoologische Abteilung des Hessischen Landesmuseums Darmstadt, Friedensplatz 1, D-6100 Darmstadt. 2000 specimens; central Europe, Africa; Rodentia, Carnivora, Artiodactyla. Person in charge is Dr. Hanns Feustel.

Zoologische Staatssammlung München (ZMS), Maria-Ward-Strasse 1b, D-8000 München 19. 100,000 specimens; number of holotypes unknown; Eurasia, South America; Primates, Carnivora, Ungulata. Person in charge is Dr. habil. E.-J. Fittkau.

Zoologisches Forschungsinstitut und Museum Alexander Koenig (ZFMK), Adenauerallee 150-164, D-5300 Bonn 1. 30,000 specimens; 52 holotypes; Europe, Asia Minor, China, Africa; Insectivora, Chiroptera, Rodentia, Artiodactyla. Person in charge is Dr. Rainer Hutterer.

Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Martin-Luther-King-Platz 3, 2000 Hamburg 13. 10,000 specimens; Europe, Africa, India; Rodentia, Pinnipedia, Artiodactyla. Person in charge is Prof. Dr. Harald Schliemann.

FINLAND

Kuopio Museum (KUO), Kauppakatu 23, SF-70100 Kuopio 10. 600 specimens; Finland. Person in charge is Dr. Eino Savolainen.

Lapin Maakuntamuseo, Luonnontieteen osasto, Hallituskatu 11, SF-96100 Rovaniemi 10. 250 specimens; Finland; Lagomorpha, Rodentia, Carnivora, Artiodactyla. Person in charge is Heikki Uotila.

Zoological Museum, University of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki 10. 13,000 specimens; Finland; Insectivora, Rodentia, Carnivora, Artiodactyla. Includes the E. J. Bonsdorff osteological collection and the Virkki collection of *Sciurus vulgaris*. Person in charge is Dr. Lasse Sammalisto.

Zoological Museum, University of Oulu, Kasarminte 8, SF-90100 Oulu 10. 20,000 specimens; Finland, northern Scandinavia; Insectivora, Rodentia, Carnivora. Includes material formerly in the zoological collections of Societas Amicorum Naturae Ouluensis. Person in charge is Eino Erkinaro.

FRANCE

Laboratoire d'Anatomie Comparée (AC), Muséum National d'Histoire Naturelle, 55 rue de Buffon, F-75005 Paris. 16,000 specimens (essentially osteological specimens); several dozen holotypes but no count available; Europe, Africa, South America; general taxonomic coverage. Person in charge is Professeur J. Anthony.

Laboratoire de Zoologie, Mammiféres et Oiseaux, Muséum National d'Histoire Naturelle (MNHN), 55 rue de Bouffon, F-75005 Paris. 10,000 specimens; numerous holotypes but no precise count available; Africa; Rodentia. Persons in charge are Dr. Francis Petter, Dr. Michel Tranier, and Jean Roche.

Musée Guimet d'Histoire Naturelle, 28 Boulevard des Belges, F-69006 Lyon. 1000 specimens; Europe. Person in charge is Monsieur Michel Philippe.

Musée d'Histoire Naturelle, Palais Longchamp, F-13001 Marseille. 483 specimens; Europe, Africa, Asia; Primates, Rodentia, Carnivora. Person in charge is M. Robert M. Jullien.

Musée des Sciences Naturelles d'Orléans, 2 rue Marcel Proust, F-45000, Orléans. 71 specimens; Europe; Carnivora, Artiodactyla. Person in charge is Madame F. Lespinasse.

Musée Zoologique, Université et de la Ville, 29 Bd de la Victoire, F-67000 Strasbourg. 3000 specimens; worldwide; Primates, Carnivora. Includes the Haensel's collection of the skulls of domestic dogs. Person in charge is G. Hildwein.

Muséum d'Histoire Naturelle, 28 rue Albert ler, F-17000 La Rochelle. 1000 specimens; 2 holotypes; France, Africa; marine mammals. Person in charge is Dr. R. Duguy.

Muséum d'Histoire Naturelle, 12 rue Voltaire, F-44000 Nantes. 463 specimens; France; Cetacea, Mustelidae. Person in charge is Madame Jacqueline Baudouin.

Muséum d'Histoire Naturelle Gabriel Foucher, Parc des Expositions, F-18000 Bourges. 115 specimens; Europe, Africa; Carnivora, Ungulata. Person in charge is Jean-Jacques Bayeul.

Muséum d'Histoire Naturelle de Nice, 60 Boulevard Risso, F-06300 Nice. 67 specimens. Person in charge is Philippe Ewald.

Muséum d'Histoire Naturelle de Saint-Denis, rue Poivre, F-97400 Saint-Denis (Ile de la Réunion). No count of specimens or holotypes given; Africa; Primates. Person in charge is M. Harry Gruchet.

GERMAN DEMOCRATIC REPUBLIC

Biologisches Institut des Bereiches Medizin der Martin-Luther-Universität Halle-Wittenberg, Universitätsplatz 7, 402 Halle. 500 specimens; *Lagurus lagurus, Ondatra zibethicus.* Person in charge is Frau Ilse Hilpert.

Mauritianum Naturkundliches Museum, Postfach 128, 74 Altenburg. 800 specimens; Germany; Insectivora, Rodentia. Direct inquiries to the Director.

Museum der Stadt Gotha, Museum der Natur, Parkallee 15, Postfach 217, 58 Gotha. 300 specimens; central Europe; Chiroptera, Rodentia. Person in charge is Wolfgang Zimmermann.

Phyletisches Museum, Sektion Biologie, Friedrich-Schiller-Universität, 69 Jena. 2000 specimens; Europe. Person in charge is Dr. D. V. Knorre.

Staatliches Museum für Naturkunde, Forschungsstelle, Am Museum 1, 89 Görlitz. 1332 specimens; central Europe. Person in charge is Siegfried Tobisch.

Staatliches Museum für Tierkunde Dresden, Augustusstrasse 2, 801 Dresden. 20,000 specimens; 20 holotypes; central Europe, Indonesia, China; Primates, Rodentia. Persons in charge are Dr. R. Hertel and Dr. Alfred Feiler.

Zoologie der Sektion Biowissenschaften der Martin-Luther-Universität, Domplatz 4, 402 Halle (Saale). 4200 specimens; 15 holotypes; Palaearctic Region, especially Mongolia; Rodentia. Person in charge is Dr. Rudolf Piechocki.

Zoologisches Museum, Ernest-Moritz-Arndt-Universität, Joh.-Seb.-Bach-Strasse 11/12, 2200 Greifswald. 600 specimens; central Europe. Person in charge is Dr. G. Müller.

GHANA

University of Ghana, Department of Zoology, P.O. Box 67, Legon, Accra. 700 specimens; Ghana; Rodentia. Person in charge is Dr. P. Grubb.

HONDURAS

Museo Animal, Departamento de Vida Silvestre, Direccion General de Recursos Naturales Renovables, Tegucigalpa, D.C. 50 specimens; Honduras. Person in charge is Wilberto Aguilar N.

HUNGARY

Bakonyi Természettudományi Múzeum (BTM), Rákóczi-tér 1, H-8420 Zirc. 756 specimens; Hungary; Insectivora, Chiroptera, Rodentia. Person in charge is Szvezsényi László.

Savaria Múzeum, Természettudományi Osztálya, Kisfaludy S. u. 9, H-9701 Szombathely. 50 specimens; Hungary; Insectivora, Rodentia, Carnivora. Person in charge is Dr. Horváth Ernó.

ICELAND

Náttúrufraedistofnun Íslands, P.O. Box 5320, 125 Reykjavík. 150 specimens; Iceland; Muridae, Canidae, Phocidae. Person in charge is Aevar Petersen.

INDIA

Bombay Natural History Society, Hornbill House, Shahid Bhagat Singh Road, Bombay-400023. 18,000 specimens; holotypes present but no count given; Indian Region; Insectivora, Chiroptera, Primates, Lagomorpha, Rodentia, Carnivora, Artiodactyla. Person in charge is Dr. Robert B. Grubh.

Central Arid Zone Research Institute (CAZRI), Jodhpur-342003, Rajasthan. 500 specimens (in fluid); Indian Desert; Rodentia. Person in charge is Dr. Ishwar Prakash.

Collections of the Zoology Section, Government Museum, Madras-600008. 150 specimens; southern India; Carnivora. Direct inquiries to Curator.

Life-Science Museum, 1066 Civil Lines, Jhansi-284001, U.P. 430 specimens; India; Insectivora, Chiroptera, Primates, Rodentia. Person in charge is Dr. Fazlulhaq Rehmani.

National Institute of Virology, Zoological Collection, 20-A Dr. Ambedkar Road, Pune-411001. 1000 specimens; 1 holotype; Indian Region; Insectivora, Chiroptera; Rodentia. Direct inquiries to the Director.

National Museum of Natural History, FICCI Museum Building, Barakhamba Road, New Delhi-110001. 100 specimens; India. Person in charge is Dr. S. M. Nair.

National Zoological Collection of India, Zoological Survey of India (ZSI), 34, Chittaranjan Ave., Calcutta 700012. 20,000 specimens; 113 holotypes; India, Pakistan, Nepal, Bhutan, Burma, Sri Lanka; Chiroptera, Rodentia. Includes material from the Asiatic Society of Bengal, Indian Museum, and a substantial portion of the mammalian collection obtained by the Bombay Natural History Society's Mammal Survey of India, Burma, and Ceylon. Person in charge is P. K. Das.

INDONESIA

Museum Zoologicum Bogoriense (MZB), LBN, J1. Raya Juanda 3, Bogor. 13,000 specimens; Indonesia; general taxonomic representation for geographic area covered. Person in charge is Boeadi.

IRAN

Muzė-ye Melli-ye Tarikh-e Tabi'i (MMTT; Iran National Museum of Natural History), Department of the Environment, P.O. Box 1430, Tehran. 900 specimens; Iran; Rodentia. Direct inquiries to the Director.

IRAQ

Natural History Research Centre and Museum, University of Baghdad, Bab Al-Muadham, Baghdad. 260 specimens; Iraq; Rodentia. Person in charge is Mrs. Nidhal Al-Hassoon.

IRELAND

Department of Zoology Museum, University College, Galway. 300 specimens; worldwide; Marsupialia, Primates, Rodentia, Carnivora. Person in charge is Dr. J. S. Fairley.

National Museum of Ireland (NMI), Natural History Division, Kildare Street, Dublin 2. 3000 specimens; western Palaearctic, Ethiopian, Oriental, and Australian regions; Marsupialia, Edentata, Pholidota, Rodentia, Carnivora, Tubulidentata, Proboscidea, Artiodactyla. Person in charge is Dr. Colm E. O'Riordan.

Zoology Museum, Department of Zoology, Trinity College, Dublin 2. 1500 specimens; worldwide; Primates, Carnivora. Person in charge is Martyn Linnie.

ISRAEL

Beth Gordon Institute, Deganya A15-120, Jordan Valley. 270 specimens; Israel; Insectivora, Chiroptera, Rodentia, Carnivora. Person in charge is Shemual Lulav.

Beth Margolin-Institute of Natural History, Haifa University, Oranim, Tivon. 2500 specimens; Israel, Sinai; Chiroptera, Rodentia, Artiodactyla. Includes part of the collection of the Biologic-Pedagogic Institute Tel-Aviv. Person in charge is Aryeh L. Aboulafia.

Sana Atallah's Natural History Museum, Beit Sahur, via Israel. 400 specimens; eastern Mediterranean Region; Chiroptera, Rodentia. Persons in charge are Issa Atallah and Mazin Butrus Qumsiyeh.

Ussishkin House, Institute for Natural History of the Huleh Valley, Dan, Upper Galilee. 210 specimens; Huleh Valley, Mt. Hermon; Rodentia. Person in charge is Elimelech Hurvitz.

Zoological Museum, Department of Zoology, Tel Aviv University, Tel Aviv. 7000 specimens; Israel and neighboring countries; Insectivora, Lagomorpha, Rodentia, Hyracoidea, Carnivora, Sirenia, Artiodactyla. Person in charge is Ms. Tsila Shariv.

Zoological Museum of the Hebrew University, Department of Zoology, Hebrew University, Jerusalem. 4500 specimens; Israel, Sinai, and Jordan Rift Valley; Rodentia. Person in charge is Prof. Eitan Tchernov.

ITALY

Centro Studi Ecologici Appenninici, Parco Nazionale d'Abruzzo, I-67032 Pescasseroli (Aq). 55 specimens; central Apennines; Canidae, Uridae, Rupicapridae. Person in charge is Dr. Sandro Lovari.

Collezione Microteriologica di Longino Contoli, Segreteria Tecnica della Commissione del C.N.R. per la Conservazione della Natura, Viala dell' Università no. 11, I-00185 Roma. 5000 specimens (all from owl pellets); Italy, Sicily; Insectivora, Rodentia. Person in charge is Dr. Longino Contoli.

Instituto Nazionale di Biologia della Selvaggina, Via Stradelli Guelfi 23/A, I-40064 Ozzano dell' Emilia (Bologna). 335 specimens; Italy; Insectivora, Chiroptera, Rodentia, Carnivora. Person in charge is Prof. Lamberto Leporati.

Museo Civico di Storia Naturale (MSNG), Via Brigata Liguria 9, I-16121 Genova. No count of specimens or holotypes given; Oriental, Ethiopian, and Palaearctic region; Marsupialia, Rodentia, Ungulata. Direct inquiries to the Director.

Museo Civico di Storia Naturale di Milano, Corso Venezia 55, I-20121 Milano. 5700 specimens; 4 holotypes; Italy, Africa, Palaearctic; Insectivora, Rodentia. Person in charge is Dr. Luigi Cagnolaro.

Museo Civico di Storia Naturale, Fontego dei Turchi-S. Croce 1730, I-30125 Venezia. 100 specimens; Italy, Africa; Carnivora, Ungulata. Person in charge is Giampaolo Rallo.

Museo Civico di Storia Naturale (CMVR), Lungadige Porta Vittoria 9, I-37100 Verona. 3500 specimens; Italy, Turkey; Insectivora, Rodentia. Includes material from the Museo P. Zangheri. Person in charge is Dr. B. G. Osella.

Museo e Instituto di Zoologia Sistematica, Università di Torino, Via Giovanni Giolitti 34, I-10123 Torino. 3500 specimens; worldwide; Chiroptera, Rodentia. Person in charge is O. Elter.

Museo Tridentino di Scienze Naturali, Via Calepina 14, I-38100 Trento. 900 specimens; Italy; Insectivora, Chiroptera, Rodentia. Person in charge is Dr. Claudio Chemini.

Museo Zoologico de "La Specola," Università di Firenze, Via Romana 17, I-50125 Firenze. 10,000 specimens; 4 holotypes; Italy, Africa; Insectivora, Rodentia. Person in charge is Dr. Maria Luisa Azzaroli.

Raccolta Craniologica Capolongo, Via Roma 8, I-80030 Roccarainola (NA). 300 specimens; Italy; Insectivora, Rodentia. Person in charge is Dr. Ing. Domenico Capolongo.

JAMAICA

Institute of Jamaica, Kingston. 75 specimens; Jamaica; Chiroptera, Rodentia. Person in charge is Tom Farr.

JAPAN

Department of Oral Anatomy, School of Dentistry, Hokkaido University, N13 W7, Sapporo 060. 4000 specimens; Hokkaido and Honshu, Japan; *Sorex, Nyctereutes, Vulpes, Phoca, Cervus*. Person in charge is Noriyuki Ohtaishi.

Dr. T. Miyao Collection, Department of Dentistry, Aichigakuin University, Chikusaku, Nagoya City. 2500 specimens (skulls); Honshu, Japan; Muridae. Person in charge is Dr. T. Miyao.

Hiro Vertebrate Pest Control Laboratory, 1-4-6 Higashi-Hirayama, Hino-shi, Tokyo 191. 100 specimens; Japan; Rodentia. Person in charge is Dr. Tatsuo Udagawa.

Laboratory of Wildlife Resource Ecology, Department of Agro-Environmental Science, Obihiro University of Agriculture and Veterinary Medicine, Inada-cho, Obihiro, Hokkaido 080. 500 specimens; Hokkaido, Japan; Rodentia, Carnivora, Artiodactyla. Person in charge is Prof. R. Haga.

Natural History Museum, Faculty of Agriculture, Hokkaido University, N. 3, W. 8, Sapporo 060. 8200 specimens; 1 holotype; Japan, Nepal, Thailand; Insectivora, Rodentia. Person in charge is Dr. Hisashi Abe.

National Science Museum, 3-23-1 Hyakunin-cho, Shinjuku-ku, Tokyo 160. 20,214 specimens; 19 holotypes; Japan and surrounding areas; Chiroptera, Rodentia. Persons in charge are Mizuto Yushiyuki (terrestrial mammals), Nobuyuki Miyazaki (marine mammals), and Shigeru Fukuda (Director-General).

Nara Deer Fund, Kasugano 160, Nara 630. 1000 specimens; Nara Park; *Cervus nippon*. Person in charge is Akio Mukaida.

Ocean Research Institute (ORI), University of Tokyo, 1-15-1, Minami-dai, Nakanoku. 490 specimens; western North Pacific Ocean; Odontoceti. Includes material from the Whale Research Institute, Tokyo. Person in charge is Toshio Kasuya.

Osaka Museum of Natural History, Nagai Park, Osaka 546. 170 specimens; central Japan; Insectivora. Person in charge is Hiroyuki Taruno.

Primate Research Institute (PRI), Kyoto University, Inuyama City, Aîchi 484. 4500 specimens; Japan, Southeast Asia, South America; Primates, Rodentia. Persons in charge are Dr. Mitsuru Aimi (general mammal collection) and Dr. Shunji Goto (primate collection).

Tsuyama Museum of Science Education, 96 Sange, Tsuyama-shi, Okayama-ken. 1000 specimens; Japan, Asia. Person in charge is Kenzo Morimoto.

KENYA

National Museum of Kenya (NMK), P.O. Box 40658, Nairobi. 8000 specimens; Kenya; Chiroptera, Rodentia. Person in charge is Issa Aggundey.

KOREA

Chang-gyeong Weon Zoological and Botanical Gardens, Seoul 110. 133 specimens; Palearctic; Carnivora. Person in charge is Oh Chang young.

National Science Museum, 2, Waryong-dong, Chongno-ku, Seoul

110. 50 specimens; Korea; Cervidae. Person in charge is Mr. Deok-Kil Rhee.

Natural History Museum, Kyung Hee University, Seoul 131. 3000 specimens; Korea; Chiroptera, Rodentia. Person in charge is Prof. Won Pyong-oh.

LEBANON

Museum of Natural History, Department of Biology, American University of Beirut, Beirut. 600 specimens; 1 holotype; Lebanon, Syria, Saudi Arabia, Jordan, Turkey; Insectivora, Chiroptera, Lagomorpha, Rodentia, Carnivora. Person in charge is Mrs. Lina Faris-Naccache.

LIBERIA

Natural History Museum, Department of Biology, University of Liberia, Monrovia. 50 specimens; Liberia. Person in charge is Miss Mary T. Bryant.

MALAYSIA

Department of Conservation of Wildlife and National Parks, Kuala Lumpur 05-05. 150 specimens; Peninsular Malaysia. Direct inquiries to Director General.

Department of Genetics and Cellular Biology, University of Malaya, Kuala Lumpur 22-11. 200 specimens; Peninsular Malaysia; Muridae. Person in charge is Yong Hoi Sen.

Institute for Medical Research, Division of Medical Ecology, USAMRU, Pahang Road, Kuala Lumpur. 8000 specimens; Peninsular Malaysia, Sabah, Sarawak; Sciuridae, Muridae. Person in charge is Dr. Inder Singh.

National Museum, Damansara Road, Kuala Lumpur. 217 specimens; Peninsular Malaysia, Sabah, Sarawak; Chiroptera, Primates, Rodentia. Person in charge is Mr. Heah Soon Hock.

Sabah Museum, P.O. Box 1239, Kota Kinabalu, Sabah. 1187 specimens; Sabah; Primates, Rodentia, Carnivora. Persons in charge are David W. McCredie and Raymond Goh.

Sarawak Museum, Kuching, Sarawak. 2502 specimens; 30 holotypes; Borneo; Chiroptera. Direct inquiries to Curator.

Zoology Department, University of Malaya, Kuala Lumpur 22-11. 1000 specimens; Peninsular Malaysia; Chiroptera, Rodentia. Person in charge is Dr. D. R. Wells.

MEXICO

Escuela Nacional de Ciencias Biológicas (ENCB), Instituto Politecnico Nacional, Carpio y Plan de Ayala, Mexico, D.F. 13,500 specimens; Mexico; Chiroptera, Rodentia. Person in charge is Ticul Alvarez.

Universidad Autónoma Metropolitana-Iztapalapa (UAMI), División de Ciencias Biológicas y de la Salud, Departamento de Biología, Apartado Postal 55-535, México 13, D.F. 2761 specimens; Puebla and Tlaxcala, Mexico; Marsupialia, Chiroptera, Lagomorpha, Rodentia, Carnivora. Person in charge is Prof. José Ramírez-Pulido.

Universidad Nacional Autónoma de México (UNAM), Instituto de Biología, Ciudad Universitaria, México 20, D.F. 18,000 specimens; 10 holotypes; Mexico; Chiroptera, Rodentia. Person in charge is Dr. Bernardo Villa-R.

MOROCCO

Museum de l'Institut Scientifique, Section Zoologie, Avenue Ibn Batouta, BP 703, Rabat Agdal. 850 specimens; Morocco; Insectivora, Chiroptera, Rodentia, Carnivora, Artiodactyla. Persons in charge are Michel Thévenot and Tahiri Hamid.

MOÇAMBIQUE

Museu de Historia Natural (MHN), Praca da Travessia do Zambeze, Maputo. 208 specimens; Mozambique. Person in charge is D. J. A. Travassos Santos Dias.

Universidade Eduardo Mondlane, Faculdade de Biologia, Dep. Zoologia, Maputo. 836 specimens; southern Mozambique; Rodentia. Person in charge is Hans Feijen.

NAMIBIA

Etosha Ecological Institute (EEEI), Etosha National Park, Okaukuejo 9224. 3689 specimens; Namibia; Insectivora, Chiroptera, Rodentia, Carnivora, Bovidae. Person in charge is John E. W. Dixon.

State Museum (SMW), P.O. Box 1203, Windhoek 9100. 7500 specimens; Namibia, Angola; Insectivora, Rodentia. Person in charge is C. G. Coetzee.

NEW ZEALAND

Auckland Institute and Museum, Private Bag, Auckland. 1000 specimens; New Zealand; Chiroptera, Pinnipedia, Cetacea. Person in charge is E. G. Turbott.

Canterbury Museum, Rolleston Avenue, Christchurch 1. 3100 specimens; New Zealand; Pinnipedia, Cetacea. Persons in charge are G. A. Tunnicliffe and R. J. Scarlett.

National Museum of New Zealand (NMNZ), Private Postal Bag, Wellington. 2000 specimens; 5 holotypes; New Zealand, Subantarctic islands; Pinnipedia, Cetacea. Person in charge is Dr. A. N. Baker.

NORTHERN IRELAND

Ulster Museum and Botanic Gardens, Zoology Department, Belfast BT9. 400 specimens; Northern Ireland; Lagomorpha, Rodentia, Carnivora. Person in charge is Marshall McKee.

NORWAY

Zoological Museum (ZMO), University of Oslo, Sarsgt. 1, Oslo 5. 12,000 specimens; 17 holotypes and lectotypes; Scandinavia, Australia. Person in charge is Jørgen A. Pedersen.

PANAMA

Museo de Ciencias Naturales, Instituto Nacional de Cultura, Apartado Postal No. 662, Panama 1. 56 specimens; Panama; Primates, Artiodactyla. Person in charge is Profesora Nuria I. Esquivel.

PAPUA NEW GUINEA

Papua New Guinea National Museum & Art Gallery (PNGM), P.O. Box 5560, Boroko. 688 specimens; Papua New Guinea; Monotremata, Marsupialia, Rodentia. Person in charge is Paul Wamas Banguinan.

University of Papua New Guinea (UPNG), % Biology Department, Box 4820 University P.O., Port Moresby. 1750 specimens; Papua New Guinea, Solomon Islands; Chiroptera, Muridae. Person in charge is Dr. John C. Pernetta.

PEOPLE'S REPUBLIC OF CHINA

Department of Vertebrate Taxonomy and Faunology, Peking Institute of Zoology, Academia Sinica, Peking. 15,000 specimens; 60 holotypes and paratypes; China; Lagomorpha, Rodentia. Person in charge is Wang Sung.

Peking Natural History Museum (PNHM), 126 Tien Chiao Street, Peking (2). 104 species represented in collection; China; general taxonomic representation of geographic area covered. No person in charge listed; address inquiries to Department of Zoology.

PHILIPPINES

Museum of Arts and Sciences, University of Santo Tomas, Manila. 2000 specimens; Philippines; Chiroptera, Rodentia, Carnivora, Artiodactyla. Person in charge is Rev. Fr. Hesus M. Merino Antolinez.

University of the Philippines at Los Baños Wildlife Collection, College of Forestry, College, Laguna 3720. 5500 specimens; Philippines. Person in charge is Dr. Dioscoro S. Rabor.

POLAND

Institute of Systematic and Experimental Zoology, Polish Academy of Sciences, ul. Stawkowska 17, 31-016 Kraków. 7300 specimens; Poland, Mongolia, Iraq, Cuba, Mexico, North Africa; Insectivora, Chiroptera, Rodentia. Includes material from the private collection of Dr. B. W. Wołoszyn. Persons in charge are Dr. Henryk Kubiak and Mrs. B. Dziurdzik.

Mammals Research Institute (MRI), Poland Academy of Sciences, 17-230 Białowieza. 145,000 specimens (plus 927 samples of owl pellets containing about 300,000 remnants of mammals); Poland and adjacent areas; Insectivora, Chiroptera, Lagomorpha, Rodentia, Carnivora, Artiodactyla. Includes material formerly in the collections of the Forestry Research Institute (approximately 13,500 specimens from the areas of the Białowieza National Park) and the Institute of Zoology in Warsaw (material collected by Professor Dehnel in 1937–1939 in that part of Poland now included in Bielorussia). Person in charge is Dr. Andrzej L. Ruprecht.

Museum, Department of Anatomy of Animals, Institute of Applied Zoology, Academy of Agriculture, Wojska Polskiego 71c, 60-625 Poznán. 414 specimens; Europe, Africa, Asia; Artiodactyla. Persons in charge are Dr. Szymon Godynicki and Hieronim Frackowiak.

PORTUGAL

Museu Bocage, Museu e Laboratório Zoológico e Antropológico, Faculdade de Ciências, Lisboa 2. The entire collection of mammals of this museum was destroyed by a fire on 18 March 1978. Person in charge is Prof. G. F. Sacarrão.

Museu e Laboratório Zoológico, Universidade de Coimbra, Coimbra. 730 specimens; Holarctic, Ethiopian; Primates, Rodentia, Carnivora, Artiodactyla. Person in charge is Maria Manuela da Gama F. Assalino.

REPUBLICA DOMINICANA

Museo Nacional de Historia Natural (MNHNSD), Plaza de la Cultura, Santo Domingo, D.N. 850 specimens; Dominican Republic; Insectivora, Chiroptera, Rodentia. Persons in charge are José Alberto Ottenwalder and David G. Robinson.

REPUBLIC OF SOUTH AFRICA

Albany Museum (AMM), Somerset Street, Grahamstown 6140. 3000 specimens; 2 holotypes; South Africa; Chrysochloridae, Muridae, Viverridae. Person in charge is Mr. B. C. Wilmot.

Department of Zoology, University of Cape Town, Rondebosch 7700. 650 specimens; South Africa, Namibia; Insectivora, Rodentia, Carnivora. Person in charge is Dr. J. U. M. Jarvis.

Department of Zoology and Entomology, Rhodes University, Grahamstown 6140. 500 specimens; South Africa; Primates, Artiodactyla. Person in charge is Dr. M. R. Perrin.

Durban Museum (DM), P.O. Box 4085, Durban 4000. 750 specimens; South Africa, Mozambique, Namibia, Zimbabwe; Insectivora, Chiroptera, Primates, Rodentia, Carnivora. Person in charge is Mr. John Mendelsohn.

East London Museum (ELM), 319 Oxford Street, East London 5201. 1000 specimens; South Africa; Rodentia. This collection is currently on long-term loan to the Kaffrarian Museum.

Faculty of Forestry, University of Stellenbosch, Stellenbosch 7600. 300 specimens; South Africa; Insectivora, Rodentia. Person in charge is D. Pepler.

Hluhluwe Game Reserve, Natal Parks, Game and Fish Preservation Board, P.O. Box 25, Mtubatuba 3935. 241 specimens; South Africa, Rodentia. Person in charge is P. J. Birkenstock.

John R. Ellerman Museum of Zoology, University of Stellenbosch, 7600. 668 specimens; South Africa; Insectivora, Rodentia, Carnivora. Person in charge is Dr. Alan Channing.

Jonkershoek Nature Conservation Station (JNCS), Cape Provincial Department of Nature and Environmental Conservation, Private Bag 5014, Stellenbosch 7600. 880 specimens; South Africa; Chiroptera. Person in charge is J. C. Herselman.

Kaffrarian Museum (KM), King William's Town 5600. 25,000 specimens; 24 holotypes; South Africa, Namibia, Zambia, Malawi. Insectivora, Chiroptera, Rodentia, Lagomorpha, Carnivora. Person in charge is Pierre Swanepoel.

Kruger National Park Museum (KNP), Private Bag X404, Skukuza 1350. 350 specimens; South Africa; Insectivora, Chiroptera, Lagomorpha, Rodentia. Person in charge is Dr. S. C. J. Joubert.

Mammal Research Institute, Department of Zoology, University of Pretoria, Pretoria 0002. 478 specimens; South Africa; Chiroptera, Rodentia. Person in charge is J. A. J. Nel.

McGregor Museum, P.O. Box 316, Kimberley 8300. 250 specimens; South Africa; Rodentia, Carnivora, Ungulata. Person in charge is P. Richardson.

Natal Museum, Loop Street, Pietermaritzburg 3201. 2000 specimens; Natal; Insectivora, Rodentia. Person in charge is J. A. Pringle.

National Museum (NM), Box 266, Bloemfontein 9300. 1500 specimens; South Africa; Rodentia, Carnivora. Person in charge is Mr. C. D. Lynch.

N. G. Palmer Collection, Private Bag X546, George 6530. 600 specimens; South Africa; Insectivora, Rodentia, Carnivora. Person in charge is N. G. Palmer.

Orange Free State Provincial Division of Nature Conservation, Orange Free State, P.O. Box 517, Bloemfontein 9300. 600 specimens; South Africa; Lagomorpha, Primates. Person in charge is N. A. Ferreira.

Port Elizabeth Museum (PEM), P.O. Box 13147, Port Elizabeth 6013. 1150 specimens; South Africa; Rodentia, Cetacea, Pinnipedia. Person in charge is Mr. G. J. B. Ross.

Rolfontein Nature Reserve, Cape Provincial Department of Nature and Environmental Conservation, P.O. Box 23, van der Kloof Dam 8771. 132 specimens; South Africa; Carnivora, Artiodactyla. Person in charge is Ken Coetzee.

Saasveld Museum, South African Department of Forestry, Saasveld Forest Research Station, Private Bag x531, George 6530. 85 specimens; South Africa; Rodentia. Person in charge is G. J. Breytenbach.

South African Institute for Medical Research, Department of Epidemiology, P.O. Box 1038, Johannesburg 2001. 350 specimens, South Africa; Primates, Rodentia, Carnivora. Person in charge is Hillary J. Keogh.

South African Museum (SAM), P.O. Box 61, Cape Town 8000. 9200 specimens; Southern Africa; Cetacea, Carnivora, Pinnipedia, Bovidae. Person in charge is Mr. P. Hirschon.

Transvaal Museum (TM), P.O. Box 413, Pretoria 0001. 28,000 specimens; 410 holotypes; Southern Africa; Insectivora, Chiroptera, Lagomorpha, Rodentia. Includes material formerly held by the D. H. S. Davis collection at the South African Institute of Medical Research. Person in charge is I. L. Rautenbach.

University of Natal at Durban, Department of Biological Sciences, King George V Avenue, Durban 4001. 173 specimens; South Africa. Person in charge is Margaret I. Keogh.

University of Natal at Pietermaritzburg (UNP), Department of Zoology, P.O. Box 375, Pietermaritzburg 3200. 1216 specimens; South Africa; Rodentia, Primates, Carnivora, Artiodactyla. Person in charge is J. Meester.

University of Witwatersrand, Bernard Price Institute for Palaeontological Research, 1 Jan Smuts Avenue, Johannesburg 2001. 700 specimens; South Africa; Rodentia, Hyracoidea, Carnivora, Artiodactyla. Person in charge is J. M. Maguire.

Vrolijkheid Nature Conservation Station, Cape Provincial Department of Nature and Environmental Conservation, Private Bag 614, Robertson 6705. 1800 specimens; South Africa; Carnivora. Person in charge is C. T. Stuart.

[Some information on South African museums was obtained from a manuscript by Wingate and Swanepoel.]

ROMANIA

"Grigore Antipa" Museum of Natural History, Sos. Kisselef nr 1, Sectorul 1, Bucharest 63, 7000. 3600 specimens; southeastern Europe; Insectivora, Rodentia. Person in charge is Stefan Forcea.

Oltenie Museum Craiova, Str. Maxim Gorki 44, cod 1100 Craiova. 55 specimens; Romania; Insectivora, Rodentia. Person in charge is Dr. Bazilescu Elena.

SAUDI ARABIA

Iyad A. Nader Collection (IAN), College of Education at Abha, P.O. Box 157, Abha. 300 specimens; Saudi Arabia; Chiroptera, Rodentia. Person in charge is Dr. Iyad A. Nader.

SCOTLAND

Aberdeen University, Natural History Museum, Tillydrone Avenue, Aberdeen. 800 specimens; Britain, Europe; Lagomorpha, Felidae. Persons in charge are Professor G. Dunnet and Dr. R. Thorpe.

Angus District Museums, Montrose Museums, Panmure Place, Montrose, Angus. 62 specimens; Europe; Carnivora. Person in charge is Norman K. Atkinson.

Dundee Museums & Art Galleries, Albert Square, Dundee DD1 1DA. 350 specimens; eastern Scotland. Person in charge is R. K. Brinklow.

Hunterian Museum, University of Glasgow, Glasgow G12 8QQ. 65 specimens; Australia; Marsupialia, Carnivora. Direct inquiries to the Director.

Paisley Museum and Art Galleries, High Street, Paisley, Renfrewshire. 80 specimens; Scotland. Direct inquiries to Keeper of Natural History.

Perth Museum and Art Gallery, George Street, Perth. 606 specimens; Scotland, South America, Africa, Australia; Pinnipedia. Includes material formerly held by Perth Literary and Antiquarian Society and Perthshire Society of Natural History. Person in charge is M. A. Taylor.

The Royal Scottish Museum (RSM), Chambers Street, Edinburgh EH1 1JF. 5000 specimens; 4 holotypes; Britain, Africa; Rodentia. Includes material formerly held by Rudd Collection, Smalley Collection of British mammals, and Turner Collection of Marine Mammals. Person in charge is Dr. A. S. Clarke.

SENEGAL

Laboratoire de Zoologie appliquée, Centre ORSTOM de Dakar, BP 1386, Dakar. 2000 specimens; Senegal; Chiroptera, Rodentia, Carnivora. Direct inquiries to the Director.

SINGAPORE

Zoological Reference Collection (ZRC), Department of Zoology, University of Singapore, Bukit Timah Road, Singapore 10. 12,000 specimens; no holotypes but about 50 paratypes; Thailand, Peninsular Malaysia, Borneo, Sumatra, Java; Chiroptera, Primates, Rodentia. This is the former reference collection of the Singapore National Museum (until 1960 the Raffles Museum). Person in charge is Mrs. Yang Chang Man.

SPAIN

Museu de Zoologia de Barcelona, Apartat de Correus 593, Parc de la Ciutadella, Barcelona 3. 600 specimens; Spain; Insectivora, Rodentia. Person in charge is Dr. Joaquim Gosàlbez.

SRI LANKA

Department of National Museums, Colombo 7. 2885 specimens; Sri Lanka; Chiroptera, Rodentia. Person in charge is Mrs. P. R. Ratnapala.

SUDAN

Sudan Natural History Museum (SNHM), P.O. Box 321, University of Khartoum, Khartoum. 1000 specimens; Sudan; Rodentia, Ungulata. Person in charge is Dr. Mohammed A. El-Rayah.

SURINAME

Universiteit van Suriname, Faculteit der Natuurtechnische Wetenschappen, Paramaribo. 250 specimens; Suriname; Chiroptera, Rodentia. Person in charge is Dr. Robert Power.

SWEDEN

Lunds Universitets Zoologiska Museum, Helgonavägen 3, S-22362 Lund. 18,700 specimens; 1 holotype; Scandinavia; Insectivora, Rodentia, Mustelidae, Artiodactyla. Person in charge is Dr. Hugo Andersson.

Zoologiska Museet, Uppsala Universitet (UUZM), Box 561, S-75122 Uppsala. 2000 specimens; 12 holotypes (11 are Linnean types); Sweden; Rodentia. Person in charge is Dr. Lars Wallin.

SWITZERLAND

Museé d'Histoire Naturelle, CH-2300 La Chaux-De-Fonds. No counts or holotypes were given; Africa; Rodentia. Includes material belonging to the Monard African collection. Person in charge is Mr. Willy Lanz.

Muséum d'Histoire Naturelle, Faculté des Sciences/Pérolles, CH-1700 Fribourg. 1000 specimens; Switzerland; Insectivora, Rodentia, Carnivora. Person in charge is André Fasel.

Muséum d'Histoire Naturelle (MHNG), Route de Malagnou, Case Postale 284, CH-1211 Geneve 6. 25,000 specimens; 68 holotypes and syntypes; Europe, Africa, South America; Insectivora, Chiroptera, Primates, Rodentia. Includes material formerly held by Fatio and Saussure. Persons in charge are Prof. Dr. W. Aellen and Dr. François J. Baud.

Naturhistorisches Museum (NMBE), Abteilung Wirbeltiere, Bernastrasse 15, CH-3005 Bern. 10,000 specimens; Switzerland, Africa, South America; Rodentia, Carnivora. Includes material from the private collection of C. A. W. Guggisberg, Nairobi. Persons in charge are Dr. Peter Lüps and Mrs. Elsbeth Büttiker-Schumacher.

Naturhistorisches Museum Basel, Augustinergasse 2, CH-4001, Basel. 6000 specimens; 9 holotypes. Persons in charge are Prof. Dr. U. Rahm (skins) and Dr. H. Schaefer (osteology).

Natur-Museum Luzern, Kasernenplatz 6, CH-6003 Lucerne. 200 specimens; Switzerland, Australia; Monotremata, Marsupialia. Person in charge is Dr. Peter Herger.

Zoologisches Museum der Universität Zürich (ZMZ), Künstlergasse 16, CH-8006 Zürich. 7000 specimens; 2 holotypes; Switzerland, Africa; Insectivora, Rodentia. Person in charge is Dr. C. Claude.

TAIWAN

Taiwan Museum, Department of Zoology, #2 Siangyang Rd., Taipei. 187 specimens; Taiwan. Person in charge is Mr. Chen Chih Wen.

TANZANIA

College of African Wildlife Management (CAWM), Mweka, P.O. Box 3031, Moshi. 100 specimens; Tanzania; Artiodactyla. Direct inquiries to the Principal.

East African Institute of Malaria and Vector-borne Diseases, P.O. Box 4, Amani. 60 specimens; Tanzania; Rodentia. Person in charge is B. S. Kilonzo.

The Serengeti Research Institute, P.O. Seronera, via Arusha. 1300 specimens; East Africa; Insectivora, Chiroptera, Rodentia. Includes material from the collection of the late Vessey Fitz-Gerald's Ecological Team, Tanzania National Parks. Direct inquiries to the Director.

University of Dar es Salaam (UDSM), Department of Zoology, P.O. Box 35064, Dar es Salaam. 300 specimens; Tanzania; Chiroptera, Rodentia. Direct inquiries to Head of Department.

THAILAND

Division of Environmental Biology, Thailand Institute of Scientific and Technological Research (TISTR), Applied Scientific Research Corporation of Thailand, 196 Phahonyothin Road, Bank Khen, Bangkok 9. 6500 specimens; 5 holotypes; Thailand, Southeast Asia; Chiroptera, Rodentia. Includes material formerly held in the collections of SEATO Medical Research Laboratory and Dr. Bodnsong Lekagul. Person in charge is Mr. Songsakdi Yenbutra.

THE NETHERLANDS

Natuurhistorisch Museum Rotterdam, P.O. Box 27020, 3003 LA Rotterdam. 700 specimens; western Europe. Person in charge is R. E. Hamstra.

Natuurhistorisch Museum Tilburg, Kloosterstraat 26, 5038 VP Tilburg. 200 specimens; The Netherlands. Person in charge is Dr. F. J. M. Ellenbroek.

Rijksmuseum van Natuurlijke Histoire (RMNH), Postbus 9517, 2300 RA Leiden. 80,000 specimens; numerous holotypes and syntypes but no count available; Netherlands, Indonesia, Suriname, Netherland Antilles; general taxonomic coverage. Person in charge is Dr. C. Smeenk.

Zoological Museum (ZMA), Institute of Taxonomic Zoology, University of Amsterdam, 36 Plantage Kerklaan, 1018 CZ Amsterdam. 21,000 specimens; 10 holotypes; Europe, Indonesia, Suriname; Chiroptera, Rodentia, Carnivora, Pinnipedia, Cetacea. Includes material formerly in the Vrolik collection. Person in charge is Dr. P. J. H. van Bree.

TUNISIA

Laboratorie de Zoologie, Institut National Agronomique, 43 Av. Charles Nicolle, Tunis. 200 specimens; 2 holotypes; Tunisia; Chiroptera, Rodentia. Person in charge is Mr. K. Dridi.

TURKEY

A. Ü. Fen Fakültesi Sistematik Zooloji, Ankara. 8606 specimens; 5 holotypes; Turkey; Insectivora, Chiroptera, Lagomorpha, Rodentia. Person in charge is Prof. Dr. Bahtiye Mursaloğlu.

UGANDA

Uganda Virus Research Institute, Vertebrate Zoology Section, P.O. Box 49, Entebbe. 266 specimens; Uganda; Chiroptera, Rodentia. Person in charge is Mr. Asarph Ogen-odoi.

Zoology Museum, Makerere University, P.O. Box 7062, Kampala. 50 specimens; Uganda. Direct inquiries to the Professor of Zoology.

URUGUAY

Departamento de Zoología Vertebrados (ZVC), Facultad de Humanidades y Ciencias, Universidad de la Republica, Calle Juan L. Cuestas 1525, Montevideo. 2000 specimens; Uruguay; Marsupialia, Chiroptera, Rodentia, Carnivora. Person in charge is Alfredo Langguth.

Museo Nacional de Historia Natural de Montevideo, Casilla de Correo 399, Montevideo. 3500 specimens; 2 holotypes; Uruguay; Chiroptera, Rodentia, Carnivora, Cetacea. Includes material from the former collections of Sociedad Taguató de Ciencias Naturales, Centro de Estudios de Ciencias Naturales, Sociedad Guazu-bira de Ciencias Naturales, Eduardo F. Acosta y Lara, and Juan J. Uraga-Blengio. Person in charge is Alvaro Mones.

USSR

All-Union Research Institute of Game Management and Fur Farming, VNIIOZ, Engels Street 79, Kirov. 3200 specimens; USSR; Lagomorpha, Rodentia, Carnivora. Person in charge is N. M. Zamakhaeva.

Collection of Prof. Panteleyev, Institute of Evolutionary Animal Morphology and Ecology, USSR Academy of Science, Moscow. Number of specimens not given; USSR; collection consist only of specimens of *Arvicola terrestris*. Person in charge is Prof. Pavel A. Panteleyev.

Zoological Institute, USSR Academy of Sciences, Universitetskaja nab. 1, 199164 Leningrad V-164. 100,000 specimens; 46 holotypes, lectotypes, and neotypes; USSR; Lagomorpha, Rodentia, Carnivora, Ungulata. Includes material from the Institute of Biology and Soil, Vladivostok. Person in charge is Dr. A. A. Gureev.

Zoological Institute, Academy of Science of USSR, Niyasov Str. 1, Tashent—95. 3303 specimens; 1 holotype; desert areas of Uzbek Republic; Rodentia, Carnivora. Person in charge is Pavlenko Tatyana Alexandrovna.

Zoological Museum, Tartu University, Vanemujse 46, Tartu. 5344 specimens; USSR; Lagomorpha, Rodentia. Includes material from the anatomical collection of Professor Alexander Dosenberg. Person in charge is Ingrid Heidemaa.

Zoology Museum of the Institute of Plant and Animal Ecology, Urals Scientific Centre, USSR Academy of Sciences, 8 Marta 202, 620008 Sverdlovsk. 48,404 specimens; 1 holotype; Urals and adjacent areas of western Siberia and Kazakhstan; Insectivora, Rodentia, Carnivora. Person in charge is Sharova Lidia Petrovna.

Zoological Museum of the Kiev's State University, Vladimirscaya 58, 252017 Kiev-17, Ukraine. 7000 specimens; Ukraine; Rodentia. Person in charge is Lydia M. Pisareva.

Zoological Museum of Moscow University (ZMMU), Herzen Str. 6, 103009 Moscow K-9. 150,000 specimens; 330 holotypes; northern Palearctic; Insectivora, Rodentia, Carnivora. Includes the private collection of Prof. S. I. Ognev. Person in charge is Dr. Olga L. Rossolimo.

YUGOSLAVIA

Hrvatski Narodni Zoološki Muzej (HNZM), Demetrova 1/II, YU-41000 Zagreb. 1500 specimens; Croatia; Insectivora, Rodentia, Carnivora. Contains material formerly in the private collections of Igalffy and Tvrthović. Person in charge is Nikola Tvrthović.

Prirodoslovni Muzej Slovenije, Prešernova 20, YU-61000 Ljubljana. 700 specimens; Yugoslavia, Nepal; Insectivora, Rodentia. Persons in charge are J. Gregori and B. Kryštufek.

Private Collection of B. Kryštufek, Valjavčeva 28, YU-64000 Kranj. 1000 specimens; Yugoslavia; Insectivora, Rodentia. Person in charge is B. Kryštufek.

Zemaljski Musej, Odjeljenje Za Prirodne Nauke—Zoološki Odsjek, Vojvode Putnika 7, YU-71000 Sarajevo. 629 specimens; 12 holotypes; Yugoslavia; Insectivora, Rodentia. Person in charge is Mr. Svjetislav Obratil.

Zoology Department Collection and **Dr. Dulić's Collection**, Zoologijski Zavod, Rooseveltov trg 6, YU-41000 Zagreb. 5000 specimens; 2 holotypes; Yugoslavia; Insectivora, Chiroptera, Rodentia. Person in charge is Prof. Dr. Beatrica Dulić.

VENEZUELA

Instituto de Investigaciones Veterinarias (IIV), Seccion de Rabia, Apartado 70, Maracay 300, Estado Aragua. 75 specimens; Venezuela; Chiroptera. Person in charge is Dr. Javier Moreno.

Museo de Biología, Universidad Central de Venezuela (MBUCV), Facultad de Ciencias, Instituto de Zoología Tropical, Apartado 59058, Los Chaguaramos, Caracas. 3000 specimens; 3 holotypes, Venezuela; Marsupialia, Chiroptera, Rodentia. Person in charge is Prof. Roger Pérez Hernández.

Museo de la Estacíon Biológica de Rancho Grande (EBRG), Maracay, Edo. Aragua. 2485 specimens; 2 holotypes; Venezuela; Edentata, Lagomorpha, Rodentia, Carnivora, Artiodactyla. Includes material formerly in the National Museum of Natural History, Washington, D.C., U.S.A. Person in charge is Lic. Gonzalo Medina Padilla.

Museo de Historia Natural La Salle (MHNLS), Sociedad de Ciencias Naturales La Salle, Apartado 8150, Caracas 101. 4500 specimens; Venezuela; Chiroptera. Persons in charge are Andrés Musso and Mercedes Salazar.

VIETNAM

Laboratory of Zoology, Hanoi University (LZUH), No. 19, Lîthauh Tôn Street, Hanoi. 2200 specimens; 7 holotypes; North Vietnam; Primates, Rodentia. Person in charge is Dao van Tiên.

ZIMBABWE

Blair Research Laboratory (BRL), Ministry of Health, P.O. Box 8105, Causeway. 2000 specimens; Zimbabwe; Rodentia. Person in charge is D. H. Gordon.

Museum of Zoology, University of Zimbabwe, Box MP 167, Mt. Pleasant, Salisburg. 2136 specimens; Zimbabwe; Chiroptera, Rodentia. Person in charge is T. Choate.

National Museum of Zimbabwe, P.O. Box 240, Bulawayo. 67,000 specimens; Zimbabwe, Zambia, Mozambique, Botswana; Lagomorpha, Primates, Rodentia, Carnivora, Bovidae. Person in charge is J. R. Peek.

Queen Victoria Museum (QVM), Box 8006, Causeway. 8030 specimens; Zimbabwe, Botswana, Mozambique; Chiroptera, Rodentia, Carnivora. Person in charge is Dr. Reay H. N. Smithers.

Umtali Museum, Victory Avenue, Umtali. 200 specimens; Zimbabwe. Person in charge is Mr. L. Mutisi.

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THE MAMMALS OF NORTHEASTERN BRAZIL: A PRELIMINARY ASSESSMENT

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ABSTRACT

Mammals were collected in northeastern Brazil between 1975 and 1978. Research was concentrated in the State of Pernambuco in the environs of the Municipality of Exu and in the State of Ceará, in the Municipality of Crato. Additionally, a representative sample of mammals collected throughout the Caatingas and housed in the National Museum in Rio de Janeiro and the Museum of Zoology of the University of São Paulo was examined. Distributional data as well as ecological notes are presented in this preliminary report. Major collecting localities are also described.

INTRODUCTION

Background

In 1974, initial efforts were made to examine various aspects of mammalian biology in the semiarid Caatingas of northeastern Brazil. This area is of particular interest because it is an extensive tropical

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Submitted 22 July 1980.

pocket of aridity bordered by more mesic habitat and may be important from a biogeographic perspective (Müller, 1973). Although the Caatingas has long played an important role in the culture and economy of Brazil (see for example James, 1942), the region has not been well studied, particularly from the point of view of its mammal fauna. Further, the entire region is greatly affected by human activities (agriculture, ranching, hunting), making it imperative to examine the area as soon as possible. Despite its broad extent and unique climate, previous studies have found that the Caatingas does not support significant numbers of endemic bird species (Sick, 1965) or lizards (Vanzolini, 1974). In this report we give a preliminary accounting of the mammals of the Caatingas, particularly those inhabiting the geographical center of the region near Exu, Pernambuco, and Crato, Ceará. We also include habitat descriptions and ecological notes on several species.

Objectives

The major objective of our research was to examine the distribution and ecology of the mammals of the Caatingas. Although we originally intended to continue the field research beyond 1978, difficulties in funding ended field work in May of that year. During the two years of greatest activity (1976–78), we were able to examine the mammal fauna of the environs of the Municipality of Exu in some detail. We were also able to initiate detailed treatments of the behavioral ecology of *Kerodon rupestris*; the habitat selection and interspecific aggression of *Thrichomys apereoides, Galea spixii, Monodelphis domestica,* and *Didelphis albiventris*; and the community ecology and reproductive biology of the bat faunas of habitats supporting Caatingas and Cerrado vegetation. Finally, we hope to be able to clarify various taxonomic problems concerning Caatingas species, as well as to offer new data on the distribution and natural history of many species of mammals from this largely unstudied region. This preliminary report on the mammals of the Northeast will be a forerunner of more extensive faunal analyses which will appear as the final preparation of specimens is completed.

Personnel

The primary field researchers involved in this study were Michael R. Willig, Karl E. Streilein, and Thomas E. Lacher, Jr. In addition, some specimens were collected by Michael A. Mares, and all of the above examined various localities throughout much of the Caatingas. Employees of AGGEU, under the direction of Celio Rodrigues de Almeida, occasionally provided specimens collected from the Municipality of Exu. Several specimens were collected by Alfred L. Gardner during a visit to Exu. Finally, some specimens were collected by Laurie J. Vitt. The project was coordinated by Mares, and at least one full-time field assistant was available for each investigator.

Collections

Most of our collecting was done in the immediate area of the Municipality of Exu, Pernambuco, and the Municipality of Crato, Ceará, particularly on the Chapada do Araripe. Occasional collecting trips were made to other areas, but in comparison with the work performed in the Exu-Crato area, these were minor in scope. In order to obtain a better idea of mammal distribution patterns in the Caatingas, we examined the extensive collection of Caatingas mammals housed in the National Museum of Rio de Janeiro and the Museum of Zoology of the University of São Paulo. We also attempted to collect specimens in most of the major macrohabitats of the Northeast. The Northeast of Brazil contains five principal vegetation zones including: Rainforest along the Atlantic coast, Cerrado, Caatingas, Cerrado-Caatingas contact zone, and Palm Forest. We were able to do some collecting in each of these regions, but our samples are far from adequate to arrive at a definitive faunal assessment for any region.

During this study, 6576 mammal specimens representing seven orders, 21 families, 56 genera, and 74 species were collected. An additional 630 specimens representing four orders, six families, 16 genera, and 17 species were examined in museum collections. Upon completion of museum specimen processing, half of our collection will be housed in the Zoology Museum of the University of São Paulo and half will be housed in the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

A complete list of species, including those observed but not captured, is as follows:

Order Marsupialia
  Family Didelphidae
    Monodelphis domestica
    Marmosa cinerea
    Marmosa karimii
    Didelphis albiventris

Order Chiroptera
  Family Emballonuridae
    Saccopteryx bilineata
    Saccopteryx leptura
    Peropteryx macrotis
  Family Noctilionidae
    Noctilio leporinus
  Family Mormoopidae
    Pteronotus davyi
    Pteronotus parnellii
    Pteronotus personatus
  Family Phyllostomatidae
   Subfamily Phyllostomatinae
    Micronycteris minuta
    Micronycteris sp.
    Lonchorhina aurita
    Tonatia bidens
    Tonatia brasiliense
    Mimon crenulatum
    Phyllostomus discolor
    Phyllostomus hastatus
    Trachops cirrhosus
   Subfamily Glossophaginae
    Glossophaga soricina
    Lonchophylla mordax
    Anoura geoffroyi
   Subfamily Carolliinae
    Carollia perspicillata
   Subfamily Sturnirinae
    Sturnira lilium
   Subfamily Stenoderminae
    Uroderma bilobatum
    Uroderma magnirostrum
    Vampyrops lineatus
    Artibeus cinereus
    Artibeus concolor
    Artibeus fuliginosus
    Artibeus jamaicensis
    Artibeus lituratus
   Subfamily Desmodontinae
    Desmodus rotundus
    Diaemus youngii
    Diphylla ecaudata
  Family Natalidae
    Natalus stramineus
  Family Furipteridae
    Furipterus horrens
  Family Vespertilionidae
    Myotis nigricans
    Eptesicus furinalis

Rhogeessa tumida
Lasiurus borealis
Lasiurus ega
Family Molossidae
Molossops abrasus
Molossops greenhalli
Molossops planirostris
Molossops temminckii
Neoplatymops mattogrossensis
Tadarida laticaudata
Tadarida sp.
Eumops sp.
Molossus ater
Molossus molossus
Promops sp.

Order Primates
Family Cebidae
Cebus apella
Family Callithricidae
Callithrix jacchus

Order Edentata
Family Myrmecophagidae
Tamandua tetradactyla
Family Dasypodidae
Euphractus sexcinctus
Dasypus novemcinctus

Order Lagomorpha
Family Leporidae
Sylvilagus brasiliensis

Order Rodentia
Family Muridae
Subfamily Cricetinae
Oryzomys eliurus
Oryzomys subflavus
Rhipidomys mastacalis
Akodon sp.
Akodon arviculoides
Bolomys lasiurus
Oxymycteris angularis
Calomys callosus
Calomys sp.
Wiedomys pyrrhorhinos
Holochilus brasiliensis
Subfamily Murinae
Rattus rattus
Mus musculus
Family Caviidae
Kerodon rupestris
Galea spixii
Family Dasyproctidae
Dasyprocta prymnolopha
Family Echimyidae
Proechimys sp.
Thrichomys apereoides

Order Carnivora
Family Canidae
Cerdocyon thous
Family Procyonidae
Procyon cancrivorus
Family Mustelidae
Galictis vittata
Conepatus semistriatus
Family Felidae
Felis concolor
Felis onca
Felis yagouaroundi

Order Artiodactyla
Family Cervidae
Mazama gouazoubira

Description of Study Sites

The Caatingas is a vast semiarid region of northeastern Brazil (Fig. 1), occurring between approximately 35° and 45° west longitude and 3° and 16° south latitude (Reis, 1976). The area encompasses about 650,000 km^2 (Frota-Pessoa et al., 1971), or about 10% of the territory of Brazil (Reis, 1976). The region is rather anomalous in that it is the largest dry region contained within the tropics and is bordered by much more mesic habitats.

The climate of the Caatingas has been extensively studied by Markham (1972; see also Markham and McLain, 1977). Most of the Caatingas receives less than 500 mm of precipitation per year, although some areas receive more than 1600 mm of rain per year. The whole region is subject to unpredictable periods of aridity when rainfall over large areas will not exceed 200 mm per year. This has given the Caatingas the name Polygon of Drought (for example, Frota-Pessoa et al., 1971), and the effects of the periodic extreme aridity on the human populace are pronounced (James, 1942), particularly in localities in which annual rainfall plummets to zero for an entire year. Gener-

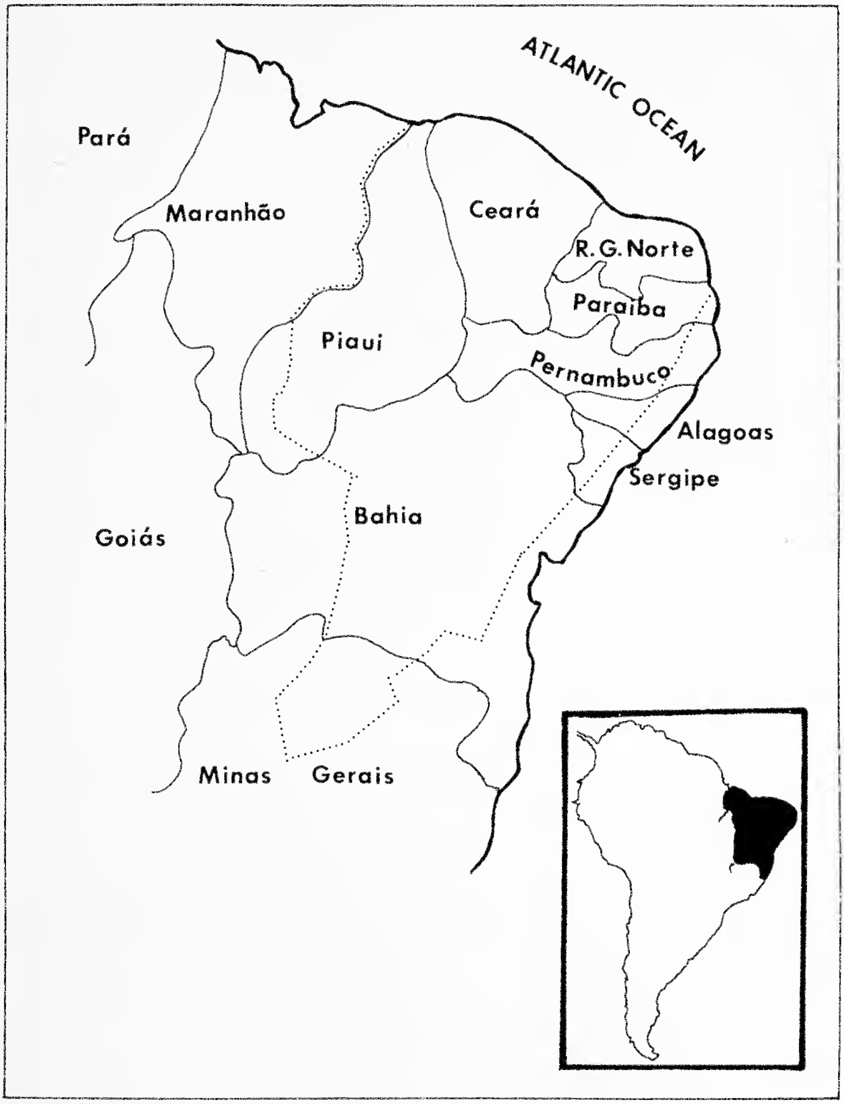


Fig. 1.—The Caatingas of Brazil (area enclosed by the dotted line) occupies an area of 650,000 km², contained for the most part in the nine states of the Northeast.

ally, most rainfall over much of the Caatingas falls between December and April or May, with showers commencing in October (James, 1942). In particularly wet years, there may be no drought period at all, although usually each year contains at least several months with little or no precipitation when deciduousness is pronounced.

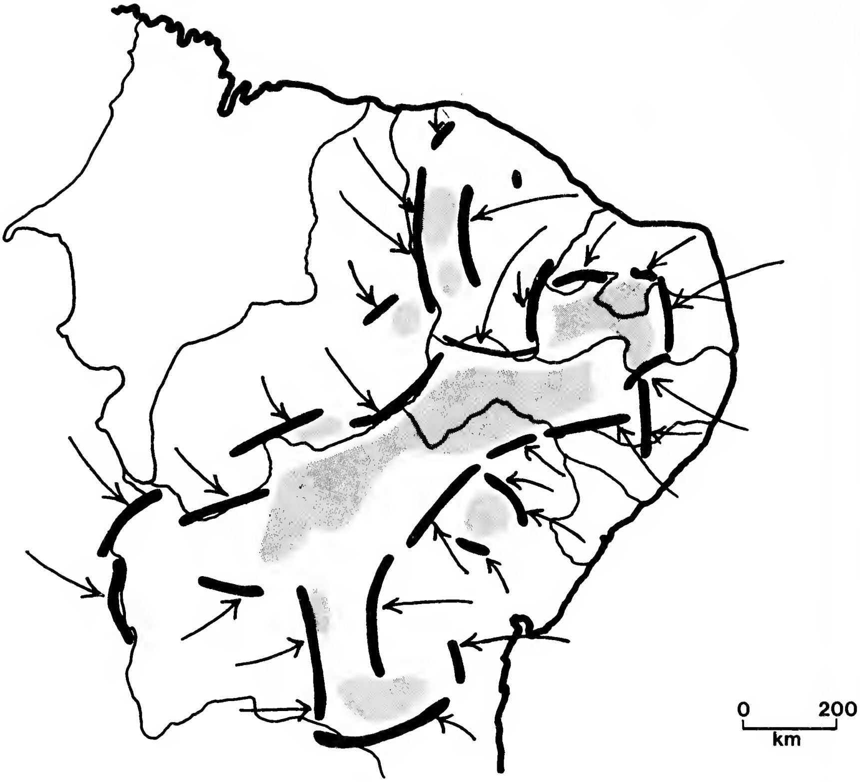


Fig. 2.—The windward side of large chapadas and serrotes (indicated by thick black lines) receive appreciable amounts of orographic rainfall due to the adibiatic cooling of rising air currents (arrows). This in turn produces a rain shadow (shaded area) throughout the interior of the Northeast which is unpredictably subject to periods of severe drought (Adapted from Markham, 1972).

There is marked topographic relief across the Caatingas as hills, low mountain ranges, and rocky knobs protrude above the gentle plain. These are all the result of differential erosion and provide sites of increased rainfall (orographic precipitation) due to upwelling air currents caused by the rocky barriers (Fig. 2). The largest of these, the Chapada do Araripe, was located within our principal collecting area and provided a mesic enclave within the overall semiarid region. Because of the effect of the Chapada do Araripe and other associated rocky hills, the Exu-Crato region provides a large diversity of habitat types, varying from very dry localities to quite mesic sites; vegetation on these sites varies in accordance with precipitation and is described below (Fig. 3). During the period of intensive study (1976–78), the Exu-Crato region experienced two years of high precipitation without a well-delineated drought period. The vegetation during this time did not undergo pronounced deciduousness.

A description of each collecting locality and a faunal list for each area follow.

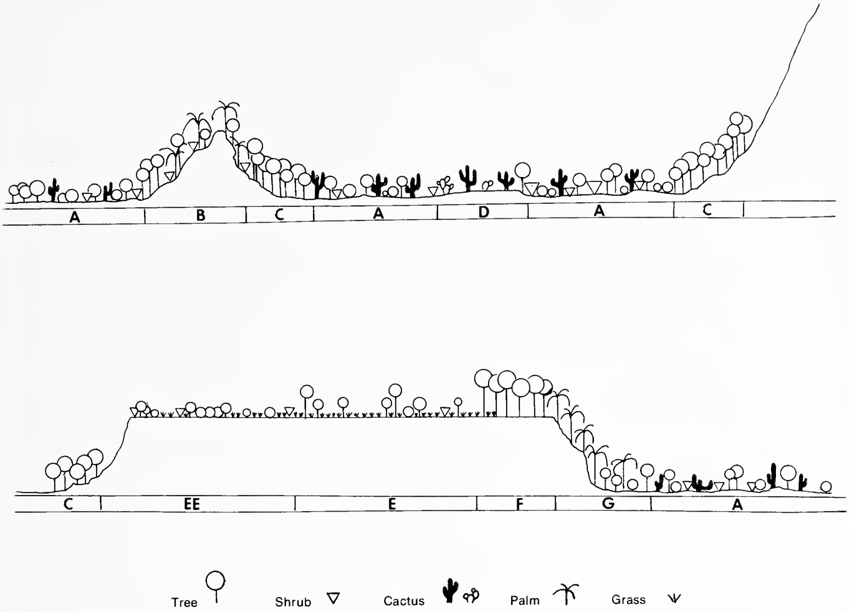


Fig. 3.—Graphic representation (adapted from Willig, unpublished manuscript) of the mosaic of habitats in the Caatingas and their proximity to cerrado vegetation on the Chapada do Araripe and to humid forest in areas of orographic rainfall. Key to habitat types—A, Caatinga Baixa; B, Serrote; C, Caatinga Alta; D, Lajeiro; E, Cerrado; EE, Disturbed areas of Cerrado; F, Cerradão; G, Humid Forest.

Table 1.—*Common plants of Caatinga Baixa habitats in the Município de Exu, Pernambuco.*

Species	Family
Cassia excelsa	Leguminosae
Cereus jamacaru	Cactaceae
Cnidoscolus urens	Euphorbiaceae
Cordia globosa	Boraginaceae
Croton campestris	Euphorbiaceae
Croton jacobinensis	Euphorbiaceae
Phaseolus peduncuclaris	Leguminosae, Papilionaceae
Piptadenia sp.	Leguminosae, Mimosoideae
Piptadenia zehntneri	Leguminosae, Mimosoideae
Ziziphus joazeiro	Rhamnaceae

I. The Remnant Atlantic Rain Forest

A short time (5 days) was spent making a preliminary survey of the mammal fauna of the Estacão Ecológico do Tapacurá, located west of Recife, Pernambuco. This area is contained within the zone of what was previously dominated by the Atlantic Rain Forest; today it is limited to only the small patches of the original vegetation which have escaped destruction (compare James, 1942; Frota-Pessoa et al., 1971). Most of the region supports sugar cane or other crops and orchards; the effect of agricultural activities on the present-day remnants of the forest fauna are unknown.

The Atlantic Rain Forest is characterized by a high diversity of mesophytic broadleafed trees. Although the canopy may reach a height of 35 m, it rarely exceeds 25 m. Within the rainforest, ground cover is sparse and vines often form complex networks from ground level through the canopy.

A list of mammal species either collected or sighted follows. For this and other localities, we have included a subjective assessment of abundance, with U = unknown, R = rare, C = common, and A = abundant.

Monodelphis domestica	(U)
Didelphis albiventris	(U)
Peropteryx macrotis	(U)
Micronycteris minuta	(U)
Phyllostomus hastatus	(U)
Glossophaga soricina	(U)
Carollia perspicillata	(U)
Sturnira lilium	(U)
Artibeus cinereus	(U)
Artibeus jamaicensis	(U)
Artibeus lituratus	(U)
Desmodus rotundus	(U)
Diaemus youngii	(U)
Myotis nigricans	(U)
Lasiurus borealis	(U)
Molossops greenhalli	(U)
Akodon sp.	(U)
Galea spixii	(U)
Thrichomys apereoides	(U)

II. Caatingas

The semiarid region of anomalous drought in the Northeast of Brazil encompasses a wide range of plant communities which are collectively known as Caatingas (Fig. 3). In general, Caatingas are assemblages of xeric-adapted plants, however, these communities need not be dominated by members of the Cactaceae.

Caatinga Baixa.—Throughout the lower elevations in Pernambuco and parts of Ceará and Bahia, Caatinga Baixa, or Low Caatinga communities predominate. Although the species composition may shift considerably between widely separated localities, trees are generally xerophytic and reach a height of 3 to 5 m with occasional emergents reaching a height of 8 m. Large cacti, such as *Cereus jamacaru* (Mandacaru), *Cephalocereus gounellei* (Xique-Xique), and *Zehntherella squamulosa* (Facheiro), are common components in Low Caatinga communities (Figs. 4 and 5). Substantial variation in the types of vegetation within a single locality is the rule rather than the exception in Caatinga Baixa. Minor differences in topography, variation in soil parameters, prior utilization by man, and differential exploitation by domestic animals are among the primary factors which generate the characteristic microhabitat mosaics. This complex of microhabitats is often too diverse to be easily categorized with a few broad generalizations. Some of the more common plants in Caatinga Baixa are listed in Table 1. The mammals of Caatinga Baixa are as follows:

Monodelphis domestica	(C)	*Rhogeessa tumida*	(U)
Marmosa karimii	(R)	*Lasiurus ega*	(R)
Didelphis albiventris	(C)	*Molossus ater*	(R)
Noctilio leporinus	(C)	*Molossus molossus*	(R-C)
Pteronotus personatus	(R)	*Callithrix jacchus*	(R)
Trachops cirrhosus	(R)	*Dasypus novemcinctus*	(C)
Glossophaga soricina	(C)	*Euphractus sexcinctus*	(C)
Lonchophylla mordax	(C)	*Sylvilagus brasiliensis*	(U)
Anoura geoffroyi	(R)	*Calomys callosus*	(R)
Carollia perspicillata	(C)	*Wiedomys pyrrhorhinos*	(R)
Uroderma bilobatum	(R)	*Galea spixii*	(R)
Vampyrops lineatus	(C)	*Cerdocyon thous*	(C)
Artibeus jamaicensis	(R)	*Procyon cancrivorus*	(R)
Artibeus lituratus	(R)	*Galictis vittata*	(U)
Desmodus rotundus	(C)	*Conepatus semistriatus*	(U)
Myotis nigricans	(R-C)	*Felis yagouaroundi*	(U)

Caatinga Alta.—Large xerophyllic trees which annually lose their leaves in synchrony during the dry season predominate and form a closed canopy in the wet season. These trees range in size from 10 to 12 m tall and are less densely packed than trees in Caatinga Baixa habitats (Fig. 6). The understory is usually poorly developed, but varies greatly in both composition and density from locality to locality. Caatinga Alta communities are restricted to higher elevations, hillsides, or the perimeters of valleys. The common plants in these communities are listed in Table 2. Locations which support Caatinga Alta communities are generally more mesic than Low Caatinga sites, but are drier than nearby serrotes. Rock outcroppings are often dispersed throughout the forest floor, but they are rarely very large. A list of mammals occurring in Caatinga Alta is as follows:

Monodelphis domestica	(C)	*Desmodus rotundus*	(A)
Didelphis albiventris	(C)	*Diphylla ecaudata*	(R)
Noctilio leporinus	(C)	*Myotis nigricans*	(R-C)
Pteronotus davyi	(R)	*Molossops planirostris*	(R)
Micronycteris minuta	(R)	*Neoplatymops mattogrossensis*	(R)
Micronycteris sp.	(R)	*Molossus molossus*	(R-C)
Tonatia bidens	(C)	*Cebus apella*	(R)
Tonatia brasiliense	(R)	*Callithrix jacchus*	(C)
Mimon crenulatum	(R)	*Tamandua tetradactyla*	(R)
Phyllostomus discolor	(R)	*Euphractus sexcinctus*	(R)
Glossophaga soricina	(C-A)	*Dasyprocta prymnolopha*	(R)
Lonchophylla mordax	(C)	*Cerdocyon thous*	(C)
Carollia perspicillata	(C-A)	*Galictis vittata*	(U)
Sturnira lilium	(R)	*Felis yagouaroundi*	(U)
Vampyrops lineatus	(C)	*Felis onca*	(U)
Artibeus jamaicensis	(C)	*Mazama gouazoubira*	(R)
Artibeus lituratus	(R-C)		

Serrotes.—The relatively flat terrain of the Caatingas contains a large number of small granitic mountains known as serrotes (Fig. 7). These serrotes appear to function as mesic refugia during the dry season. Palms, such as *Syargus oleracea* and *Accrocomia intumescens,* are typically restricted to serrotes. In many places, serrotes contain the

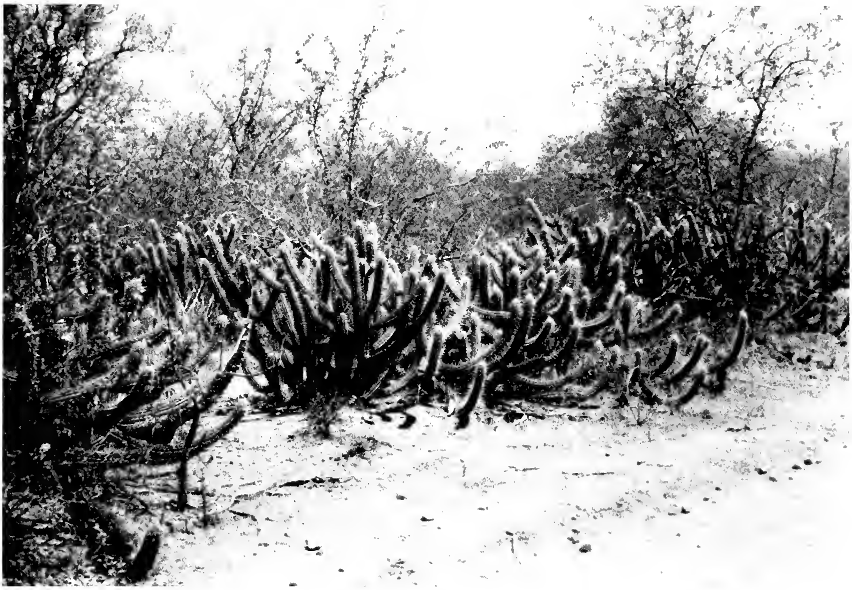


Fig. 4.—Although dense deciduous trees and shrubs form the dominant thorn scrub component of Caatinga Baixa, cacti such as Xique-Xique (shown in this photograph) are prevalent in many localities. Município de Serra Talhada, Pernambuco.

Fig. 5.—Much of the Caatingas is being altered by human activities. The effects of slash and burn agriculture (on the right of the photograph) are contrasted with the dense vegetation of Caatinga Baixa. Município de Exu, Pernambuco.

Fig. 6.—Granitic substrates (seen in the foreground) often delimit the edge of Caatinga Alta habitats at higher elevations on serrotes. Notice the large trees (seen in the background) typical of Caatinga Alta vegetation. Município de Exu, Pernambuco.

Fig. 7.—A rocky serrote interrupts the flat plain of Caatinga Baixa habitat. Photograph taken during the dry season of 1975. Município de Serra Talhada, Pernambuco.

Fig. 8.—Extensive lajeiros studded with cacti (Mandacaru and Palma) and bromeliads are frequently encountered in the Caatingas. At this particular site, the top of the lajeiro is slightly elevated above the plain of the surrounding thorn scrub. Depressions and crevices on the surface often fill with water in the wet season and persist for a variable amount of time in the dry season. Município de Senhor do Bom Fim, Bahia.

upper limit of Caatinga Alta habitat; hence the vegetation of the serrotes may be considered a mixture of Caatinga Alta and more mesic elements such as palm trees. The mammals of the serrotes include the following:

Monodelphis domestica	(A)
Didelphis albiventris	(A)
Peropteryx macrotis	(R)
Micronycteris sp.	(R)
Tonatia bidens	(C)
Tonatia brasiliense	(R)
Phyllostomus discolor	(R)
Phyllostomus hastatus	(R)
Trachops cirrhosus	(C)
Glossophaga soricina	(A)
Lonchophylla mordax	(C)
Anoura geoffroyi	(R-C)
Carollia perspicillata	(A)
Vampyrops lineatus	(A)
Artibeus jamaicensis	(A)
Artibeus lituratus	(C)
Desmodus rotundus	(A)
Diphylla ecaudata	(R)
Furipterus horrens	(R)
Myotis nigricans	(R-C)
Molossops temminckii	(R)
Neoplatymops mattogrossensis	(R)
Euphractus sexcinctus	(R)
Kerodon rupestris	(A)
Thrichomys apereoides	(A)
Cerdocyon thous	(C)
Galictis vittata	(C)
Conepatus semistriatus	(U)
Felis yagouaroundi	(U)

Lajeiros.—Lajeiros are rock outcroppings primarily distributed throughout low lying areas of the Caatingas. They vary in complexity from simple unbroken rock faces, to

Fig. 9.—Lajeiros composed of large boulders are also common in the Caatingas (background of photograph). The foreground is occupied by an abandoned agricultural field which is in an early successional stage of development, while the lajeiro harbors a flora more typical of Caatinga Baixa vegetation. Município de Senhor do Bom Fim, Bahia.

a complex of many fissured rock faces studded with cacti and strewn with boulders of variable sizes and shapes (Figs. 8 and 9). The predominant cacti associated with these outcroppings are *Pilosocereus gounellei, Cereus jamacaru,* and *Opuntia palmadora* (Palma). Most lajeiros are located near serrotes; however, some may be isolated by a distance of several kilometers from other lajeiros or serrotes. Lajeiros occupy a broad

Table 2.—*Common plants of Caatinga Alta habitats in the Município de Exu, Pernambuco.*

Species	Family
Bauhinia sp.	Leguminosae, Caesalpinioidae
Cavanillesia arborea	Bombacaceae
Cordia sp.	Boraginaceae
Craetava tapia	Capparaceae
Croton argyrophylloides	Euphorbiaceae
Croton jacobinensis	Euphorbiaceae
Erythroxylum sp.	Erythroxylaceae
Piptadenia zehntneri	Leguminosae, Mimosoideae
Pterogyne nitens	Leguminosae, Papilionoideae
Schinus terebinthifolius	Anacardiaceae

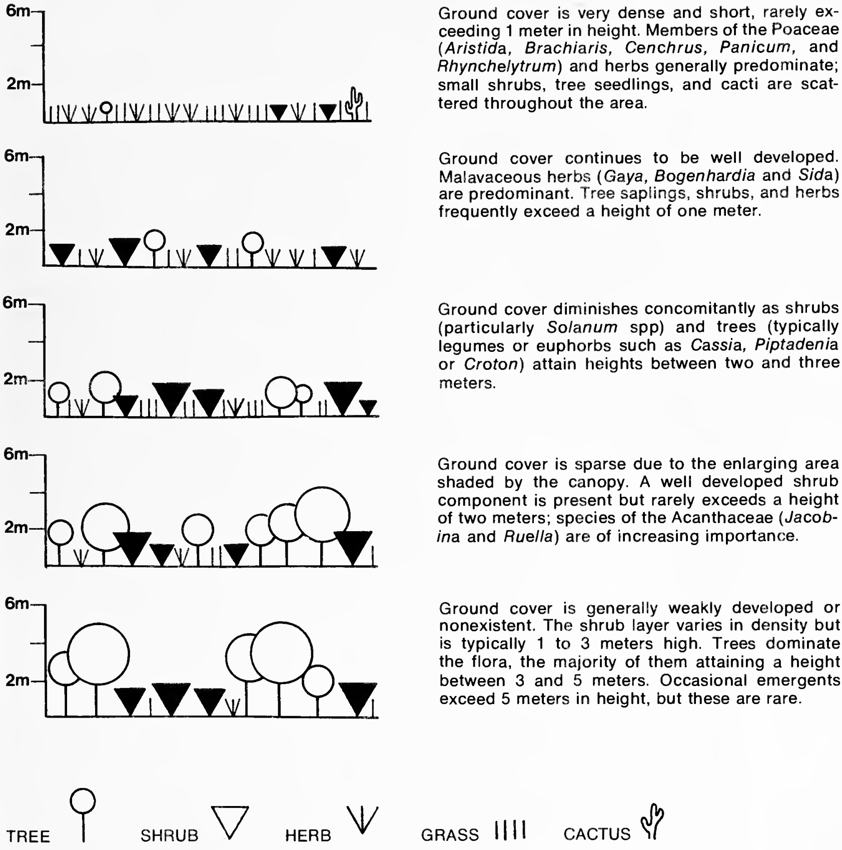
Fig. 10.—A planted agricultural field dominates the foreground, with characteristic Caatinga vegetation occupying steep slopes on the sides of hills (seen in the background). Município de Senhor do Bom Fim, Bahía.

range of sizes whose upper limit includes extensive formations best measured in hectares. Complex lajeiros greatly enhance the horizontal and vertical complexity of the Caatingas. Mammals frequenting lajeiros include the following:

Monodelphis domestica	(A)	*Molossops temminckii*	(R)
Didelphis albiventris	(A)	*Neoplatymops mattogrossensis*	(C)
Peropteryx macrotis	(R)	*Kerodon rupestris*	(A)
Micronycteris sp.	(R)	*Galea spixii*	(C)
Glossophaga soricina	(C)	*Trichomys apereoides*	(A)
Carollia perspicillata	(C-A)	*Cerdocyon thous*	(C)
Vampyrops lineatus	(C)	*Galictis vittata*	(C)

Areas dominated by human activity.—Agricultural practices have greatly altered the natural state of the Caatingas (Fig. 10). Fruit orchards may predominate in the more mesic areas, especially along streams, where a wide variety of fruits such as oranges, papayas, bananas, and mangos are cultivated.

The standard procedure for establishing an agricultural field entails clear-cutting sections of Low or High Caatinga, removing the large pieces of wood for fuel, and burning the remaining material on the site. Subsequent utilization varies, depending upon both the site and crop planted. Corn and beans are the most common and transient crops grown in Low Caatinga habitats, whereas cotton and *Opuntia* plantings may persist for years. Grass pastures also last for many years, due in part to occasional burning and constant grazing by cattle and horses, which prevent the reestablishment of Caatingas vegetation.



Ground cover is very dense and short, rarely exceeding 1 meter in height. Members of the Poaceae (*Aristida, Brachiaris, Cenchrus, Panicum,* and *Rhynchelytrum*) and herbs generally predominate; small shrubs, tree seedlings, and cacti are scattered throughout the area.

Ground cover continues to be well developed. Malavaceous herbs (*Gaya, Bogenhardia* and *Sida*) are predominant. Tree saplings, shrubs, and herbs frequently exceed a height of one meter.

Ground cover diminishes concomitantly as shrubs (particularly *Solanum* spp) and trees (typically legumes or euphorbs such as *Cassia, Piptadenia* or *Croton*) attain heights between two and three meters.

Ground cover is sparse due to the enlarging area shaded by the canopy. A well developed shrub component is present but rarely exceeds a height of two meters; species of the Acanthaceae (*Jacobina* and *Ruella*) are of increasing importance.

Ground cover is generally weakly developed or nonexistent. The shrub layer varies in density but is typically 1 to 3 meters high. Trees dominate the flora, the majority of them attaining a height between 3 and 5 meters. Occasional emergents exceed 5 meters in height, but these are rare.

Fig. 11.—Much of the Caatingas occurs in one of the seral stages of ecological succession graphically illustrated above. (Adapted from Willig et al., unpublished manuscript.)

Abandoned agricultural fields proceed through a number of successional stages. The amount of time during which a particular sere persists is extremely variable, primarily because vegetative growth is directly linked to the amount and timing of annual rainfall. Due to the magnitude of human activity in recent history, much of the Caatingas is in a disturbed state, existing in one of the seral stages discussed in Fig. 11. Mammals found in disturbed habitats include the following:

Buildings

Monodelphis domestica	(R)	*Tadarida laticaudata*	(R)
Didelphis albiventris	(R)	*Molossus ater*	(R)
Peropteryx macrotis	(R)	*Molossus molossus*	(A)
Glossophaga soricina	(A)	*Promops* sp.	(R)
Carollia perspicillata	(C)	*Rattus rattus*	(A)
Myotis nigricans	(C-A)	*Mus musculus*	(R)

Fig. 12.—Cerrado vegetation on the Chapada do Araripe in the Floresta Naçional Araripe-Apodí is dominated by grass and trees and is quite similar to the savanna of Africa. Município de Crato, Ceará.

Agricultural fields

Monodelphis domestica	(R)	*Oryzomys subflavus*	(R-C)
Didelphis albiventris	(R)	*Bolomys lasiurus*	(R-A)
Oryzomys eliurus	(R)	*Galea spixii*	(A)

Fruit orchards

Monodelphis domestica	(R)	*Anoura geoffroyi*	(R)
Didelphis albiventris	(C)	*Carollia perspicillata*	(C)
Phyllostomus discolor	(C)	*Vampyrops lineatus*	(C)
Glossophaga soricina	(C)	*Lasiurus ega*	(R)

Abandoned fields

Monodelphis domestica	(C)	*Bolomys lasiurus*	(R-A)
Marmosa karimii	(R)	*Calomys callosus*	(R)
Didelphis albiventris	(C)	*Galea spixii*	(A)
Dasypus novemcinctus	(U)	*Cerdoyon thous*	(C)
Euphractus sexçinctus	(U)		

III. The Chapada do Araripe

The Floresta Naçional Araripe-Apodí contains most of the collection sites examined on the Chapada do Araripe. The topography of the plateau is exceedingly flat, with a thin layer of sandy red soil covering a hard sandstone substrate. Permanent bodies of

Fig. 13.—Humid forest occupies areas of orographic rainfall on the windward side of the Chapada do Araripe. Município de Crato, Ceará.

water of any size are absent from the Chapada do Araripe; during the rainy season, temporary pools of water may form in low-lying depressions. There are no rocks, boulders or even stones on the top of the Chapada. In general, the vegetation is sclerophyllous and semideciduous. Trees and shrubs may lose their leaves each year, but leaf loss is asynchronous both inter- and intraspecifically.

Cerrado.—The Cerrado of the Chapada do Araripe is physiognomically an open tree and shrub woodland with a pervasive grass component (Figs. 3 and 12). Taller trees, rarely exceeding a height of 15 m, are scattered throughout the area. Smaller trees of various sizes (3 m to 5 m) and shrubs (.5 m to 3 m) comprise about 50% of the plant

Table 3.—*Common plants in Cerrado and Cerradão habitats of the Chapada do Araripe in the Floresta Naçional Araripe-Apodí.*

Species	Family
Anonna sp.	Annonaceae
Byrsonima sericea	Malpighiaceae
Caryocar coreaceum	Caryocaraceae
Casearia dentata	Flacourtiaceae
Casearia grandiflora	Flacourtiaceae
Cassia speciosa	Leguminosae, Caesalpiniodeae
Cassia splendida	Leguminosae, Caesalpiniodeae
Dioclea bicolor	Leguminosae, Papilionoideae
Fagara gardneri	Rutaceae
Hirtela glandulosa	Chrysobalanaceae
Hirtela racemosa	Chrysobalanaceae
Hyptis umbrosa	Labiatae
Miconia c.f. *albicans*	Melastomaceae
Miconia ligustroides	Melastomaceae
Myrcia sp.	Myrtaceae
Ocotea pallida	Lauraceae
Parkia platicephala	Leguminosae, Mimosoideae
Stygmaphillon	Malpighiaceae
Vismia	Guttiferae

cover, while grass species occupy the remaining area. As such, the canopy is irregular and undulating in profile, with numerous areas lacking woody plants. Taller trees and shrubs often have characteristically twisted trunks and branches. The most common trees, shrubs, and grasses are noted in Table 3, while the mammals of the Cerrado portion of the Chapada do Araripe include the following:

Didelphis albiventris	(A)	*Eptesicus brasiliensis*	(R)
Pteronotus davyi	(R)	*Lasiurus borealis*	(R)
Micronycteris sp.	(R)	*Lasiurus ega*	(R)
Micronycteris minuta	(R)	*Molossops temminckii*	(R)
Phyllostomus discolor	(A)	*Molossus molossus*	(R-C)
Phyllostomus hastatus	(A)	*Callithrix jacchus*	(U)
Glossophaga soricina	(A)	*Tamandua tetradactyla*	(U)
Anoura geoffroyi	(A)	*Euphractus sexcinctus*	(A)
Carollia perspicillata	(A)	*Dasypus novemcinctus*	(A)
Sturnira lilium	(R-C)	*Oryzomys eliurus*	(R)
Uroderma bilobatum	(R)	*Bolomys lasiurus*	(R)
Vampyrops lineatus	(A)	*Wiedomys pyrrhorhinos*	(R)
Artibeus concolor	(R)	*Dasyprocta prymnolopha*	(U)
Artibeus jamaicensis	(A)	*Cerdocyon thous*	(C)
Artibeus lituratus	(A)	*Felis concolor*	(U)
Desmodus rotundus	(R)	*Felis onca*	(U)
Natalus stramineus	(R)	*Mazama gouazoubira*	(C)
Myotis nigricans	(R-C)		

Cerradão.—Certain sections in the Floresta Naçional Araripe-Apodí differ substantially from the Cerrado vegetation in both density, physiognomy, and species composition. Stands with many trees, few shrubs and little grass are herein referred to as Cerradão. The Cerradão is composed of larger trees which form a more or less continuous canopy between 12 and 17 m high, and the trees do not have the twisted appearance characteristic of the Cerrado. Tree density is much greater in the Cerradão than in the Cerrado. The understory may vary considerably from quite dense to sparse; in either case however, shrubs less than 1 m in height and grasses are quite rare. Mammals of the Cerradão portion of the Chapada are as follows:

Didelphis albiventris	(A)	*Artibeus jamaicensis*	(A)
Saccopteryx bilineata	(R)	*Desmodus rotundus*	(R)
Noctilio leporinus	(R)	*Myotis nigricans*	(R-C)
Pteronotus davyi	(R)	*Eptesicus brasiliensis*	(R)
Micronycteris sp.	(R)	*Lasiurus borealis*	(R)
Micronycteris minuta	(R)	*Molossops temminckii*	(R)
Phyllostomus discolor	(A)	*Tadarida* sp.	(R)
Phyllostomus hastatus	(A)	*Molossus molossus*	(R-C)
Glossophaga soricina	(A)	*Callithrix jacchus*	(R-C)
Anoura geoffroyi	(A)	*Euphractus sexcinctus*	(U)
Carollia perspicillata	(A)	*Dasyprocta prymnolopha*	(C)
Sturnira lilium	(R-C)	*Proechimys* sp.	(U)
Vampyrops lineatus	(A)	*Cerdocyon thous*	(C)
Artibeus concolor	(R)	*Felis concolor*	(U)
Artibeus lituratus	(A)	*Mazama gouazoubira*	(R-C)

IV. Cerrado-Caatingas Contact Zone

The area around Valença do Piauí, Piauí, was chosen as a Caatingas-Cerrado contact zone because it had been previously used by Vanzolini (1976) in his analysis of the herpetofauna of the Caatingas and Cerrado of Brasil. Vanzolini discussed the flora and geomorphology of the area in some detail; it is sufficient here to point out that the area contains a number of contact zones between Caatingas and Cerrado habitats (that is, Cerrado without Caatingas enclaves, Cerrado with Caatingas enclaves at upper elevational limits, and Cerrado with Caatingas enclaves at the lower elevational limits). The total amount of time spent in the area of Valença do Piauí was limited, hence the absence of a species from the collection is not indicative of its absence from the area. More intensive field work is required to substantiate the abundance and distribution of mammals in these contact zones. Mammals whose occurrence in this region we were able to document include:

Monodelphis domestica	(U)	*Lasiurus ega*	(U)
Didelphis albiventris	(U)	*Molossops abrasus*	(U)
Pteronotus davyi	(U)	*Molossus ater*	(U)
Pteronotus parnellii	(U)	*Molossus molossus*	(U)
Pteronotus personatus	(U)	*Eumops* sp.	(U)
Phyllostomus discolor	(U)	*Kerodon rupestris*	(U)
Lonchorhina aurita	(U)	*Galea spixii*	(U)
Glossophaga soricina	(U)	*Thrichomys apereoides*	(U)
Artibeus jamaicensis	(U)		

V. Humid Forest

The plant community along the base of the Chapada do Araripe in the Municipality of Crato, Ceará, may be classified as a humid forest. The forest forms an irregular band

Fig. 14.—More mesic inland portions of the Northeast may support extensive palm forests such as that seen here. The sandy area in the foreground is a dried river bed. Across the state border from Teresina, Piauí, in the state of Maranhão.

which circumscribes the base of the Chapada do Araripe in the state of Ceará. Precipitation on the Crato side of the Chapada do Araripe is higher than in contiguous areas due to orographic rainfall patterns (Markham, 1972). Only a small amount of time was spent in the area, so extensive information about the vegetation is lacking. Many planted palms were evident, and the vegetation was dense and luxuriant (Fig. 13). Substantial areas that were once forested have been altered by human activity. A preliminary list of mammals of the humid forest is as follows:

Didelphis albiventris	(U)	*Vampyrops lineatus*	(C)
Saccopteryx leptura	(U)	*Artibeus jamaicensis*	(C)
Micronycteris sp.	(U)	*Artibeus lituratus*	(U)
Phyllostomus hastatus	(C)	*Desmodus rotundus*	(U)
Glossophaga soricina	(A)	*Myotis nigricans*	(U)
Lonchophylla mordax	(U)	*Molossus molossus*	(C-A)
Anoura geoffroyi	(U)	*Callithrix jacchus*	(U)
Carollia perspicillata	(A)	*Cerdocyon thous*	(U)
Sturnira lilium	(U)		

VI. Palm Groves

In the extreme northwest of the Caatingas an extensive forest of palm groves occurs in the more mesic areas (Fig. 14). In an attempt to make a preliminary collection of specimens from the area and select possible future study sites, we visited a few locations in the Municipality of Terezina, Piauí. More extensive work is required to characterize the flora and fauna of the area, although we were able to establish the occurrence of a few species of mammals, including:

Glossophaga soricina	(U)
Carollia perspicillata	(U)
Uroderma magnirostrum	(U)
Artibeus cinereus	(U)
Artibeus fuliginosus	(U)
Artibeus jamaicensis	(U)
Artibeus lituratus	(U)

Accounts of Species

Order Marsupialia

Family Didelphidae

Monodelphis domestica Wagner, 1842

This marsupial is a common inhabitant of the Caatingas. Favored habitats include rocky serrotes and lowland rock outcroppings. Reproduction is relatively aseasonal; the young are not protected by a marsupium. Although they are good climbers, they are principally terrestrial; they are also nocturnal. Laboratory animals accepted a wide variety of food items including various vertebrates, invertebrates, and fruits.

Specimens collected.—Pernambuco (Município de Exu), Escola Agrícola de Exu, 0.7 km S of Exu (26); Fazenda Batente, 5.5 km SE of Exu (12); Fazenda Pinheira, 1.5 km SW of Exu (13); Município de Exu (11); (Município de Serra Talhada), Fazenda Saco, 6.6 km N of Serra Talhada (5). Piauí (Município de Valença do Piauí), Fazenda Olho da Agua, 2 km N of Valença do Piauí (1).

Specimens examined.—Alagoas (Limoeiro da Anadia), Sítio Barracão (1); (Palmeira dos Indios), Sítio Capuma (1); Sítio Dormião (1); Sítio Panelas (1); Sítio Riveira (1); Sítio Sabiá (3); (Santana do Ipanema), Sítio Lagoinha (1); (Viçosa), Sítio Cachoeira Grande (1). Bahia (Feira), Fazenda Capoeira do Rosario (1); Fazenda Cazumba (1); Fazenda Jacú (1); Fazenda Salgado (1); (Serrinha), Fazenda Cacuá (1); Fazenda Oiteiro (2); Fazenda Umburana (1); no locality (2). Ceará (Campo Sales), Sítio Volta (1); (Crato), Sítio Constantino (1); no locality (1); Sítio Olaria (1); (Jardim), Sítio Cereado (1); (Milagres), Sítio Camara (1); (Missão Velho), Sítio Araruna (1); Sítio Emboscada (1); Sítio Lapinha (1); (São Benidito), Sítio Cinta da Solidade (1). Pernambuco (Bodocó), Sítio Belem (1); Sítio Lopes (1); Sítio Paus Preto (1); Sítio São Gonçalo (1); Sítio Xique-Xique (1); (Garanhuns), Sítio Riacho Fundo (1); no locality (1); (Pesqueira), Fazenda Caianinha (1); Fazenda Sororoca (1); (Triunfo), Sítio Boa Esperança de Jerico (1); Sítio Borgens (2); Sítio Cana Brava de Jerico (2); Sítio Corredor do Vento (1); Sítio Macaco de Baixa Verde (1); Sítio Novo (1); Sítio Oiti (2); Sitio São Mateus (1).

Marmosa cinerea Temminck, 1824

Specimens examined.—Bahia (Ilheus), Aritaqua Urucutuca (1); Banco da Vitoria, Pirataquisse (1); Buerarema Ribeirão da Fortuna (1); Rio do Braço, Fazenda Almeida (1); No locality, (11). Pernambuco (dois Irmãos) (1).

Marmosa karimii Petter, 1968

This small marsupial was rare. Specimens were collected only in Low Caatinga and perennial shrub/low tree dominated successional stages. An individual kept in the laboratory was adept at capturing insects and subsisted on insects and occasional hylid frogs and geckos; small amounts of fruit were eaten at times.

Specimens collected.—PERNAMBUCO (Município de Exu), 0.5 km S of Exu (1); Escola Agrícola de Exu, 0.7 km S of Exu (1); Fazenda Guaraní, 2.9 km N of Exu (1); Município de Exu (1).

Didelphis albiventris Lund, 1841

This large marsupial is a habitat generalist and ranges throughout the Caatingas. In the Exu area, it inhabited all microhabitats in addition to more mesic Cerrado localities, such as the Chapada do Araripe (occurring there both in Cerrado and Cerradão habitats). Microhabitat utilization and population density may exhibit seasonal shifts in Caatinga habitats corresponding to seasonal climatic changes. Reproduction is strongly synchronized, with the birth peak occurring during November and December; a marsupium is present. This species is mostly nocturnal and terrestrial in the Caatingas, and is broadly omnivorous.

Specimens collected.—CEARÁ (Município de Crato), Floresta Naçional Araripe-Apodí (13). PERNAMBUCO (Município de Exu), Escola Agrícola de Exu, 0.7 km S of Exu (3); Fazenda Batente, 5.5 km SE of Exu (5); Fazenda Uruguai, 4.8 km NE of Exu (1); Município de Exu (9); Serrote das Lages, 18 km S of Exu (3).
Specimens examined.—PERNAMBUCO (Garanhuns) (1).

Order Chiroptera

Family Emballonuridae

Saccopteryx bilineata (Temminck, 1838)

Absent from the Caatingas; rare on the Chapada do Araripe.

Specimens collected.—CEARÁ (Município de Crato), Floresta Naçional Araripe-Apodí, 9 km S of Crato (1); Floresta Naçional Araripe-Apodí, 10 km SW of Crato (1).

Saccopteryx leptura Schreber, 1774

Specimen collected.—CEARÁ (Município de Crato), Sítio Luanda, 4 km S of Crato (1).

Peropteryx macrotis (Wagner, 1843)

Uncommon in the Caatingas. Roosts in small groups of up to 10 individuals, often occupying large openings inside rockpiles or culverts. Absent from Cerradão and Cerrado habitats on the Chapada do Araripe.

Specimens collected.—BAHIA (Município de Senhor do Bom Fim), Fazenda Lajeido, km 147 on Route BA 130 (5). PERNAMBUCO (Município de Exu), Escola Agrícola de Exu, 0.7 km S of Exu (1); Fazenda Batente, 5.5 km SE of Exu (3); Fazenda Pomonha, 21 km SSW of Exu (7); Serrote Gambá, 19 km SSW of Exu (4); (Município de São Lourenço da Mata), Estação Ecológico do Tapacurá (2); Mata do Camocim (7).

Family Noctilionidae

Noctilio leporinus (Linnaeus, 1758)

Rare in the Cerradão of the Chapada do Araripe where it probably occurs as a transient in the dry season. Common in the Caatingas where it roosts during the day in groups of up to 30 individuals in large hollow hardwood trees. A single night roost under a bridge containing over 100 individuals was consistently utilized from 1976 to 1978. The large accumulation of fecal material under the roost suggests that it had been in use for many years previous to our arrival in 1976.

Specimens collected.—CEARÁ (Município de Crato), Floresta Naçional Araripe-Apodí, 9 km S of Crato (4); Floresta Naçional Araripe-Apodí, 21 km SSW of Crato (1). PERNAMBUCO (Município de Exu), Escola Agrícola de Exu, 0.7 km S of Exu (1); Fazenda Alto de Ferreira, 5 km SW of Exu (14); Fazenda Batente, 5.5 km SE of Exu (1); Fazenda Colônia, 5.5 km S of Exu (136); Fazenda Guarani, 2.9 km N of Exu (6); Fazenda Pinheira, 1.5 km SW of Exu (12); Fazenda São José, 1.5 km N of Exu (2).

Family Mormoopidae

Pteronotus davyi Gray, 1838

Very rare in the Caatingas where it is found only in Caatinga Alta habitats. Also rare in Cerrado and Cerradão habitats of the Chapada do Araripe.

Specimens collected.—CEARÁ (Município de Crato), Floresta Naçional Araripe-Apodí, 8 km S of Crato (1); Foresta Naçional Araripe-Apodí, 9 km S of Crato (4); Floresta Naçional Araripe-Apodí, 8 km SSW of Crato (5); Floresta Naçional Araripe-Apodí, 17 km SSW of Crato (1). PERNAMBUCO (Município de Exu), Fazenda Cantareno, 4.5 km NNE of Exu (1). PIAUÍ (Município de Valença do Piauí), Fazenda Olho da Agua, 2 km N of Valença do Piauí (1).

Pteronotus parnellii (Gray, 1843)

Absent from the Chapada do Araripe and the Caatingas. Netted only in a mesic Caatinga-Cerrado contact zone in Piauí.

Specimens collected.—PIAUÍ (Município de Valença do Piauí), Fazenda Olho da Agua, 2 km N of Valença do Piauí (2).

Pteronotus personatus (Wagner, 1843)

Absent from the Chapada do Araripe; present, but rare, in some localities of the Caatingas. In all cases it has been netted near streams or lakes.

Specimens collected.—PERNAMBUCO (Município de Serra Talhada), Fazenda Saco (I.P.A.), 6.6 km NNE of Serra Talhada (1). PIAUÍ (Município de Valença do Piauí), Fazenda Olho da Agua, 2 km N of Valença do Piauí (3).

Family Phyllostomatidae

Subfamily Phyllostomatinae

Micronycteris minuta (Gervais, 1855)

Specimens collected.—CEARÁ (Município de Crato), Floresta Naçional Araripe-Apodí, 9 km S of Crato (1); Floresta Naçional Araripe-Apodí, 8 km SSW of Crato (1). PERNAMBUCO (Município de Exu), Fazenda Cantareno, 4.5 km NNE of Exu (2); Serrote das Lajes, 17 km S of Exu (5); Serrote Gamba, 19 km SSW of Exu (1); (Município de São Lourenço da Mata), Estação Ecológica do Tapacurá (1).

Micronycteris sp.

Rare in the Caatingas where it was usually captured near serrotes or lajeiros. Rare on the Chapada do Araripe. This group of specimens appears not to conform in detail with the presently recognized species in the genus; further analysis is required to define the systematic affinities of this collection.

Specimens collected.—CEARÁ (Município de Crato), Floresta Naçional Araripe-Apodí, 8 km SSW of Crato (1); Sitio Luanda (Itaiteira), 4 km S of Crato (1); (Município de Nova Olinda), km 19 on Route CE 96, 4 km SE of Nova Olinda (3). PERNAMBUCO (Município de Exu), Fazenda Alto de Ferreira, 5 km SW of Exu (2); Fazenda Cantareno, 4.5 km NNE of Exu (1); Fazenda Pomonha, 21 km SSW of Exu (5); Serrote das Lajes, 17 km S of Exu (2).

Lonchorhina aurita Tomes, 1863

Absent from the Chapada do Araripe and the Caatingas. Present in areas of the Caatinga-Cerrado contact zone in Piauí.

Specimen collected.—PIAUÍ (Município de Valença do Piauí), Fazenda Olho da Agua, 2 km N of Valença do Piauí (1).

Tonatia bidens (Spix, 1823)

Absent from the Chapada do Araripe. Distribution primarily restricted to serrotes in the Caatingas.

Specimens collected.—PERNAMBUCO (Município de Exu), Fazenda Maniçoba, 13.7 km SSW of Exu (5); Fazenda Pomonha, 21 km SSW of Exu (5); Serrote das Lajes, 17 km S of Exu (8); Serrote das Lajes, 17.7 km S of Exu (21); Serrote Gamba, 19 km SSW of Exu (6); Serrote Gritadeira, 18 km SSW of Exu (4).

Tonatia brasiliense (Peters, 1866b)

Absent from the Chapada do Araripe. Uncommon in the Caatingas where it is found either in Caatinga Alta habitats or near serrotes.

Specimens collected.—PERNAMBUCO (Município de Exu), Fazenda Batente, 5.5 km SE of Exu (1); Fazenda Cantareno, 4.5 km NNE of Exu (2); Fazenda Guarani, 2.9 km N of Exu (1); Serrote Gritadeira, 18 km SSW of Exu (2).

Mimon crenulatum (E. Geoffroy, 1810)

Rare in the Caatingas where it is found almost exclusively in Caatinga Alta habitats. Absent from the Chapada do Araripe.

Specimens collected.—PERNAMBUCO (Município de Exu), Fazenda Cantareno, 4.5 km NNE of Exu (3); Fazenda Colônia, 5.5 km S of Exu (1); Fazenda Paus Grandes, 14.2 km E of Exu (3).

Phyllostomus discolor (Wagner, 1843)

Locally common in banana and mango orchards in the Caatingas. Abundant and widespread throughout both Cerrado and Cerradão habitats of the Chapada do Araripe. It feeds primarily on fruits, although at least part of the year it appears to be nectarivorous and/or pollenivorous.

Specimens collected.—CEARÁ (Município de Crato), Aeroporto de Crato, 10 km SW of Crato (3); Floresta Naçional Araripe-Apodí, 8 km S of Crato (7); Floresta Naçional Araripe-Apodí, 9 km S of Crato (113); Floresta Naçional Araripe-Apodí, 10 km SSW of Crato (3); Floresta Naçional Araripe-Apodí, 11 km SSW of Crato (1); Floresta Naçional Araripe-Apodí, 13 km SSW of Crato (5); Floresta Naçional Araripe-Apodí, 17 km SSW of Crato (18); Floresta Naçional Araripe-Apodí, 21 km SSW of Crato (1); Floresta Naçional Araripe-Apodí, 10 km SW of Crato (14). PERNAMBUCO (Município de Exu), Fazenda Alto de Ferreira, 5 km SW of Exu (1); Fazenda Bom Jesus, 8 km NNW of Exu (11); Fazenda Maniçoba, 13.7 km SSW of Exu (9); Fazenda São José, 1.5 km N of Exu (4); Serrote das Lajes, 17 km S of Exu (1); Serrote das Lajes, 17.7 km S of Exu (1); Serrote Gambá, 19 km SSW of Exu (3); Serrote Gritadeira, 18 km SSW of Exu (1). PIAUÍ (Município de Valença do Piauí), Fazenda Olho da Agua, 2 km N of Valença do Piauí (1).

Phyllostomus hastatus (Pallas, 1767)

Occasionally present in the Caatingas, but probably a transient from the Chapada do Araripe. Widespread and common throughout the Chapada in both Cerrado and Cerradão habitats. A colony of over 100 individuals of both sexes was found roosting inside an archway at the entrance to the Colégio Agrícola de Crato. The diet appears to be primarily frugivorous, although some insect remains were observed in its feces.

Specimens collected.—BAHIA (Município de Juazeiro da Bahia), Fazenda Barrinha (2). CEARÁ (Município de Crato), Colégio Agrícola de Crato, 5 km W of Crato (102); Floresta Naçional Araripe-Apodí, 8 km S of Crato (1); Floresta Naçional Araripe-Apodí, 13 km SSW of Crato (3); Floresta Naçional Araripe-Apodí, 17 km SSW of Crato (1); Floresta Naçional Araripe-Apodí, 9 km SW of Crato (1); Floresta Naçional Araripe-Apodí, 10 km SW of Crato (16); Floresta Naçional Araripe-Apodí, 9 km W of Crato (1); Floresta Naçional Araripe-Apodí, 10 km W of Crato (2). PERNAMBUCO (Município de Exu), Fazenda Bom Jesus, 0.8 km NNW of Exu (1); Fazenda Colônia, 5.5 km S of Exu (1); Serrote das Lajes, 17 km S of Exu (1); Serrote Gambá, 19 km SSW of Exu (1); (Município de São Lourenço da Mata), Estação Ecológico do Tapacurá (3).

Trachops cirrhosus (Spix, 1823)

Absent from the Chapada do Araripe. Distribution in the Caatingas restricted to serrotes or areas containing rocky outcroppings.

Specimens collected.—BAHIA (Município de Juazeiro da Bahia), Fazenda São Raimundo, km 216 on Route BA 130 (1). PERNAMBUCO (Município de Exu), Fazenda Batente, 5.5 km SE of Exu (5); Fazenda Colônia, 5.5 km S of Exu (1); Fazenda Guaraní, 2.9 km N of Exu (3); Serrote das Lajes, 17 km S of Exu (26); Serrote das Lajes, 17.7 km S of Exu (1); Serrote Gritadeira, 18 km SSW of Exu (2).

Subfamily Glossophaginae

Glossophaga soricina (Pallas, 1766)

Abundant and ubiquitous in Cerrado, Cerradão, and most habitats of the Caatingas. At times found roosting with *Carollia perspicillata* in caves and man-made structures. Present in all other major vegetation zones of the Northeast.

Specimens collected.—BAHIA (Município de Senhor do Bom Fim), Fazenda Flamengo, km 150 on Route BA 130 (1); Fazenda Morro da Imburana, km 145 on Route BA 130 (1). CEARÁ (Município de Crato), Aeroporto de Crato, 10 km SW of Crato (14); Colégio Agrícola de Crato, 5 km W of Crato (285); Fazenda Fundão, 3 km SSE of Crato (11); Floresta Naçional Araripe-Apodí, 8 km S of Crato (21); Floresta Naçional Araripe-Apodí, 9 km S of Crato (52); Floresta Naçional Araripe-Apodí, 8 km SSW of Crato (25); Floresta Naçional Araripe-Apodí, 10 km SSW of Crato (10); Floresta Naçional Araripe-Apodí, 11 km SSW of Crato (1); Floresta Naçional Araripe-Apodí, 13 km SSW of Crato (35); Floresta Naçional Araripe-Apodí, 17 km SSW of Crato (3); Floresta Naçional Araripe-Apodí, 21 km SSW of Crato (3); Floresta Naçional Araripe-Apodí, 9 km SW of Crato (1); Floresta Naçional Araripe-Apodí, 10 km SW of Crato (18); Floresta Naçional Araripe-Apodí, 11 km SW of Crato (3); Floresta Naçional Araripe-Apodí, 14 km SW of Crato (10); (Município de Nova Olinda), km 19 on Route CE 96, 4 km SE of Nova Olinda (9). PERNAMBUCO (Município de Exu), Escola Agrícola de Exu, 0.7 km S of Exu (236); Fazenda Barracão, 19.8 km SW of Exu (2); Fazenda Batente, 5.5 km SE of Exu (3); Fazenda Bom Jesus, 0.8 km NNW of Exu (23); Fazenda Colônia, 5.5 km S of Exu (1); Fazenda Guarani, 2.9 km N of Exu (3); Fazenda Maniçoba, 13.7 km SSW of Exu (3); Fazenda Pomonha, 21 km SSW of Exu (13); Fazenda São José, 1.5 km N of Exu (22); Serrote das Lajes, 17 km S of Exu (22); Serrote das Lajes, 17.7 km S of Exu (3); Serrote Gamba, 19 km SSW of Exu (5); Serrote Gritadeira, 18 km SSW of Exu (12); (Município de São Lourenço da Mata) Estação Ecológico do Tapacurá (13); (Município de Serra Talhada), Fazenda Salto, 35 km NNE of Serra Talhada (1). PIAUÍ (Município de Teresina), km 18 on Route BR 316 (1); (Município de Valença do Piauí), Fazenda Olho da Agua, 2 km N of Valença do Piauí (2); (Watering hole), 5 km W of Valença do Piauí (1).

Lonchophylla mordax Thomas, 1903

Common in the Caatingas, especially near serrotes. Absent from Cerradão and Cerrado habitats of the Chapada do Araripe.

Specimens collected.—BAHIA (Município de Juazeiro da Bahia), Fazenda São Raimundo, km 216 on Route BA 130, (1). CEARÁ (Município de Nova Olinda), km 19 on Route CE 96, 4 km SE of Nova Olinda (9). PERNAMBUCO (Município de Exu), Fazenda

Cantareno, 4.5 km NE of Exu (1); Fazenda Colônia, 5.5 km S of Exu (2); Fazenda Guaraní, 2.9 km N of Exu (1); Fazenda Maniçoba, 13.7 km SSW of Exu (2); Fazenda Pomonha, 21 km SSW of Exu (9); Serrote das Lajes, 17 km S of Exu (41); Serrote das Lajes, 17.7 km S of Exu (6); Serrote Gambá, 19 km SSW of Exu (5); Serrote Gritadeira, 18 km SSW of Exu (5).

Anoura geoffroyi Gray, 1838

Uncommon in the Caatingas where it is usually associated with serrote habitats. Locally abundant in more open areas of Cerradão or in the Cerrado areas of the Chapada do Araripe.

Specimens collected.—CEARÁ (Município de Crato), Floresta Naçional Araripe-Apodí, 8 km S of Crato (1); Floresta Naçional Araripe-Apodí, 9 km S of Crato (3); Floresta Naçional Araripe-Apodí, 8 km SSW of Crato (59); Floresta Naçional Araripe-Apodí, 10 km SSW of Crato (1); Floresta Naçional Araripe-Apodí, 21 km SSW of Crato (1); Floresta Naçional Araripe-Apodí, 11 km SW of Crato (1); Floresta Naçional Araripe-Apodí, 10 km W of Crato (1); Sítio Luanda (Itaiteira), 4 km S of Crato (1); (Município de Nova Olinda), km 19 on Route CE 96, 4 km SE of Nova Olinda (23). PERNAMBUCO (Município de Exu), Escola Agrícola de Exu, 0.7 km S of Exu (1); Fazenda Bom Jesus, 0.8 km NNW of Exu (4); Fazenda Pomonha, 21 km SSW of Exu (10); Fazenda São José, 1.5 km N of Exu (1); Serrote das Lajes, 17 km S of Exu (1); Serrote das Lajes, 17.7 km S of Exu (1).

Subfamily Carolliinae

Carollia perspicillata (Linnaeus, 1758)

Abundant and ubiquitous in all habitats of the Caatingas, Cerrado, and Cerradão. Present in all other major vegetation zones. Found roosting in both man-made structures and caves, sometimes in association with *Glossophaga soricina*.

Specimens collected.—CEARÁ (Município de Crato), Aeroporto de Crato, 10 km SW of Crato (19); Colégio Agrícola de Crato, 5 km W of Crato (19); Fazenda Fundão, 3 km SSE of Crato (1); Floresta Naçional Araripe-Apodí, 8 km S of Crato (51); Floresta Naçional Araripe-Apodí, 9 km S of Crato (181); Floresta Naçional Araripe-Apodí, 8 km SSW of Crato (58); Floresta Naçional Araripe-Apodí, 10 km SSW of Crato (37); Floresta Naçional Araripe-Apodí, 13 km SSW of Crato (22); Floresta Naçional Araripe-Apodí, 17 km SSW of Crato (23); Floresta Naçional Araripe-Apodí, 21 km SSW of Crato (7); Floresta Naçional Araripe-Apodí, 9 km SW of Crato (16); Floresta Naçional Araripe-Apodí, 10 km SW of Crato (120); Floresta Naçional Araripe-Apodí, 11 km SW of Crato (12); Floresta Naçional Araripe-Apodí, 9 km W of Crato (36); (Município de Nova Olinda), km 19 on Route CE 96, 4 km SE of Nova Olinda (1). PERNAMBUCO (Município de Exu), Escola Agrícola de Exu, 0.7 km S of Exu (10); Fazenda Alto de Ferreira, 5 km SW of Exu (1); Fazenda Cantareno, 4.5 km NNE of Exu (11); Fazenda Colônia, 5.5 km S of Exu (14); Fazenda Guaraní, 2.9 km N of Exu (5); Fazenda Maniçoba, 13.7 km SSW of Exu (22); Fazenda Paus Grandes, 14.2 km E of Exu (1); Fazenda Pomonha, 21 km SSW of Exu (26); Fazenda São José, 1.5 km N of Exu (2); Fazenda São Pedro, 1 km ESE of Exu (1); Fazenda Santa Helena, 1 km NE of Exu (1); Serrote das Lajes, 17 km S of Exu (108); Serrote das Lajes, 17.7 km S of Exu (35); Serrote Gambá, 19 km SSW of Exu (5); Serrote Gritadeira, 18 km SSW of Exu (28); (Município de São Lourenço da Mata), Estação Ecológico do Tapacurá (19). PIAUÍ (Município de Teresina), km 18 on

Route BR 316 (9); (Município de Valença do Piauí), Fazenda Olho da Agua, 2 km N of Valença do Piauí (15).

Subfamily Sturnirinae

Sturnira lilium (E. Geoffroy, 1810)

Uncommon in the Caatingas where it is primarily restricted to Caatinga Alta habitats. Uncommon in both Cerradão and Cerrado habitats of the Chapada do Araripe.

Specimens collected.—CEARÁ (Município de Crato), Aeroporto de Crato, 10 km SW of Crato (2); Floresta Naçional Araripe-Apodí, 9 km S of Crato (4); Floresta Naçional Araripe-Apodí, 8 km SSW of Crato (7); Floresta Naçional Araripe-Apodí, 10 km SSW of Crato (1); Floresta Naçional Araripe-Apodí, 10 km SW of Crato (2); Floresta Naçional Araripe-Apodí, 11 km SW of Crato (4); Floresta Naçional Araripe-Apodí, 9 km W of Crato (1); Sítio Luanda (Itaiteira), 4 km S of Crato (9). PERNAMBUCO (Município de Exu), Fazenda Batente, 5.5 km SE of Exu (1); Fazenda Cantareno, 4.5 km NNE of Exu (3); Fazenda Maniçoba, 13.7 km SSW of Exu (3); (Município de São Lourenço da Mata), Estação Ecológico do Tapacurá (4).

Subfamily Stenodermatinae

Uroderma bilobatum Peters, 1866*a*

Very rare both in the Caatingas and on the Chapada do Araripe.

Specimens collected.—CEARÁ (Município de Crato), Floresta Naçional Araripe-Apodí, 8 km SSW of Crato (1); Floresta Naçional Araripe-Apodí, 11 km SW of Crato (1). PERNAMBUCO (Município de Exu), Açude Itamaragí, 0.5 km S of Exu (1); Fazenda Pomonha, 21 km SSW of Exu (1).

Uroderma magnirostrum Davis, 1968

Specimen collected.—PIAUÍ (Município de Terezina), km 18 on Route BR 316 (1).

Vampyrops lineatus (E. Geoffroy, 1810)

Very abundant and widespread in both Caatingas and Chapada habitats. In the Caatingas, it has been found roosting in caves in groups of no more than 12 individuals.

Specimens collected.—CEARÁ (Município de Crato), Aeroporto de Crato, 10 km SW of Crato (31); Colégio Agrícola de Crato, 5 km W of Crato (18); Floresta Naçional Araripe-Apodí, 8 km S of Crato (4); Floresta Naçional Araripe-Apodí, 9 km S of Crato (18); Floresta Naçional Araripe-Apodí, 8 km SSW of Crato (35); Floresta Naçional Araripe-Apodí, 10 km SSW of Crato (43); Floresta Naçional Araripe-Apodí, 13 km SSW of Crato (6); Floresta Naçional Araripe-Apodí, 17 km SSW of Crato (16); Floresta Naçional Araripe-Apodí, 21 km SSW of Crato (8); Floresta Naçional Araripe-Apodí, 9 km SW of Crato (4); Floresta Naçional Araripe-Apodí, 10 km SW of Crato (9); Floresta Naçional Araripe-Apodí, 11 km SW of Crato (20); Floresta Naçional Araripe-Apodí, 9 km W of Crato (6); Sítio Luanda (Itaiteira), 4 km S of Crato (10); (Município de Nova Olinda), km 19 on Route CE 96, 4 km SE of Nova Olinda (6). PERNAMBUCO (Município de Exu), Escola Agrícola de Exu, 0.7 km S of Exu (4); Fazenda Batente, 5.5 km SE of Exu (4); Fazenda Bom Jesus, 0.8 km NNW of Exu (8); Fazenda Cantareno, 4.5 km

NNE of Exu (2); Fazenda Colônia, 5.5 km S of Exu (4); Fazenda Gravata, 3.1 km NW of Exu (2); Fazenda Guaraní, 2.9 km N of Exu (16); Fazenda Maniçoba, 13.7 km SSW of Exu (9); Fazenda Pomonha, 21 km SSW of Exu (49); Fazenda São José, 1.5 km N of Exu (42); Fazenda Santa Helena, 1 km NE of Exu (8); Serrote das Lajes, 17 km S of Exu (108); Serrote das Lajes, 17.7 km S of Exu (20); Serrote Gambá, 19 km SSW of Exu (13); Serrote Gritadeira, 18 km SSW of Exu (13).

Artibeus cinereus (Gervais, 1856)

Absent from habitats in both the Caatingas and the Chapada do Araripe. Present in remnant Atlantic Tropical Forest and in palm groves.

Specimens collected.—PERNAMBUCO (Município de São Lourenço da Mata), Estação Ecológico do Tapacurá (6). PIAUÍ (Município de Teresina), km 18 on Route BR 316 (5).

Artibeus concolor Peters, 1865*a*

Present but rare on the Chapada do Araripe in Cerrado habitats. Absent from all habitats of the Caatingas.

Specimens collected.—CEARÁ (Município de Crato), Aeroporto de Crato, 10 km SW of Crato (1); Floresta Naçional Araripe-Apodí, 8 km SSW of Crato (3); Floresta Naçional Araripe-Apodí, 10 km SSW of Crato (3); Floresta Naçional Araripe-Apodí, 10 km SW of Crato (4); Floresta Naçional Araripe-Apodí, 11 km SW of Crato (1).

Artibeus fuliginosus Gray, 1838

Present in palm groves but absent from all habitats of the Caatingas and Chapada do Araripe.

Specimen collected.—PIAUÍ (Município de Teresina), km 18 on Route BR 316 (1).

Artibeus jamaicensis Leach, 1821

Abundant and ubiquitous in both Cerrado and Cerradão habitats; present throughout the Caatingas but locally abundant on, or near, serrotes. Present in all other major vegetation zones.

Specimens collected.—BAHIA (Município de Juazeiro da Bahia), Fazenda Barrinha (5); Fazenda São Raimundo, km 216 on Route BA 130 (1). CEARÁ (Município de Crato), Colégio Agrícola de Crato, 5 km W of Crato (10); Floresta Naçional Araripe-Apodí, 8 km S of Crato (37); Floresta Naçional Araripe-Apodí, 9 km S of Crato (66); Floresta Naçional Araripe-Apodí, 8 km SSW of Crato (1); Floresta Naçional Araripe-Apodí, 10 km SSW of Crato (50); Floresta Naçional Araripe-Apodí, 11 km SSW of Crato (1); Floresta Naçional Araripe-Apodí, 13 km SSW of Crato (3); Floresta Naçional Araripe-Apodí, 17 km SSW of Crato (8); Floresta Naçional Araripe-Apodí, 21 km SSW of Crato (3); Floresta Naçional Araripe-Apodí, 10 km SW of Crato (11); Floresta Naçional Araripe-Apodí, 11 km SW of Crato (4); Floresta Naçional Araripe-Apodí, 9 km W of Crato (5); Sítio Luanda (Itaiteira), 4 km S of Crato (5); (Município de Nova Olinda), km 19 on Route CE 96, 4 km SE of Nova Olinda (9). PERNAMBUCO (Município de Exu), Escola Agrícola de Exu, 0.7 km S of Exu (1); Fazenda Alto de Ferreira, 5 km SW of Exu (1); Fazenda Cantareno, 4.5 km NNE of Exu (5); Fazenda Colônia, 5.5 km S of Exu (4);

Fazenda Guaraní, 2.9 km N of Exu (4); Fazenda Pomonha, 21 km SSW of Exu (44); Fazenda São José, 1.5 km N of Exu (2); Serrote das Lajes, 17 km S of Exu (79); Serrote das Lajes, 17.7 km S of Exu (34); Serrote Gamba, 19 km SSW of Exu (5); Serrote Gritadeira, 18 km SSW of Exu (28); (Município de São Lourenço da Mata), Estação Ecológico do Tapacurá (23). PIAUÍ (Município de Teresina), km 18 on Route BR 316 (2); (Município de Valença do Piauí), Fazenda Olho da Agua, 2 km N of Valença do Piaui (17).

Artibeus lituratus (Olfers, 1818)

Abundant and widespread on the Chapada do Araripe in both Cerradão and Cerrado habitats. Widespread, but uncommon, throughout the Caatingas. Present in remnant Atlantic Forest and palm grove habitats.

Specimens collected.—CEARÁ (Município de Crato), Aeroporto de Crato, 10 km SW of Crato (24); Floresta Naçional Araripe-Apodí, 8 km S of Crato (24); Floresta Naçional Araripe-Apodí, 9 km S of Crato (43); Floresta Naçional Araripe-Apodí, 8 km SSW of Crato (8); Floresta Naçional Araripe-Apodí, 10 km SSW of Crato (5); Floresta Naçional Araripe-Apodí, 13 km SSW of Crato (8); Floresta Naçional Araripe-Apodí, 17 km SSW of Crato (14); Floresta Naçional Araripe-Apodí, 21 SSW of Crato (12); Floresta Naçional Araripe-Apodí, 9 km SW of Crato (5); Floresta Naçional Araripe-Apodí, 10 km SW of Crato (90); Floresta Naçional Araripe-Apodí, 11 km SW of Crato (16); Floresta Naçional Araripe-Apodí, 14 km SW of Crato (1); Floresta Naçional Araripe-Apodí, 19 km SW of Crato (1); Floresta Naçional Araripe-Apodí, 9 km W of Crato (25); (Município de Nova Olinda), km 19 on Route CE 96, 4 km SE of Nova Olinda (2). PERNAMBUCO (Município de Exu), Escola Agrícola de Exu, 0.7 km S of Exu (2); Fazenda Bom Jesus, 0.8 km NNW of Exu (2); Fazenda Cantareno, 4.5 km NNE of Exu (9); Fazenda Guarani, 2.9 km N of Exu (12); Fazenda Maniçoba, 13.7 km SSW of Exu (2); Fazenda Paus Grandes, 14.2 km E of Exu (2); Fazenda Pomonha, 21 km SSW of Exu (11); Fazenda São José, 1.5 km N of Exu (3); Serrote das Lajes, 17 km S of Exu (2); Serrote Gamba, 19 km SSW of Exu (2); (Município de São Lourenço da Mata), Estação Ecológico do Tapacurá (2). PIAUÍ (Município de Teresina), km 18 on Route BR 316 (4).

Subfamily Desmodontinae

Desmodus rotundus (E. Geoffroy, 1810)

Common in the Caatingas where it is locally abundant on serrotes. Rare on the Chapada do Araripe, perhaps due to the paucity of livestock.

Specimens collected.—BAHIA (Município de Senhor do Bom Fim), Morro da Imburana, km 145 on Route BA 130 (1). CEARÁ (Município de Crato), Floresta Naçional Araripe-Apodí, 8 km S of Crato (1); Floresta Naçional Araripe-Apodí, 9 km S of Crato (4); Floresta Naçional Araripe-Apodí, 8 km SSW of Crato (2); Floresta Naçional Araripe-Apodí, 10 km SSW of Crato (1); Floresta Naçional Araripe-Apodí, 13 km SSW of Crato (1); Floresta Naçional Araripe-Apodí, 17 km SSW of Crato (3); Floresta Naçional Araripe-Apodí, 10 km SW of Crato (1); (Município de Nova Olinda), km 19 on Route CE 96, 4 km SE of Nova Olinda (32). PERNAMBUCO (Município de Exu), Fazenda Alto de Ferreira, 5 km SW of Exu (3); Fazenda Batente, 5.5 km SE of Exu (2); Fazenda Bom Jesus, 0.8 km NNW of Exu (3); Fazenda Cantareno, 4.5 km NNE of Exu (1); Fazenda Maniçoba, 13.7 km SSW of Exu (73); Fazenda Paus Grandes, 14.2 km E of Exu (4);

Fazenda Pomonha, 21 km SSW of Exu (2); Serrote das Lajes, 17 km S of Exu (49); Serrote das Lajes, 17.7 km S of Exu (225); Serrote Gamba, 19 km SSW of Exu (4); Serrote Gritadeira, 18 km SSW of Exu (5); (Município de São Lourenço da Mata), Estação Ecológico do Tapacurá (5).

Diaemus youngii (Jentink, 1893)

Absent from both Caatinga and Chapada habitats. Present in remnant Atlantic Rain Forest.

Specimen collected.—PERNAMBUCO (Município de São Lourenço da Mata), Estação Ecológico do Tapacurá (1).

Diphylla ecaudata Spix, 1823

Rare in the Caatingas; absent from the Chapada do Araripe.

Specimens collected.—PERNAMBUCO (Município de Exu), Fazenda Maniçoba, 13.7 km SSW of Exu (2); Serrote das Lajes, 17 km S of Exu (1); Serrote Gritadeira, 18 km SSW of Exu (1).

Family Natalidae

Natalus stramineus Gray, 1838

Rare on the Chapada do Araripe; absent from the Caatingas.

Specimens collected.—CEARÁ (Município de Crato), Floresta Naçional Araripe-Apodí, 8 km S of Crato (2); Floresta Naçional Araripe-Apodí, 9 km S of Crato (1).

Family Furipteridae

Furipterus horrens (F. Cuvier, 1828)

Absent from the Chapada do Araripe. Rare in the Caatingas, where it was only captured on serrotes. Flies at dusk.

Specimens collected.—PERNAMBUCO (Município de Exu), Serrote das Lajes, 17 km S of Exu (1); Serrote das Lajes, 17.7 km S of Exu (1).

Family Vespertilionidae

Myotis nigricans (Schinz, 1821)

Rare to common in both Caatinga and Chapada habitats where it was found to roost in buildings under roofing tiles.

Specimens collected.—CEARÁ (Município de Crato), Aeroporto de Crato, 10 km SW of Crato (9); Floresta Naçional Araripe-Apodí, 9 km S of Crato (13); Floresta Naçional Araripe-Apodí, 8 km SSW of Crato (10); Floresta Naçional Araripe-Apodí, 11 km SSW of Crato (1); Floresta Naçional Araripe-Apodí, 13 km SSW of Crato (2); Floresta Naçional Araripe-Apodí, 17 km SSW of Crato (1); Floresta Naçional Araripe-Apodí, 10 km SW of Crato (12); Sítio Luanda (Itaiteira), 4 km S of Crato (8). PERNAMBUCO (Município de Exu), Escola Agrícola de Exu, 0.7 km S of Exu (184); Fazenda Batente, 5.5 km SE of Exu (11); Fazenda Bom Jesus, 0.8 km NNW of Exu (1); Fazenda Cantareno, 4.5 km NNE of Exu (5); Fazenda Pomonha, 21 km SSW of Exu (1); Fazenda São José, 1.5 km

N of Exu (2); Serrote das Lajes, 17 km S of Exu (2); (Município de São Lourenço da Mata), Estação Ecológico do Tapacurá (3); (Município de Serra Talhada), Fazenda Saco (I.P.A.), 6.6 km NNE of Serra Talhada (2).

Eptesicus furinalis D'Orbigny and Gervais, 1847

Absent from the Caatingas. Present on the Chapada do Araripe where it is found roosting in buildings.

Specimens collected.—CEARÁ (Município de Crato), Aeroporto de Crato, 10 km SW of Crato (2); Floresta Naçional Araripe-Apodí, 9 km S of Crato (4); Floresta Naçional Araripe-Apodí, 10 km SW of Crato (16); Floresta Naçional Araripe-Apodí, 11 km SW of Crato (1).

Rhogeessa tumida H. Allen, 1866

Absent from habitats of the Chapada do Araripe and from the Caatingas in the vicinity of Exu, Pernambuco.

Specimen collected.—BAHIA (Município de Juazeiro da Bahia), Fazenda São Raimundo, km 216 on Route BA 130 (1).

Lasiurus borealis (Müller, 1776)

Absent from the Caatingas; rare on the Chapada do Araripe.

Specimens collected.—CEARÁ (Município de Crato), Aeroporto de Crato, 10 km SW of Crato (1); Floresta Naçional Araripe-Apodí, 9 km S of Crato (2); Floresta Naçional Araripe-Apodí, 10 km SW of Crato (2); Floresta Naçional Araripe-Apodí, 9 km W of Crato (5).

Lasiurus ega (Gervais, 1856)

Present, but rare, in both Caatinga and Chapada habitats.

Specimens collected.—CEARÁ (Município de Crato), Aeroporto de Crato, 10 km SW of Crato (1); Floresta Naçional Araripe-Apodí, 10 km SW of Crato (1). PERNAMBUCO (Município de Exu), Fazenda Batente, 5.5 km SE of Exu (1); Fazenda Bom Jesus, 0.8 km NNW of Exu (3); Fazenda São José, 1.5 km N of Exu (1). PIAUÍ (Município de Valença do Piauí), Fazenda Olho da Agua, 2 km N of Valença do Piauí (1).

Family Molossidae

Molossops abrasus (Temminck, 1826)

Absent from both the Chapada do Araripe and the Caatingas. Present in the Caatinga-Cerrado contact zone of Piauí.

Specimens collected.—PIAUÍ (Município de Valença do Piauí), Fazenda Olho da Agua, 2 km N of Valença do Piauí (3).

Molossops greenhalli (Goodwin, 1958)

Absent from both Caatinga and Chapada habitats. Present in remnant Atlantic Rain Forest.

Specimen collected.—PERNAMBUCO (Município de São Lourenço da Mata), Estação Ecológico do Tapacurá (1).

Molossops planirostris (Peters, 1865)

Rare in the Caatingas; absent from the Chapada do Araripe.

Specimens collected.—PERNAMBUCO (Município de Exu), Fazenda Pau Ferrado, 2.6 km E of Exu (3).

Molossops teminckii (Burmeister, 1854)

Rare in the Caatingas, caught exclusively on serrotes or near rocky outcroppings. Most active at dusk and early evening.

Specimens collected.—CEARÁ (Município de Crato), Floresta Naçional Araripe-Apodí, 9 km S of Crato (4); Floresta Naçional Araripe-Apodí, 10 km SSW of Crato (2); Floresta Naçional Araripe-Apodí, 8 km SSW of Crato (1). PERNAMBUCO (Município de Exu), Fazenda Batente, 5.5 km SE of Exu (2); Serrote Gambá, 19 km SSW of Exu (2).

Neoplatymops mattogrossensis (Vieira, 1942)

Absent from the Chapada do Araripe. Common in rocky habitats and on serrotes in the Caatingas. Roosts in low-lying rock crevices; flies at dusk and early evening.

Specimens collected.—PERNAMBUCO (Município de Exu), Fazenda Batente, 5.5 km SE of Exu (23); Fazenda Cantareno, 4.5 km NNE of Exu (11); Fazenda Maniçoba, 13.7 km SSW of Exu (5); Fazenda Pinheira, 1.5 km SW of Exu (1); Fazenda Pomonha, 21 km SSW of Exu (1); Serrote Gambá, 19 km SSW of Exu (3); Serrote Gritadeira, 18 km SSW of Exu (8).

Tadarida laticaudata (Geoffroy, 1805)

Specimens collected.—PERNAMBUCO (Município de Exu), Escola Agrícola de Exu, 0.7 km S of Exu (3).

Tadarida sp.

Specimens collected.—CEARÁ (Município de Crato), Floresta Naçional Araripe-Apodí, 9 km W of Crato (1).

Eumops sp.

Absent from the Chapada do Araripe and the Caatingas. Present in the Caatinga-Cerrado contact zone of Piauí.

Specimen collected.—PIAUÍ (Município de Valença do Piauí), (Watering hole), 5 km W of Valença do Piauí (1).

Molossus ater (E. Geoffroy, 1805)

Rare in the Caatingas.

Specimens collected.—CEARÁ (Município de Nova Olinda), km 19 on Route CE 96, 4 km SE of Nova Olinda (1). PERNAMBUCO (Município de Exu), Fazenda Batente, 5.5 km SE of Exu (1); Fazenda Guaraní, 2.9 km N of Exu (1). PIAUÍ (Município de Valença do Piauí), Fazenda Olho da Agua, 2 km N of Valença do Piauí (1); (Watering hole), 5 km W of Valença do Piaui (3).

Molossus molossus (Pallas, 1766)

More or less common in both the Caatingas and Chapada habitats. It may, however, be locally abundant in either habitat near man-made structures which it utilizes as roosts.

Specimens collected.—CEARÁ (Município de Crato), Aeroporto de Crato, 10 km SW of Crato (11); Colégio Agrícola de Crato, 5 km W of Crato (138); Floresta Naçional Araripe-Apodí, 10 km SW of Crato (4). PERNAMBUCO (Município de Exu), Escola Agrícola de Exu, 0.7 km S of Exu (62); Fazenda Batente, 5.5 km SE of Exu (1); Serrote das Lajes, 17 km S of Exu (1); (Município de Serra Talhada), Fazenda Saco (I.P.A.), 6.6 km NNE of Serra Talhada (45). PIAUÍ (Município de Valença do Piauí), Fazenda Olho da Agua, 2 km N of Valença do Piauí (13); (Watering hole), 5 km W of Valença do Piaui (2).

Promops sp.

Very rare in the Caatingas; found only in association with man-made structures. Absent from the Chapada do Araripe.

Specimens collected.—PERNAMBUCO (Município de Exu), Cidade de Exu (1); Escola Agrícola de Exu, 0.7 km S of Exu (2).

Order Primates

Family Cebidae

Cebus apella Linnaeus, 1758

In general, *C. apella* is currently restricted to the more extensive, remnant pockets of Caatinga Alta. In the past, this species probably occurred in areas with riverine vegetation and palm forests (associated with the higher serrotes) which are contiguous with high Caatinga.

Specimens collected.—PERNAMBUCO (Município de Exu), Fazenda Cantareno, 4.5 km NNE of Exu (3).

Family Callithricidae

Callithrix jacchus Linnaeus, 1758

This species may be locally abundant in the remaining pockets of Caatinga Alta which also harbor *Cebus apella* and in smaller pockets where *Cebus* is absent. The ability to utilize Caatinga Baixa to some extent accounts in part for the greater abundance of *C. jacchus*. Laboratory specimens accepted various insects and fruits as food.

Specimens collected.—PERNAMBUCO (Município de Exu), Escola Agrícola de Exu, 0.7 km S of Exu (2); Fazenda Paus Grande, 14.2 km E of Exu (1); Fazenda Cantareno, 4.5 km NNE of Exu (8).

Specimens examined.—ALAGOAS (Manga Beiras), Usina Sinimbu (3); (Quebrangulo), Engenho Riachão (1). BAHIA (No locality), (1); (Rio Preto), Santa Rita de Cassia (1). CEARÁ (Crato), Chapada Araripe (1); (Pacoti), Sítio Alvoredo (1); Sítio Baixa Verde (3); Sítio Boa Vista (1); Sítio Coati (1); Sítio Flor (3); Sítio Goiabeira (2); Sítio Lorena (2); Sítio Mendoza (1); Sítio Umquaiana (5).

Order Edentata

Family Myrmecophagidae

Tamandua tetradactyla Linnaeus, 1758

Occurs primarily in pockets of Caatinga Alta and in the Cerrado portions of the Chapada do Araripe. Its distribution in the Caatingas is limited due to heavy hunting pressure.

Specimens collected.—PERNAMBUCO (Município de Exu), Fazenda Cantareno, 4.5 km NNE of Exu (2); Município de Exu (1).

Family Dasypodidae

Euphractus sexcinctus Linnaeus, 1758

This armadillo may be found in a wider range of habitats and soil types than *Dasypus* and may even extend onto the bases of rocky serrotes. It is not as readily eaten as is *Dasypus*, and thus it experiences less hunting pressure.

Specimen collected.—PERNAMBUCO (Município de Exu), Município de Exu (1).

Dasypus novemcinctus Linnaeus, 1758

Uncommon in Caatingas and Cerrado habitats due to heavy hunting pressures. In protected areas, such as the Floresta Naçional Araripe-Apodí, it may be locally abundant. Prefers open areas with soft soils.

Specimen collected.—PERNAMBUCO (Município de Exu), Município de Exu (1).

Order Lagomorpha

Family Leporidae

Sylvilagus brasiliensis Linnaeus, 1758

The single specimen was collected in a complex area of interdigitating cultivated fields, abandoned fields of various ages and low Caatinga.

Specimen collected.—BAHIA (Município de Senhor do Bom Fim), Route BA 130 (1).

Specimens examined.—ALAGOAS (Quebrangulo), Engenho Juliana (1); (Viçosa), Fazenda São José (1). BAHIA (Campo Formosa), Fazenda Rapousa (1). PERNAMBUCO (Garanhuns), Sítio Cavaquinho (1); Sítio Inhumas (1).

Order Rodentia

Family Muridae

Subfamily Cricetinae

Oryzomys eliurus Wagner, 1845

Found in interface areas of thick brush and cultivated fields of grass with a relatively mesic microclimate. This species is less frequently encountered than *O. subflavus.*

Specimens collected.—CEARÁ (Município de Crato), Colégio Agrícola de Crato, 5 km W of Crato (1); Floresta Naçional Araripe-Apodí (2). PERNAMBUCO (Município de Exu), Município de Exu (1).

Specimens examined.—ALAGOAS (Limoeiro de Anadia), Sítio Brêu (2); (Quebrangulo), Fazenda Lagoa dos Bois (2); (Viçosa), Sítio Canárias (1); Sítio Cachoeira Grande (1); Fazenda Pedra de Fogo (4). BAHIA (Seabra), Fazenda Cochó do Malheiros (2); Fazenda Furados (8). CEARÁ (Itapagé), Sítio Bom Jesus (1); Sítio Maia (2); Sítio Trata (1); (Itapipoca), Sítio Jacú (1); (Pacoti), Sítio Boa Esperança do Lapis (2); Sítio Espinho Vermelho (2); Sítio Ouro (1). MINAS GERAIS (Belo Horizonte), Bairro Gameleira (1); Secão Formecimento Agrícola (1); (Jaboticabas) (1); (Ouro Preto) (1). PERNAMBUCO (Garanhuns), Fazenda Caldeirão (1); Sítio Canhoto (1); Sítio Capim (1); Sítio Cavaquinho (1); Sítio Frexeira (1); Sítio Jambelo (1); Sítio Lajeiro (1); Sítio Riacho Seco (1); Fazenda São Paulo (1); Fazenda Velha (1).

Oryzomys subflavus Wagner, 1842

This rodent is essentially a commensal. The distribution typically is limited to plots of sugarcane although other cultivated fields may harbor a few individuals.

Specimens collected.—CEARÁ (Município de Crato), Colégio Agrícola de Crato, 5 km W of Crato (1); Floresta Naçional Araripe-Apodí (1). PERNAMBUCO (Município de Exu), Escola Agrícola de Exu, 0.7 km S of Exu (1); Município de Exu (25); Fazenda Cana Mansa, 13.4 km SW of Exu (1); (Município de Serra Talhada), Fazenda Saco (I.P.A.), 6 km N of Serra Talhada (2); SUCAM (in the town of Triunfo), 28 km NNE of Serra Talhada (8).

Specimens examined.—ALAGOAS (Anadia), Sítio Brejo do Boi (1); (Palmeira dos Indios), Sítio Ribeiro (1); (Quebrangulo), Sítio Barro Preto (1); Sítio Olho d'Agua do Monteiro (1); Fazenda Peri-peri (1); (Santana do Ipanema), Sítio Goiabeira (1); (Viçosa), Sítio São José (1); Fazenda São Pedro (1); Sítio Tangil 2° (2). BAHIA (Feira), Fazenda Cazumba (1); Sítio Tomba (1); Fazenda Três Riachos (3); (Serrinha), Sítio Baixa d'Agua (1); Fazenda Outeiro (1); Fazenda Tiririca (8); Fazenda Umburana (1). CEARÁ (Crato), Sítio Arisco (2); Sítio Constantino (1); Sítio Crispin (1); Sítio Grangeiro (1); Sítio Passagem (2); (Guaraciaba), Sítio Mazagão (1); (Pacoti), Sítio Ladeira (1); (São Benidito), Sítio Barra (1); Sítio Chora (3); Sítio Piraguara (1). PERNAMBUCO (Garanhuns), Sítio Cajarana (1); Sítio Cavaquinho (1); Fazenda Colônia da Serra (1); Sítio Engenho do Maneão (1); Sítio Flamengo (1); Sítio Inhumas (1); Sítio Saco (1); Fazenda Serra da Pedra (1); Sítio Varzea-Ingá (1); Sítio Varzea-Redonda (1).

Rhipodomys mastacalis Lund, 1841

Specimens examined.—CEARÁ (Crato), Sítio Belo Horizonte (2); Sítio Caiano (1); Sítio Parque (1); Sítio Passagem (1); (São Benedito), Sítio Barros (1); Sítio Cantinho (1); Sítio Cegarro (1); Sítio Guaribas do Amaral (2); Sítio Macapá (1); Sítio Piraguará (3); Sítio São José da Boa Vista (1). PERNAMBUCO (Caruaru), Sítio Brejo do Buraco (3); Sítio Quandús (5); Fazenda Santa Maria (3); Sítio Serra dos Cavalos (4).

Akodon sp.

Specimens collected.—PERNAMBUCO (Município de São Lourenço da Mata), Estação Ecológico do Tapacurá (20).

Akodon arviculoides (Wagner, 1842)

Specimens examined.—ALAGOAS (Anadia), Sítio Brejo do Boi (1); (Viçosa), Fazenda Gitirana (4); Sítio Pedra da Fazenda dos Pereiras (3); Fazenda Poço-Feio (1); Sítio Timbó 2° (1). BAHIA (Serrinha), Fazenda Alagadiço Grande (1); Fazenda Europa (1); Fazenda João Congo (2); Fazenda Montanha (1); Fazendo Riacho Grande (1); Fazenda Tiririca (2). MINAS GERAIS (Conceição do Mato Dentro), Boca da Mata (2); Bocada Mulata (1); Mata do Dr. Daniel (7). PERNAMBUCO (Garanhuns), Sítio Brejo Grande (1); Sítio Camaratuba (1); Sítio Cavaquinho (3); Sítio Varzea do Ingá (3).

Bolomys lasiurus (Lund, 1841)

This species undergoes population eruptions of great magnitude at irregular intervals. Individuals inhabit cultivated (especially corn) and grass (maintained by grazing) fields or recently abandoned fields with thick ground cover. They are strictly terrestrial and sometimes construct "runways." Captive specimens were essentially omnivorous.

Specimens collected.—CEARÁ (Município do Crato), Floresta Naçional Araripe-Apodí (1). PERNAMBUCO (Município de Exu), 0.5 km SW of Exu (3); 1 km S of Exu (10); 1 km SW of Exu (4); 1.5 km S of Exu (2); 1.5 km SW of Exu (6); Escola Agrícola de Exu (AGGEU lab specimens), 0.7 km S of Exu (429); Fazenda Pinheira, 1.5 km SW of Exu (12); Município de Exu (60); Town of Exu (6); (Município de Serra Talhada), Fazenda Saco, 6 km N of Serra Talhada (10); SUCAM (in the town of Triunfo), 28 km NNE of Serra Talhada (9).

Specimens examined.—ALAGOAS (Capela), Fazenda Serra Alegre (1); (Quebrangulo), Fazenda Dourado (4); Sítio Olho d'Agua do Monteiro (1); Fazenda Peri-peri (1); Fazenda Poço da Serra (1); Fazenda Santa Cruz (3). BAHIA (Conquista), Fazenda Barra Moranga (1); (Palmeiras), Sítio Bouqueirão (6); Campo de São João (3); Fazenda Conceição (1). CEARÁ (Itapagé), Camará (3); Sítio São João II (7). MINAS GERAIS (Alem Paraiba), Fazenda São Geraldo (5); (Volta Grande), Fazenda Paraiso (1); Fazenda Pombal (1). PERNAMBUCO (Caruaru), Sítio Pitombeira (1); Sítio Riacho dos Mocós (2); Fazenda Salgado (1); (Triunfo), Sítio Brejinho (1); Sítio Monte Alegre (1); Sítio Novo (1); Sítio Peri-peri (1); Sítio Salva Terra (1); Sítio São Bartolomeu (1).

Oxymycteris angularis (Thomas, 1909)

Specimens examined.—ALAGOAS (Quebrangulo), Engenho Riachão (2); (Viçosa), Sítio Amazonas (3); Sítio Bauauas (1); Fazenda Cachoeira Grande (1); Sítio Cambuim II (2); Sítio Engenho São José (1); Sítio Estrada Nova (2); Sítio Gravatá (2); Sítio Pedra de F. dos Pereiros (1); Fazenda Pindobinha (2); Fazenda Poço Feio (1); Fazenda Riachão

II (1); Fazenda São Manoel (3); Sítio Tamandua (1); Sítio Urucuba (1); Sítio Vila Maria Lia (2). CEARÁ (São Benidito), Sítio Pedra de Côco (1). PERNAMBUCO (Bonito), Sítio Rodiadouro (1); (Caruaru), Sítio Brejinho de Serra dos Cavalos (1); Sítio Brejo do Buraco (2); Sítio Capoeira (1); Fazenda Caruaru (7); Fazenda Santa Maria (3); Sítio Serra dos Cavalos (9).

Calomys callosus Rengger, 1830

Caatinga Baixa and the latter stages of old field succession are preferred habitats. *Calomys* is nocturnal and an agile, active climber.

Specimens collected.—PERNAMBUCO (Município de Exu), 0.5 km S of Exu (1); Escola Agrícola de Exu, 0.7 km S of Exu (8); Fazenda Santa Helena, 1 km N of Exu (1); Município de Exu (7).

Calomys sp.

Specimens examined.—BAHIA (Conquista), Fazenda Agrião (3); Sítio Batalha (2); Fazenda Espirito Santo (6); Fazenda Felícia (2); (Jequié), Fazenda Santa Maria (11); Fazenda Pedra Redonda (1); (No locality) (14).

Wiedomys pyrrhorhinos (Wied, 1821)

Caatinga Baixa is the typical habitat of *Wiedomys*. This species is nocturnal and relatively rare.

Specimens collected.—BAHIA (Município de Juazeiro da Bahia), Fazenda São Raimundo, km 216 on Route BA 130 (1). CEARÁ (Município de Crato), Floresta Naçional Araripe-Apodí (1). PERNAMBUCO (Município de Exu), Escola Agrícola de Exu, 0.7 km S of Exu (12); Fazenda Pinheira, 1.5 km SW of Exu (3); Município de Exu (2).

Specimens examined.—ALAGOAS (Palmeira dos Indios), Sítio Ribeira (1); (Quebrangulo), Fazenda Lagoas dos Bois (1); Fazenda Santa Cruz II (6); (Santana do Ipanema), Sítio Lagoinha (2). BAHIA (Feira), Fazenda Tanque do Pasto (1); Fazenda Trez Riacho (3); (Seabra), Lagoa Seca (3); Varzea da Canabrava (3). CEARÁ (Campo Sales), Sítio Cantos (1); (Ipú), Cidade (1); Fazenda Lages (3); Sítio Pereiros (1); (Missão Velha), Sítio Açude Velho (1); Sítio Cachoeira (1); (São Benedito), Sítio Alto (1); Sítio Barros (1). PERNAMBUCO (Caruaru), Sítio Canhoto (2); Sítio Gravatá (2); Pingueiras (6); Sítio Preguiça (6); Sítio Roncaria (1); Fazenda Serraria (4).

Holochilus brasiliensis (Desmarest, 1819)

Specimens examined.—ALAGOAS (Quebrangulo), Fazenda Bento de Barros (2); Sítio Mauiras (1); Fazenda Peri-peri (3); (Viçosa), Fazenda Pindobinha (1); Sítio Tangil (3). BAHIA (Bom Jesus-Lapa), Ilha do Medo (7). CEARÁ (Barbalha), Sítio Barreiras (1); Sítio Tupinamba (3); (Crato), Sítio Passagem (4); (Ipú), Sítio Gagas (1); (Joazeiro), Sítio Boca das Cobras (5); (Pacoti), Sítio Espinho Vermelho (2); (São Benidito), Sítio Carangueijo (1); Sítio Catinguinha (1); Sítio Muricatuba (1). MINAS GERAIS (Santa), Bicas Lagoa (3). PERNAMBUCO (Garanhuns), Sítio Cavaquinho (1); Fazenda Cristovão (1); Sítio Frixeira (1); Sítio Inhumas (5); Sítio Laranja (1); Fazenda Trairas (1).

Subfamily Murinae

Rattus rattus Linnaeus, 1758

This species is a common commensal. The current distribution includes man-made dwellings in towns and outlying fazendas. *R. rattus* is of particular interest because it is a vector of an endemic form of bubonic plague.

Specimens collected.—PERNAMBUCO (Município de Exu), Escola Agrícola de Exu, 0.7 km S of Exu (4); Fazenda Batente, 5.5 km SE of Exu (2); Fazenda Pinheira, 1.5 km SW of Exu (7); Município de Exu (170).

Mus musculus (Linnaeus, 1758)

This species is another commensal. Populations are concentrated in towns, but population levels are much lower than those of *Rattus*.

Specimens collected.—PERNAMBUCO (Município de Exu) (23).

Family Caviidae

Kerodon rupestris (Wied, 1820)

This species is normally found only on lajeiros and rocky serrotes. A population was established near Parnamirim, Pernambuco, in an old quixaba forest by introducing individuals. The relatively large size (up to 1,000 g), hunting pressure, and restrictive habitat requirements have contributed to localized extirpations throughout much of the Caatingas. Reproduction is not synchronized and animals are active both day and night. This species may be the only endemic Caatinga rodent.

Specimens collected.—PERNAMBUCO (Município de Exu), Escola Agrícola de Exu, 0.7 km S of Exu (4); Fazenda Batente, 5.5 km SE of Exu (5); Fazenda Cantareno, 4.3 km NE of Exu (5); Município de Exu (9); Serrote das Lages, 17.7 km S of Exu (1); (Município de Parnamirim) (1).

Specimens examined.—ALAGOAS (Santana do Ipanema), Sítio Goiabeira (1); Sítio Lagoinha (12); Sítio Riacho do Bode (2). BAHIA (Joazeiro) (1); (Vila Nova) (2). CEARÁ (Araripe), Sítio Cachoeira (1); (Assaré), Sítio Caraco (1); Sítio Manuel Inaçio (2); (Campo Sales), Sítio Acoci (18); Sítio Canto (8); (Crato), Serra do Juá (1); Sítio Boa Vista (2); (Itapagé), Sítio São João (1); (Milagres), Sítio Espinho de Judeu (2); (Missão Velho), Sítio Lapinha (2). MINAS GERAIS (Barro Alto) (1); (Riacho da Cruz) (1). PERNAMBUCO (Bodocó), Sítio Belem (2); Sítio Lopes (2); Sítio Riacho da Melancia (1); Sítio Sabonete (6); Sítio Serra do Brejo (2); (Exu), Sítio Gravatá (4); (Pesqueira), Sítio Ceguinha (1).

Galea spixii (Wagler, 1831)

This is the only rodent in the Caatingas which utilizes a network of well-worn runways. Individuals are found only in low-lying areas. Peak densities are reached in certain cultivated or recently abandoned fields. Reproduction occurs throughout the year. Activity is mostly crepuscular although short periods of activity may occur at any time.

Specimens collected.—PERNAMBUCO (Município de Exu), 0.5 km S of Exu (3); 0.5 km SW of Exu (4); 1.0 km S of Exu (5); 4.0 km S of Exu (1); Escola Agrícola de Exu, 0.7 km S of Exu (27); Fazenda Batente, 5.5 km SE of Exu (10); Fazenda Pinheira, 1.5 km SW of Exu (6); Fazenda Maniçoba, 10 km S of Exu (1); Município de Exu (106); (Município de São Lourenço da Mata), Estação Ecológico do Tapacurá (170 m) (1).

Specimens examined.—ALAGOAS (Limoeiro de Anadia), Sítio Brejo (2); Sítio Brêu

(3); Sítio Gameleira (1); (Quebrangulo), Fazenda Poço da Serra (1); Sítio Barra (1); Sítio Olho d'Agua do Monteiro (2). BAHIA (Mundo Novo), Sítio Barra de Mundo Novo (1); (Serrinha), Fazenda Cruzeiro (3); Sítio Totonio (1). CEARÁ (Barbalha), Sítio São Pedro (1); (Brejo Santo), Sítio Cancela (3); Sítio Massape (1); (Crato), Sítio Fabrica (1); Sítio Miranda (1); Sítio Oiteiro (1); Sítio Sapuinho (2); (Jardim), Sítio Engenho d'Agua (1); Sítio Olho d'Agua (1); (Missão Velho), Sítio Yamaleira (1); (Santana do Cariri) (1); (Solonopole), Sítio Cedrão (1); Sítio Inhuma (1); Sítio Passa Corrente (1); Sítio Veneza (4). PERNAMBUCO (Exu), Sítio Alto do Umbuzeiro (1); Sítio Gravatá (1); (Bodocó), Sítio Roncador (3); (Pesqueira), Fazenda Caçimba Nova (1); Fazenda Caianinha (1); Sítio Carrapato (1); Sítio Isabel Dias (1); Sítio Maravilha (2); Fazenda Pitanquinha (6); Fazenda Quatro Cantos (1); Sítio Serrinha (1); (Triunfo), Sítio Lagoa do Almeida (1).

Family Dasyproctidae

Dasyprocta prymnolopha (Wagler, 1831*b*)

Heavy hunting pressure has greatly reduced or eliminated populations in many localities. Remnant populations still persist in some pockets of Caatinga Alta and on isolated serrotes. In areas subject to minimal hunting pressure, such as the Floresta Naçional Araripe-Apodí, these large rodents may still be common residents.

Specimens collected.—PERNAMBUCO (Município de Exu), Fazenda Marçal, 14.2 km NW of Exu (2).

Specimen examined.—PERNAMBUCO (Dois Irmãos) (1).

Family Echimyidae

Thrichomys apereoides Lund, 1841 (see Petter, 1973)

This echimyid is strictly associated with rocky habitats, such as serrotes and lajeiros. Reproductive periods are relatively synchronized and the young are very precocial. *Thrichomys* may be active for brief periods at any time but it is generally crepuscular. These animals are scansorial and are good climbers.

Specimens collected.—BAHIA (Município de Senhor do Bom Fim), Fazenda Flamengo, 10 km N of Jaguarari (3); Fazenda Morro da Imburana, 15 km N of Jaguarari (2). PERNAMBUCO (Município de Exu), Escola Agrícola de Exu, 0.7 km S of Exu (25); Fazenda Batente, 5.5 km SE of Exu (13); Fazenda Guaraní, 2.9 km N of Exu (5); Fazenda Pinheira, 1.5 km SW of Exu (4); Fazenda Santa Helena, 1 km N of Exu (2); Município de Exu (48); (Município de São Lourenço da Mata), Estação Ecológico do Tapacurá (170 m) (3).

Order Carnivora

Family Canidae

Cerdocyon thous (Linnaeus, 1766)

This species is ubiquitous and fairly common. Currently, *Cerdocyon* is the most abundant terrestrial predator (placental) in the Caatingas and on the Chapada do Araripe.

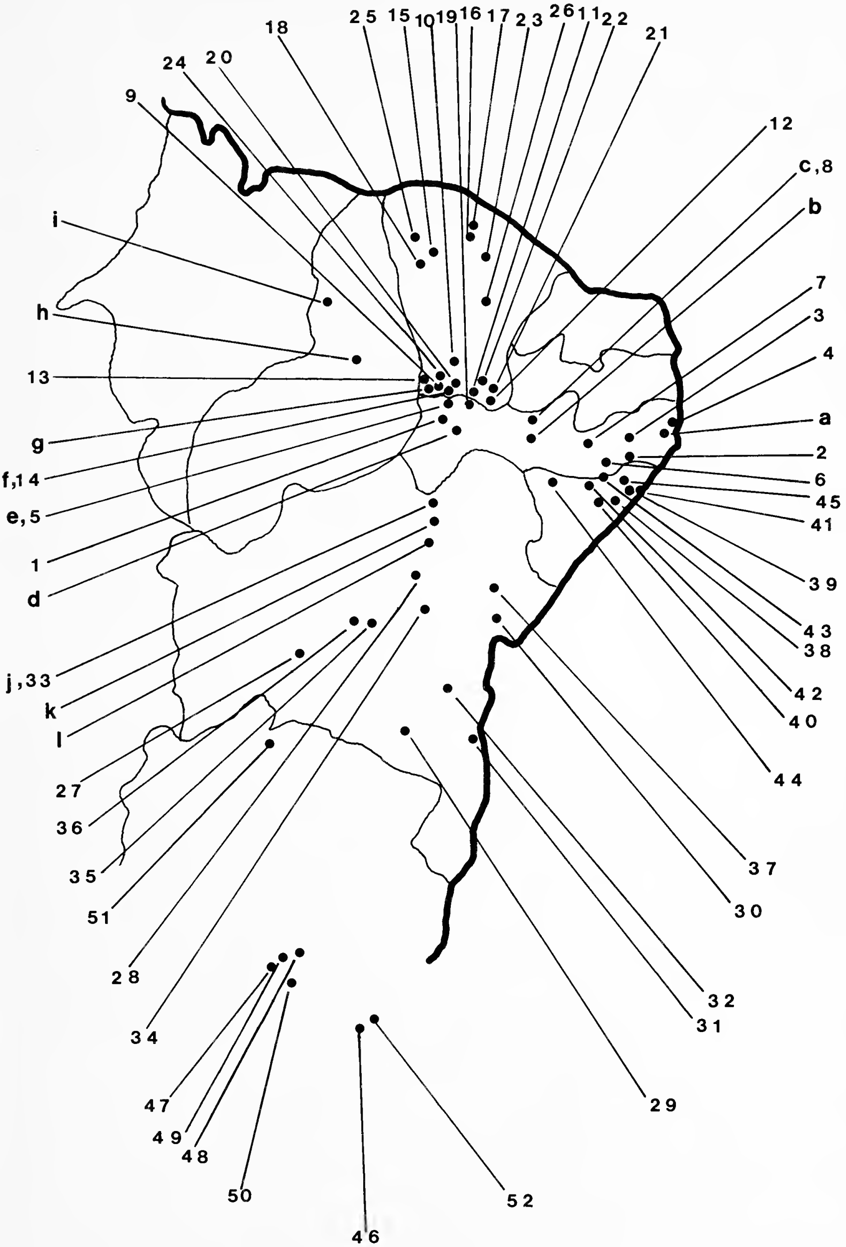


Fig. 15.—Mammal specimens were examined or collected from a broad area throughout most of the Northeast of Brazil. Major localities are indicated by a dot, with the appropriate numeral referencing the set of specific sites enumerated in the Gazetteer.

Specimens collected.—CEARÁ (Município de Crato), Floresta Naçional Araripe-Apodí, 9 km W of Crato (1). PERNAMBUCO (Município de Exu), Escola Agrícola de Exu (1); (Município de Serra Talhada), Município de Serra Talhada (1).

Family Mustelidae

Galictis vittata (Schreber, 1776)

Highest densities are apparently reached in rocky areas. This species is probably the most important mammalian predator of the rock-dwelling rodents *Kerodon* and *Thrichomys*.

Specimens collected.—PERNAMBUCO (Município de Exu), Fazenda Batente, 5.5 km SE of Exu (2).

Family Felidae

Felis yagouaroundi (E. Geoffroy, 1803)

Areas currently disturbed by man's activities are usually not frequented by this species. It may occur in any of a variety of Caatingas and Chapada habitats.

Specimen collected.—PERNAMBUCO (Município de Exu), Escola Agrícola de Exu (1).

GAZETTEER

All sites in the Gazetteer are represented by an alphanumeric code and are organized by municipality and state separately for specimens collected and specimens examined. For collected specimens, each site is indexed by a letter (A through L) followed by a number. The letter refers to a general locality (that is, a municipality), while the number refers to a distinct site within the locality. For specimens examined, each site represented is indexed by a number (1–52) followed by a letter. The number refers to a general locality written on the museum tags (presumably a municipality or city), while the letter refers to distinct sites within the locality. Sites may be located on the map in Fig. 15 by referring to the general locality index (the letter for specimens collected, the number for specimens examined).

Specimens Collected

Município de São Lourenço da Mata
Pernambuco

A1 Mata do Camocim (170 m)
A2 Estação Ecológico do Tapacurá (170 m)

Município de Serra Talhada
Pernambuco

B1 Fazenda Saco (I.B.A.), 6.6 km NNE of Serra Talhada
C1 Fazenda Salto, 35 km NNE of Serra Talhada
C2 SUCAM (in the town of Triunfo), 28 km NNE of Serra Talhada

Município de Parnamirim
Pernambuco

D1 Town of Parnamirim, 47.6 km W of Salgeiro

Município de Exu
Pernambuco

E1 Açude Itamaragí, .5 km S of Exu
E2 Escola Agrícola de Exu, .7 km S of Exu
E3 Fazenda Alto de Ferreira, 5.0 km SW of Exu
E4 Fazenda Alto do Umbuzeiro, 1.4 km NW of Exu
E5 Fazenda Barracão, 19.8 km SW of Exu
E6 Fazenda Batente, 5.5 km SE of Exu
E7 Fazenda Bom Jesus, .8 km NNW of Exu
E8 Fazenda Cachoeira, 13.1 km SSW of Exu
E9 Fazenda Cana Mansa, 13.4 km SW of Exu
E10 Fazenda Cantareno, 4.5 km NNE of Exu
E11 Fazenda Colônia, 5.5 km S of Exu
E12 Fazenda Gravatá, 3.1 km NW of Exu
E13 Fazenda Guaraní, 2.9 km N of Exu
E14 Fazenda Marçal, 10.5 km NW of Exu
E15 Fazenda Maniçoba, 13.7 km SSW of Exu
E16 Fazenda Pau Ferrado, 2.6 km E of Exu
E17 Fazenda Paus Grandes, 14.2 km E of Exu
E18 Fazenda Pinheira, 1.5 km SW of Exu
E19 Fazenda Pomonha, 21 km SSW of Exu
E20 Fazenda São José, 1.5 km N of Exu
E21 Fazenda São Pedro, 1 km ESE of Exu
E22 Fazenda Santa Helena, 1 km NE of Exu
E23 Fazenda Uruguai, 4.8 km NE of Exu
E24 Serrote das Lajes, 17.0 km S of Exu
E25 Serrote das Lajes, 17.7 km S of Exu
E26 Serrote Gambá, 19 km SSW of Exu
E27 Serrote Gritadeira, 18 km SSW of Exu

Município de Crato
Ceará

F1 Aeroporto de Crato, 10 km SW of Crato
F2 Colégio Agrícola de Crato, 5 km W of Crato
F3 Fazenda Fundão, 3 km SSW of Crato
F4 Floresta Naçional Araripe-Apodí, 8 km S of Crato
F5 Floresta Naçional Araripe-Apodí, 9 km S of Crato
F6 Floresta Naçional Araripe-Apodí, 8 km SSW of Crato
F7 Floresta Naçional Araripe-Apodí, 10 km SSW of Crato

F8 Floresta Naçional Araripe-Apodí, 11 km SSW of Crato
F9 Floresta Naçional Araripe-Apodí, 13 km SSW of Crato
F10 Floresta Naçional Araripe-Apdoí, 17 km SSW of Crato
F11 Floresta Naçional Araripe-Apodí, 21 km SSW of Crato
F12 Floresta Naçional Araripe-Apodí, 9 km SW of Crato
F13 Floresta Naçional Araripe-Apodí, 10 km SW of Crato
F14 Floresta Naçional Araripe-Apodí, 11 km SW of Crato
F15 Floresta Naçional Araripe-Apodí, 14 km SW of Crato
F16 Floresta Naçional Araripe-Apodí, 19 km SW of Crato
F17 Floresta Naçional Araripe-Apodí, 9 km W of Crato
F18 Floresta Naçional Araripe-Apodí, 10 km W of Crato
F19 Sítio Luanda (Itaiteira), 4 km S of Crato

Município de Nova Olinda
Ceará

G1 Km 19 on Route CE 96 (outside of the town of Nova Olinda)

Município de Valença do Piauí
Piauí

H1 Fazenda Olho da Agua, 2 km N of Valença do Piauí
H2 (Watering Hole) 5 km W of Valença do Piauí

Município de Teresina
Piauí

I1 Km 18 on Route BR 316 (outside of the city of Teresina)

Município de Juazeiro da Bahia
Bahia

J1 Fazenda Barrinha
J2 Fazenda São Raimundo, Km 216 on Route BA 130

Município de Senhor do Bom Fim
Bahia

K1 Fazenda Flamengo, Km 150 on Route BA 130, 10 km N of the town of Jaguarari
K2 Fazenda Lajeido, Km 147 on Route BA 130
K3 Fazenda Morro da Imburana, Km 145 on Route BA 130
L1 Distrito de Juacema (on Route BA 130)

Specimens Examined

(National Museum in Rio de Janeiro)
Bodocó

Pernambuco

1a Sítio Belem
1b Sítio Lopes

1c Sítio Paus Pretio
1d Sítio Riacho da Melançia
1e Sítio Roncador
1f Sítio São Gonçalo
1g Sítio Sabonete
1h Sítio Serra do Brejo
1i Sítio Xique-xique

Bonito
Pernambuco

2a Sítio Rodiadouro

Caruaru
Pernambuco

3a Sítio Brejinha de Serra dos Cavalos
3b Sítio Brejo do Buraco
3c Sítio Canhoto
3d Sítio Capoeira
3e Fazenda Caruaru
3f Sítio Gravatá
3g Pingueiras
3h Sítio Pitombeira
3i Sítio Preguica
3j Sítio Quandús
3k Sítio Riacho dos Mocós
3l Sítio Roncaria
3m Fazenda Salgado
3n Fazenda Santa Maria
3o Sítio Serra dos Cavalos
3p Fazenda Serraria
3q No locality

Dois Irmãos
Pernambuco

4a No locality

Exu
Pernambuco

5a Sítio Gravatá
5b Sítio Alto do Umbuzeiro

Garanhuns
Pernambuco

6a Sítio Brejo Grande
6b Sítio Cajarana

6c	Fazenda Caldeirão
6d	Sítio Camaratuba
6e	Sítio Canhoto
6f	Sítio Capim
6g	Sítio Cavaquinho
6h	Fazenda Colônia da Serra
6i	Fazenda Cristovão
6j	Sítio Engenho do Manião
6k	Sítio Flamengo
6l	Sítio Frixeira
6m	Sítio Inhumas
6n	Sítio Jambelo
6o	Sítio Lajeiro
6p	Sítio Laranja
6q	Sítio Riacho Fundo
6r	Sítio Riacho Seco
6s	Sítio Saco
6t	Fazenda São Paulo
6u	Fazenda Serra da Pedra
6v	Fazenda Trairas
6w	Sítio Varzea do Ingá
6x	Sítio Varzea-Ingá
6y	Sítio Varzea-Redonda
6z	Fazenda Velha
6aa	No locality

No Area
Pernambuco

No locality

Pesqueira
Pernambuco

7a	Fazenda Caçimba Nova
7b	Fazenda Caianinha
7c	Sítio Carrapato
7d	Sítio Isabel Dias
7e	Sítio Maravilha
7f	Fazenda Pitanquinha
7g	Fazenda Quatro Cantos
7h	Sítio Serrinha
7i	Fazenda Sororoca

Triunfo
Pernambuco

8a	Sítio Boa Esperança de Jérico
8b	Sítio Borgens

8c Sítio Brejinho
8d Sítio Cana Brava de Jérico
8e Sítio Corredor do Vento
8f Sítio Lagoa do Almeida
8g Sítio Macaco de Baixa Verde
8h Sítio Monte Alegre
8i Sítio Novo
8j Sítio Oiti
8k Sítio Peri-peri
8l Sítio Salva Terra
8m Sítio São Bartolomeu
8n Sítio São Mateus

Araripe
Ceará

9a Sítio Cachoeira

Assare
Ceará

10a Sítio Caraco
10b Sítio Manuel Inacio

Barbalha
Ceará

11a Sítio Barreiras
11b Sítio São Pedro
11c Sítio Tupinamba

Brejo Santo
Ceará

12a Sítio Cancela
12b Sítio Massape

Campo Sales
Ceará

13a Sítio Acoci
13b Sítio Canto(s)
13c Sítio Volta

Crato
Ceará

14a Sítio Arisco
14b Sítio Belo Horizonte
14c Sítio Boa Vista
14d Sítio Caiano
14e Chapada Araripe
14f Sítio Constantino

14g Sítio Crispin
14h Sítio Fabrica
14i Sítio Grangeiro
14j Sítio Miranda
14k Sítio Oiteiro
14l Sítio Olaria
14m Sítio Parque
14n Sítio Passagem
14o Sítio Sapuinho
14p Serra do Juá
14q No locality

Guaraciaba
Ceará

15a Sítio Mazagão

Itapagé
Ceará

16a Sítio Bom Jesus
16b Camará
16c Sítio Maia
16d Sítio São João II
16e Sítio São José
16f Sítio Trata

Itapipoca
Ceará

17a Sítio Jacú

Ipíu
Ceará

18a Cidade de Ipíu
18b Sítio Gagas
18c Fazenda Lages
18d Sítio Pereiros

Jardim
Ceará

19a Sítio Cereado
19b Sítio Engenho d'Agua
19c Sítio Olho d'Agua

Joazeiro
Ceará

20a Sítio Boca das Cobras

Milagres
Ceará

21a Sítio Camará
21b Sítio Espinho de Judeu

Missão Velho
Ceará

22a Sítio Açude Velho
22b Sítio Araruna
22c Sítio Cachoeira
22d Sítio Emboscada
22e Sítio Lapinha
22f Sítio Yamaleira

Pacoti
Ceará

23a Sítio Alvoredo
23b Sítio Baixa Verde
23c Sítio Boa Esperança do Lapis
23d Sítio Boa Vista
23e Sítio Coati
23f Sítio Espinho Vermelho
23g Sítio Flor
23h Sítio Goiabeira
23i Sítio Ladeira
23j Sítio Lorena
23k Sítio Mendoza
23l Sítio Ouro
23m Sítio Umquaiana

Santana do Cariri
Ceará

24a Cidade de Santana do Cariri

São Benidito
Ceará

25a Sítio Alto
25b Sítio Barra
25c Sítio Barros
25d Sítio Cantinho
25e Sítio Carangueijo
25f Sítio Catinguinha
25g Sítio Cegarro
25h Sítio Chora

25i Sítio Cinta da Solidade
25j Sítio Guaribas do Amaral
25k Sítio Macapá
25l Sítio Muricatuba
25m Sítio Pedra de Côco
25n Sítio Piraguará
25o Sítio São José da Boa Vista

Solonopole
Ceará

26a Sítio Cedrão
26b Sítio Inhuma
26c Sítio Passa Corrente
26d Sítio Veneza

Bom Jesus de Lapa
Bahia

27a Ilha do Medo

Campo Formosa
Bahia

28a Fazenda Rapousa

Conquista
Bahia

29a Fazenda Agrião
29b Fazenda Barra Morangoa
29c Sítio Batalha
29d Fazenda Espirito Santo
29e Fazenda Felícia

Feira
Bahia

30a Fazenda Capoeira do Rosario
30b Fazenda Cazumba
30c Fazenda Jacú
30d Fazenda Salgado
30e Fazenda Tanque do Pasto
30f Sítio Tomba
30g Fazenda Três Riachos

Ilheus
Bahia

31a Aritaque Urucutuca
31b Banco da Vitória, Pirataquissé

31c Buerarema Riberão da Fortuna
31d Rio do Braço, Fazenda Almeida

Jequié
Bahia
32a Fazenda Pedra Redonda
32b Fazenda Santa Maria

Joazeiro
Bahia
33a No locality

Mundo Novo
Bahia
34a Sítio Barra de Mundo Novo

No Area
Bahia
No locality

Palmeiras
Bahia
35a Sítio Bouqueirão
35b Campo de São José
35c Fazenda Conceição

Seabra
Bahia
36a Varzea da Canabrava
36b Fazenda Cochó do Malheiros
36c Fazenda Furados
36d Lagoa Seca

Serrinha
Bahia
37a Fazenda Alagadiço Grande
37b Sítio Baixa d'Agua
37c Fazenda Cacuá
37d Fazenda Bruzeiro
37e Fazenda Europa
37f Fazenda João Congo
37g Fazenda Montanha
37h Fazenda Oiteiro
37i Fazenda Riacho Grande
37j Fazenda Tiririca

37k Sítio Totonio
37l Fazenda Umburana

Vila Nova
Bahia

No locality

Anadia
Alagoas

38a Sítio Brejo do Boi

Capela
Alagoas

39a Fazenda Serra Alegre

Limoeira de Anadia
Alagoas

40a Sítio Barracão
40b Sítio Brejo
40c Sítio Brêu
40d Sítio Gameleira

Managabeiras (=Manguaba)
Alagoas

41a Usina Sinimbu

Palmeiras dos Indios
Alagoas

42a Sítio Capuma
42b Sítio Dormião
42c Sítio Panelas
42d Sítio Ribeira
42e Sítio Sabiá

Quebrangulo
Alagoas

43a Sítio Barra
43b Sítio Barra Preto
43c Fazenda Bento de Barros
43d Fazenda Dourado
43e Engenho Juliana
43f Engenho Riachão
43g Fazenda Lagoa dos Bois
43h Sítio Mauiras
43i Sítio Olho d'Agua do Monteiro

43j Fazenda Peri-peri
43k Fazenda Poço da Serra
43l Fazenda Santa Cruz II

Santana do Ipanema
Alagoas

44a Sítio Goiabeira
44b Sítio Lagoinha
44c Sítio Riacho do Bode

Viçosa
Alagoas

45a Sítio Amazonas
45b Sítio Bauauas
45c Sítio Cachoeira Grande
45d Sítio Cambuim II
45e Sítio Canárias
45f Sítio Estrada Nova
45g Sítio Engenho São José
45h Fazenda Gitirana
45i Sítio Gravatá
45j Sítio Pedra da Fazenda das Pereiras
45k Fazenda Pedra do Fogo
45l Fazenda Pindobinha
45m Fazenda Poço Feio
45n Fazenda Riachão II
45o Sítio São José
45p Fazenda São Manoel
45q Fazenda São Pedro
45r Sítio Tamanduá
45s Sítio Tangil
45t Sítio Tangil 2°
45u Sítio Timbó 2°
45v Sítio Urucuba
45w Sítio Vila Maria Lia

Alem Paraiba
Minas Gerais

46a Fazenda São Geraldo

Barro Alto
Minas Gerais

No locality

Belo Horizonte
Minas Gerais

47a Bairro Gameleira
47b Secão Fornecimento Agrícola

Conceição do Mato Dentro
Minas Gerais

48a Boca da Mata
48b Bocada Mulata
48c Mata do Dr. Daniel

Jaboticabas (=Jaboticatubas?)
Minas Gerais

49a No locality

Ouro Preto
Minas Gerais

50a No locality

Riacho da Cruz
Minas Gerais

51a No locality

Santa
Minas Gerais

Bicas Lagoa

Volta Grande
Minas Gerais

52a Fazenda Paraiso
52b Fazenda Pombal

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MODELING THE DEVELOPMENT OF SEDENTARY MARITIME ECONOMIES ON THE COAST OF PERU: A PRELIMINARY STATEMENT

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Curator, Section of Man

Abstract

The date of 5000 B.P. is crucial to the understanding of the development of complex societies on the Peruvian coast. It is at this time that modern sea level was attained and the present coastline stabilized. The rise of complex societies on the coast is discussed in relation to the above factors.

Introduction

There have been numerous discussions of the origins of maritime subsistence patterns on the central and north coast of Peru; all of which invoke "land based" environmental factors, to explain the shift from hunting and gathering to a maritime subsistence economy at circa 5000 B.P. Lanning (1963) was the first investigator to recognize that extensive maritime subsistence patterns were established by 5000 B.P. and he proposed that littoral economies developed as a response to decreasing animal and plant resources in the lomas, brought on by increased aridity.

Many authors have addressed the question of post-Pleistocene environmental change in the Peruvian coast, either rejecting (Craig and Psuty, 1968; Parson, 1970; Osborn, 1977) or supporting Holocene climate change (Richardson, 1978*a*). All previous investigators, including myself, were concentrating their explanations of maritime origins from inland when, in reality, the answer lay beneath the continental shelf.

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The following discussion will present a model to explain the origins of intensive maritime economies on the Peruvian coast for it is now clear that highly complex societies arose on the central and north Peruvian coast with a maritime subsistence base by 5000 B.P. (Moseley, 1975). As will be demonstrated, the main causal factor in this development was sea level rise and the submergence of the continental shelf prior to 5000 B.P.

SEA LEVEL

Various authors (Shepard, 1964; Milliman and Emery, 1968; Gill, 1971; Clark and Lingle, 1979; Dillion and Oldale, 1978; Morner, 1971; Clark et al., 1978) have estimated the rise of ocean levels since the last glacial maximum at 15,000 years ago. The estimates range from a rise of 85 m to 135 m, with most authors using the latter figure.

From 15,000 B.P., meltice began to increase the volume of water in the ocean basins and by 7000 B.P. sea level was within 20 m of modern sea level which was attained by 5000 B.P. After 5000 B.P. sea level remained constant (Shepard, 1964) or fluctuated several meters above and below the modern level (Fairbridge, 1976). The post-5000 B.P. sea level fluctuation question is not relevant to this discussion but the vertical rise of circa 135 m of sea level and the subsequent submergence of the continental shelf on the west coast of South America has profound implications for understanding the processes of the development of maritime economies on the coast of Peru (Richardson, 1978*b*).

Simpson (1975*a,b*) has stated that the lowering of sea level would have affected the late Pleistocene weather patterns. In the Indo-Australian area, large expanses of continental shelf were exposed, thus preventing the vernal mixing of waters between the eastern and western Pacific. Thus the Pacific anticyclone did not weaken during the glacial summer, which meant that the eastern anticyclone and southeast trade winds would have remained constant throughout the glacial summer and winter (Simpson, 1975*a*:34). The result would have been that the coast of Peru would have been arid during the last glacial and rain would have fallen continuously throughout the summer and winter in the high Andes. The evidence for Simpson's conclusions comes from the recent work on the Galapagos (Colinvaux, 1972) where there was an increase in aridity at high elevations during the Pleistocene. In addition, there is now evidence that there was an increase in upwelling along the Peruvian coast at the zone of equatorial divergence. Luz (1973, 1977) has demonstrated from core data from the South Pacific that the ocean waters were 5–6 degrees cooler than today, and Gates (1976) has postulated that the ocean surface temperatures were lower at 18,000 B.P. If this model proposed by Simpson is a valid one, the various explanations for increase or decrease in rainfall in the central Andes, due to the shifting of the Intertropical Covergence Zone north or south of the equator (for example, Paskoff, 1977; Fairbridge, 1972; Hastenrath, 1971) have no validity.

It can also be suggested that the El Niño phenomenon did not occur during the Pleistocene, because the low pressure center over Indonesia would have not weakened to allow this warm water current to move across the Pacific and down the coast of Peru. In essence the El Niño countercurrent would then be a post-Pleistocene development. The origins of the El Niño current is being debated by oceanographers at present, but most agree that the El Niño current is not a local west coast South American phenomenon, but is part of the overall weather system of the Pacific. Wrytki, Quinn, and others conclude that the El Niño has its origins in the southeast tradewinds and when these trades are strong, they pile up water against the southeast Asian coast where the water level rises 0.5 m above that of the South American coast. With the shift in weather patterns, the low pressure area over Indonesia and the high pressure area near Easter Island, the trade winds decrease in intensity and the ". . . piled up water sloshes back toward South America" (Cromie, 1980:42; Hartline, 1980; Wyrtki et al., 1976). This warm current can be detected by ocean temperatures and sea levels along the line islands in the Pacific; and when it reaches South America, it moves south along the coast as the El Niño current. It has also been discovered that the warm countercurrent can occur at anytime of the year, but that it only affects the Peruvian coast when it arrives during the winter, for at other times the ocean temperature is already high.

BATHYMETRIC DATA

The key to our understanding of the rise of complex societies on the Peruvian coast, with a maritime economy, are the dates of the submergence of the continental shelf and the establishment of essentially modern coastal configurations. Bathymetric charts for west coast South America are not precise enough yet to compute the rate of submergence of the continental shelf as the post-glacial seas rose as has been accomplished for the California coast, where 400 to 500 m of shelf were lost every hundred years (Bickel, 1978:8). On the Atlantic coast of North America, the rise of sea level has been computed at 160 cm per 100 years and Edwards and Merrill (1977) feel that the inland movement of the sea would have been apparent to the prehistoric inhabitant.

The recently published bathymetric maps of the Peru-Chile continental margin and the trench by the Geological Society of America, provide 100 and 200 m depth measurements on the continental shelf

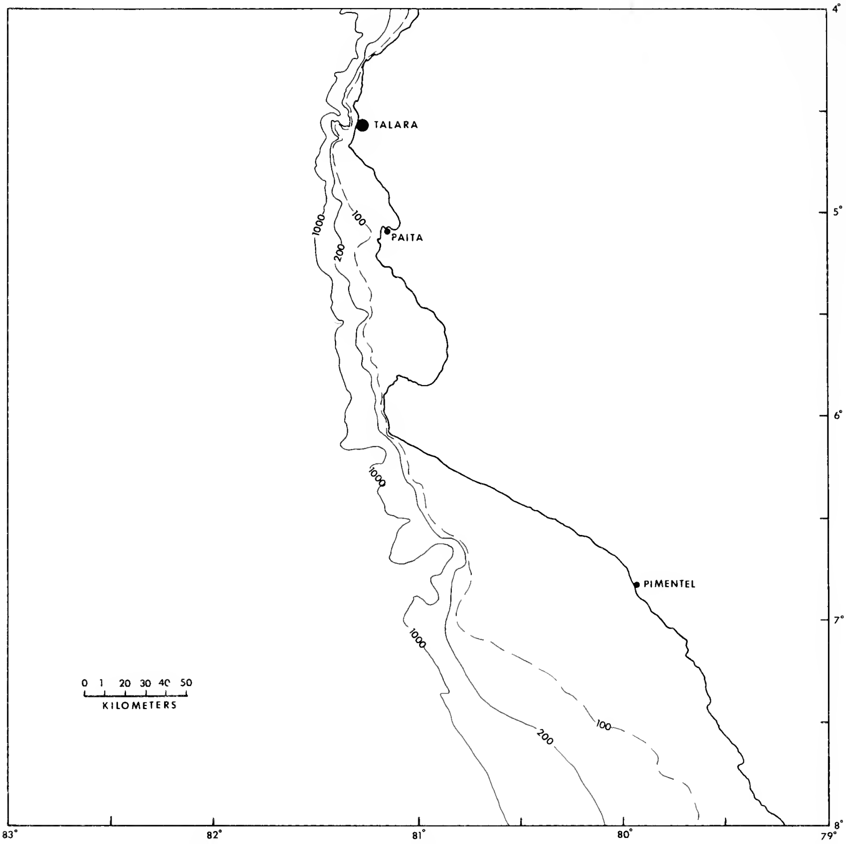

Fig. 1.—Map of the continental shelf and the coast of Peru from 4° to 8° south latitude. Adapted from Prince et al. (1980). Contour intervals in meters.

of western South America (Prince et al., 1980). Maps with less than 100 m depth measurements are restricted to either island groups or shipping ports.

Using the 100 m depth measurement, but keeping in mind that sea level was lowered by 135 m at 15,000 B.P., the expanse of the continental shelf exposed at the 100 m depth interval is over 100 km in some areas. The largest extent of the continental shelf at the 100 m depth is from 6° (Llescus Peninsula) to 12° (Callao) south latitude and it ranges from a width of 20 to 100 km with the widest portion between 6.5° (Pimentel) and 9° (Chimbote) south latitude (Figs. 1–3). For the remainder of the Peruvian south coast the 100 meter depth is at 10–30

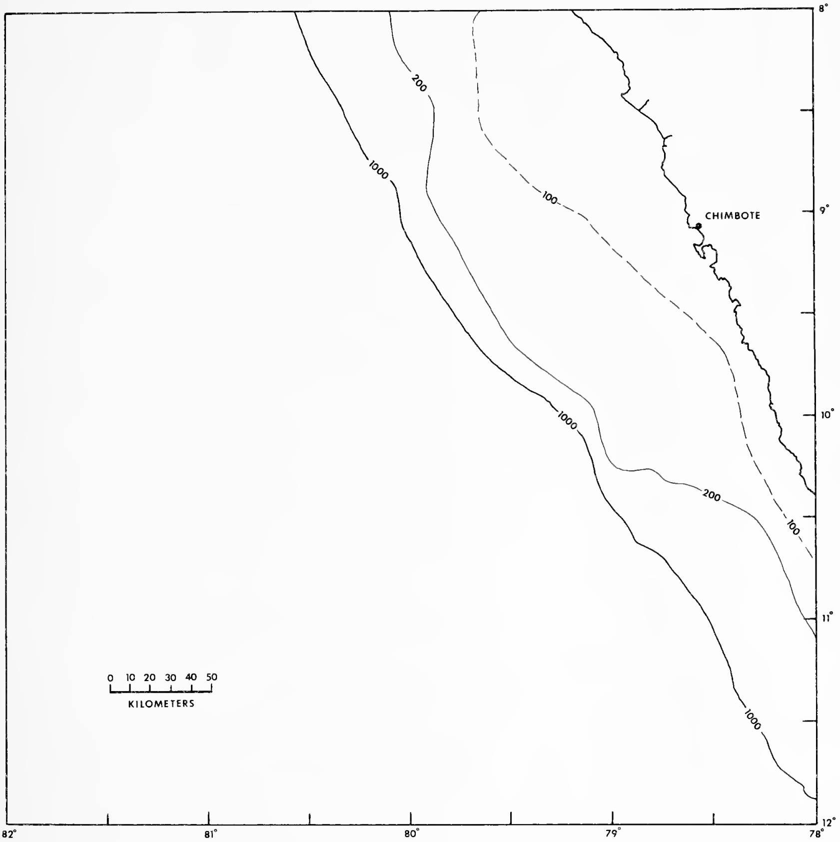

Fig. 2.—Map of the continental shelf and the coast of Peru from 8° to 12° south latitude. Adapted from Prince et al. (1980). Contour intervals in meters.

kilometers, while along the Chilean coast, where the 100 depth is rarely designated, the 200 meter depth is 5 to 10 kilometers from the modern shore, in most cases (Fig. 4).

The best evidence for the date of the establishment of modern coastline along the western South American coast are the beach lines on the Peruvian north coast. The Piura/Chira beach ridges consist of three major sets of raised beaches—the Chira ridges, the Colán ridges, and the Piura ridges. The nine Chira ridges have been dated and the oldest ridge fronting the Pleistocene lobitos marine terrace is dated to 4305 B.P., and the artifact assemblage on this oldest ridge is preceramic

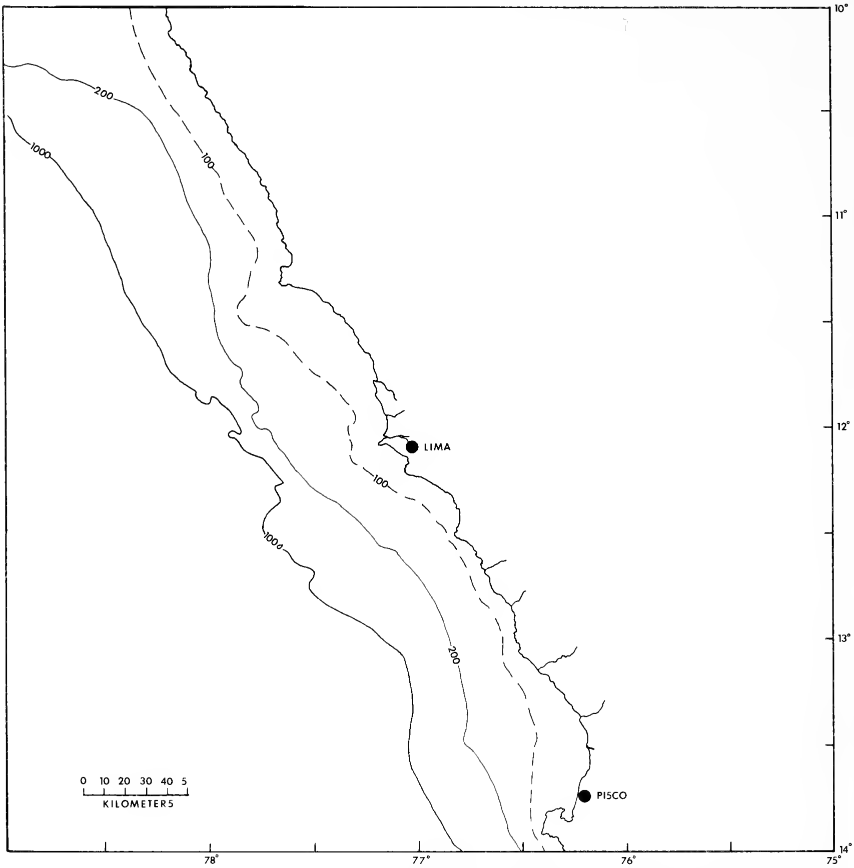

Fig. 3.—Map of the continental shelf and the coast of Peru from 10° to 14° south latitude. Adapted from Prince et al. (1980). Contour intervals in meters.

(Richardson, 1974; Chigne, 1975). The shell caped beach lines were formed by the transport of sediments from the Chira River, which were distributed northward, building up in back of Punta Balcones and Punta Pariñas. The subsequent beach ridges were raised by tectonic uplift and as a consequence a stranded beach system 2.7 km wide resulted.

The point to be stressed here is that the Chira beach ridges began forming only when modern sea level (5000 B.P.) was attained and the present coastline established. Certainly, beach lines were formed prior to 5000 B.P., but these were either submerged as the ocean rose or destroyed by wave action as the sea encroached landward. The Colón ridges are formed of Pleistocene marine pebbles resulting from a geologic structure above the present town of Colán, due to as yet unexplained process. The Piura ridges have a similar sequence to the Chira ridges (McConaughy, personal communication). The only other large set of ridges, are those that emanate out of the Santa River, which have yet to be fully explored. It can be speculated that all Holocene beach ridges on the western South American coast originated *after* modern sea level was reached.

By 5000–5500 B.P., modern shellfish, fish, and sea mammal resources were stabilized and possibly underwent population explosions. Prior to 5000 B.P. these resources were constantly adjusting to the progressive submergence on the continental shelf, but after 5000 B.P. these resources no longer were forced to adapt to increasing depths or changing shorelines as sea level rose, and thus after 5000 B.P., they may well have increased considerably over their previous population levels.

ARCHAEOLOGICAL RECORD

The following four locations on the west coast of South America provide information on the utilization of maritime resources prior to 5000–5500 B.P.—the Vegas complex of the Santa Elena Peninsula, Ecuador; the Amotape/Siches complex of the Talara region of northwest Peru; the Paijan complex of Pampas de Cupisnique on the Peruvian north coast; Quebrada las Conchas site, near Antofagasta, Chile.

The Vegas complex (7000–10,000 B.P.) is best known from the type site (Site 80) near the western end of the Santa Elena Peninsula and from the analysis of the midden deposits, the mangrove mollusk (*Anadara tuberculosa*) represented 24% of the diet, fish 30%, and terrestrial mammals 46% (Stothert, 1977:3; 1980). By 7000 B.P., sea level was within 10 to 20 m below its present level and the continental shelf may have supported a wider zone of mangrove vegetation. The majority of the Vegas middens are situated on the margins of an extensive drainage system at 10 m above current sea level and Site 80, the largest, was located to take advantage of an underground water resource. The question of freshwater support for mangrove vegetation has been thought to have been due to increased rainfall during the Holocene (Sarma, 1974); however, as has been pointed out in the previous section, there is increasing evidence that the Peruvian and Ecuadorian coasts were arid during the late Pleistocene and probably the early Holocene.

Mangroves can survive in hypersaline areas with little or no freshwater for a large part of the year and thus, rainfall may not be a factor

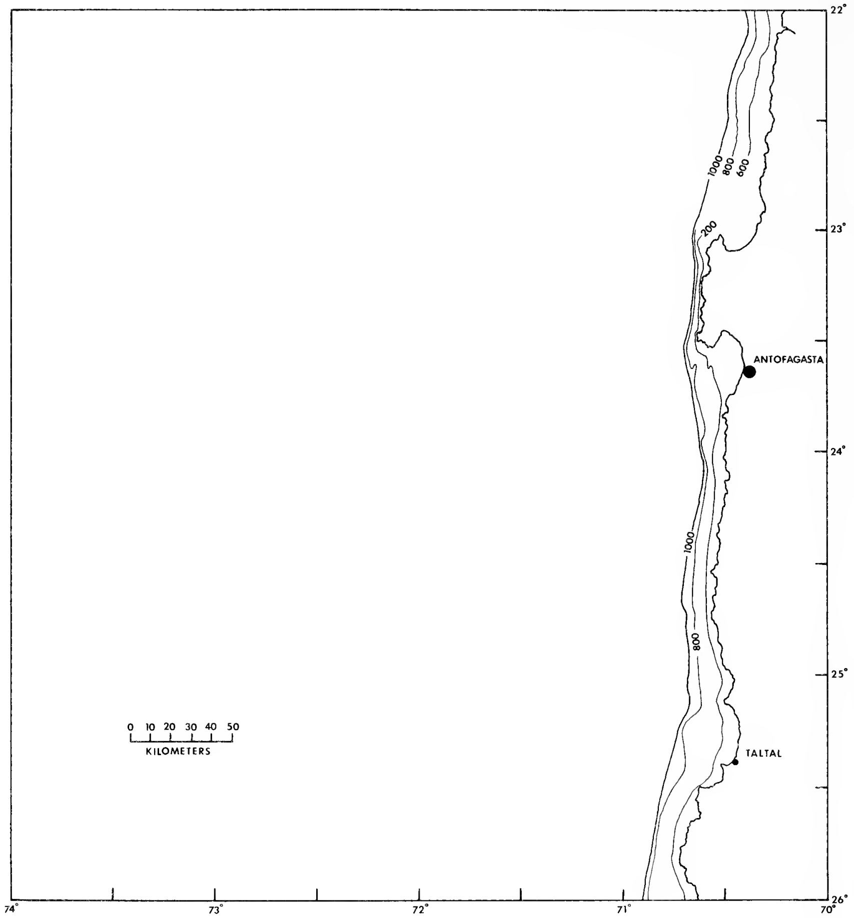

Fig. 4.—Map of the continental shelf and the coast of Peru from 22° to 26° south latitude. Adapted from Prince et al. (1980). Contour intervals in meters.

in the maintenance of mangrove forests. The increase in the meltice runoff may also have been a factor in contributing fresh water for mangrove development on the Eduadorian coast.

In the Talara area, all the Amotape sites are located on the Pleistocene tablazo at 50 m above sea level and 8 km from the present shoreline. These small campsites have scatterings of the mangrove mollusk *Anadara tuberculosa* and two radiocarbon dates place this occupation of the Talara Tar Seep area at 11,200 B.P. and 8125 B.P. For the better known Siches (8–6000 B.P.) period there are numerous sites with middens composed of the mangrove mollusk, all of which are located on the high Pleistocene marine floors overlooking Quebrada Pariñas, Talara Harbor, and the mouth of the Chira River. The largest of the Siches site (PV7-18) is located at the head of the quebrada where fresh water from Tertiary deposits form pools today.

The 100 m sea level depth on the Continental Shelf is at 8 km from the present shoreline at Talara (Fig. 1). With a sea level of minus 20 m the former Holocene Talara shoreline at 7000 B.P. would have been 5 km from the present coast. At 11,000 B.P., the Amotape hunters were using mangrove resources which were approximately 16 km from the beach and the small campsites probably represent small groups of hunters using the Talara Tar Pit zone as part of their seasonal round (Richardson, 1978*a*).

On the Peruvian coast in the Chicama Valley at Quebrada de Cupisnique 15 km from the present coast, Chauchat (1978*a*; 1978*b*; personal communication 1979) excavated two sites with midden accumulations of the Paijan period (PV22-12 and 13). These sites provide the first associated subsistence date with Paijan artifacts, which include marine fish, snails, lizards, desert fox, and the scapula of a deer. It is unclear whether marine shellfish were present, but the analysis has yet to be completed. Site 13 dates at 9810 B.P. and 7740 B.P. Chauchat feels that the Paijan projectile points may have functioned as fish spears. Turnbaugh (1975) has suggested a similar function for broadpoints during the transitional period in the eastern United States. In the Moche Valley, the Paijan sites of La Cumbre and Quirquiac Shelter could have exploited an exposed continental shelf of 100 km wide between 10,000–12,000 B.P. (Ossa and Moseley, 1971). At 12,000 B.P. the 100 m depth level was 100 km from the current coast and it can be postulated that the existing inland Paijan sites, functioned for hunting purposes, while on the former Holocene coast, Paijan populations may certainly have been utilizing or in fact been adapted to a maritime subsistence pattern, whose evidence is now submerged due to the continued rise of sea level.

The only other site with an early date for the use of maritime resources is that of Quebrada las Conchas near Antofogasta, Chile, located 3000 m from the present coastline and dated to 9400 B.P. and 9600 B.P. At this site, extensive shellfish, sea lion, and fish remains were recovered suggesting a reliance upon maritime resources (Llagostera M., 1979; manuscript). The next earliest date for Chilean maritime adaptation is from the Quiani site near Arica with a date 6170 B.P. (Willey, 1971:203). The late Pleistocene shoreline in this area and the modern one were not much different, for the 100 m depth is within 2 km of the present shore.

The exploitation of marine resources is very early on the West Coast of South America, but the evidence for such an early adaptation has only remained in those few areas where the present coastline either approximated or was close to the Holocene coast further out on the continental shelf. The Paijan discovery is very significant for it illustrates that the earliest known populations on the Peruvian coast, included marine resources as part of their overall subsistence pattern. One can postulate that there may be drowned Paijan middens along the north coast 100 km from the present coastline.

The earliest use of maritime resources on the Peruvian coast south of the Sechura Desert, excluding the Paijan example, cannot be dated older than circa 5000 B.P. In the Moche Valley, Alto Salaverry, and Padre Aban reflect a subsistence strategy of the use of rocky headlines and near shore resources, between 4500–3800 B.P., whereas the succeeding Gramalote complex (3800 B.P.) included deep burrowing clams for the first time as well as the large mussel (*Chormytius chorus*) which were mainly adults forms, leading the excavators to speculate that the Gramolote population was exploiting a previously unused resource (Pozorski and Pozorski, 1979*a*; 1979*b*). Thus the total width at 10,000–12,000 B.P. of the area that could have been exploited was enormous as compared to the present desert strip which is a narrow band of 4 to 6 km.

It is only in those areas where the modern coastline is within several kilometers or closer to the former 100 m depth that the evidence for early exploitation of marine resources will be found. If the dates for the Chilean coast are correct, more sites of this time range should exist.

CONCLUSION

The date of 5000 B.P. is critical to our understanding of the rise of complex maritime societies on the coast of Peru for it is at this crucial juncture in Central Andean cultural development that 1) sea level approximates modern levels; 2) modern coastlines are formed; and 3) the modern distribution of modern shellfish, fish, and sea mammal resources were established. The rise of complex maritime societies on the Peruvian central and north coast is then a response to the above set of conditions.

It is now clear, that the earliest populations to inhabit the coast of Peru utilized maritime resources and that much of the evidence for developing maritime economic systems, leading up to 5000 B.P., lies submerged on the continental shelf.

ACKNOWLEDGMENTS

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OBSERVATIONS ON THE DISTRIBUTION AND ECOLOGY OF THE MAMMALS OF SALTA PROVINCE, ARGENTINA

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Abstract

Distributional and ecological observations of mammals of Salta Province, Argentina, are summarized in this preliminary report. Data are presented which pertain to macro- and microhabitat preferences, molting, reproduction, and natural history, as well as standard external and cranial morphological measurements. Fifty-eight species belonging to 19 families and seven orders are considered in this paper; this represents 41% of the total mammal fauna of the province. Fieldwork was conducted over an 8-year period and included all major macrohabitats of the province (that is, Puna, Precordillera, Chaco, Moist Forest, and Transitional Forest). Species accounts are included, and the current status of all species occurring within the province is discussed. The ranges of two species (*Tadarida laticaudata* and *Auliscomys sublimis*) are extended.

Introduction

Salta Province is in extreme northwestern Argentina and lies between 22° and 26° south latitude and 62° and 66° west longitude (Fig. 1). The province encompasses more than 155,000 km^2 of a region that

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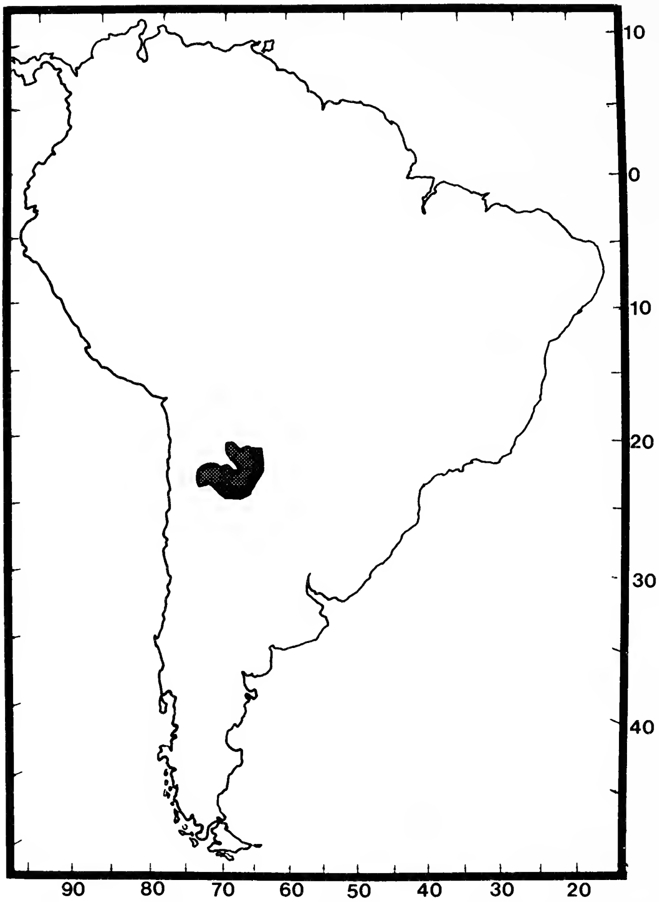

Fig. 1.—A map showing the position of Salta Province in South America. Its position along the Andean chain and astride the Tropic of Capricorn results in a great diversity of habitats occurring within the provincial boundaries.

is geologically, climatologically, and vegetationally diverse. In its eastern portion, the province supports thorn forest vegetation, or dry Chaco, on a vast flat plain. Temperatures in this area are high in summer (air temperature may exceed 50°C), which also coincides with the rainy season (for example, see Adamoli et al., 1972; A. L. Cabrera, 1976). Precipitation in this area varies from about 500 mm to 800 mm and increases from east to west (Fig. 2). Topographic relief also increases from east to west as the low eastern plain meets low-lying mountain ranges in the central portions of the province (with heights reaching

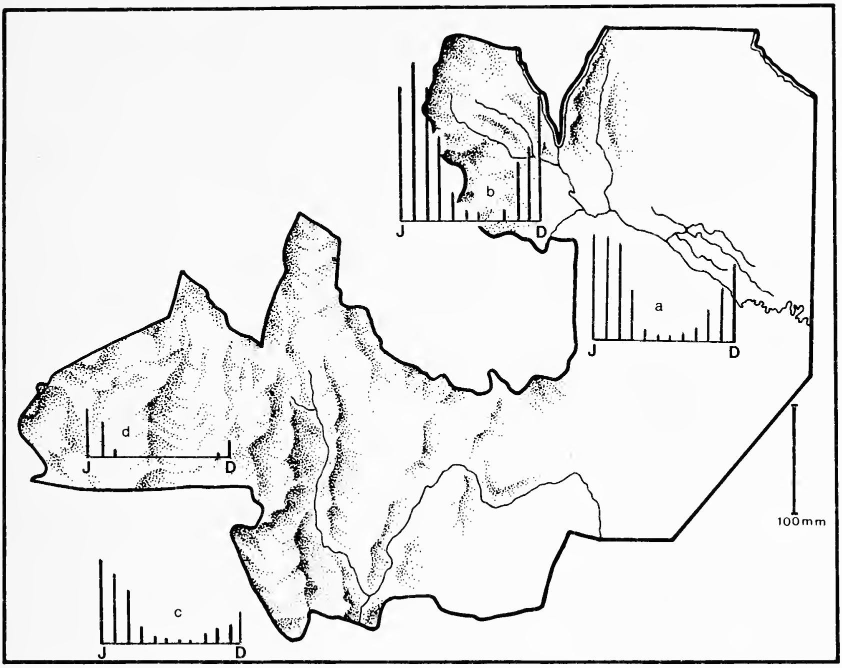

Fig. 2.—Rainfall within four major macrohabitats of Salta Province: a) a Chacoan locality (Rivadavia); b) a moist forest site (Orán); c) a Monte Desert site (Andalgalá, Catamarca Province); d) a Puna locality (San Antonio de los Cobres). Summer rainfall (October–March) predominates over the entire province.

approximately 1500 m). Continuing westward, taller ranges (with tops reaching 3000 m) are encountered, and still further west mountains reaching 5000 m form a geographic barrier to easterly winds. Finally, in the westernmost parts of the province, the Andean mountain chain, with peaks exceeding 6700 m, forms the western boundary of the province. Thus Salta offers an elevational gradient of more than 6000 m. As expected, climatic patterns are influenced by this varied topographic relief and are also complex, resulting in a mosaic of major vegetation communities including thorn scrub (or Chaco), moist forest, Monte Desert, and Puna (or high Andean steppe) (Fig. 3). Within each of these macrohabitats, there are several distinct vegetational associations, thus the province as a whole offers one of the richest areas on the continent from the viewpoint of habitat diversity.

Mammal investigations within Salta have largely been limited to collecting data of early naturalists and basic taxonomic studies (for example, Thomas, 1897, 1918, 1919; Yepes, 1944; Llanos, 1944; Romaña

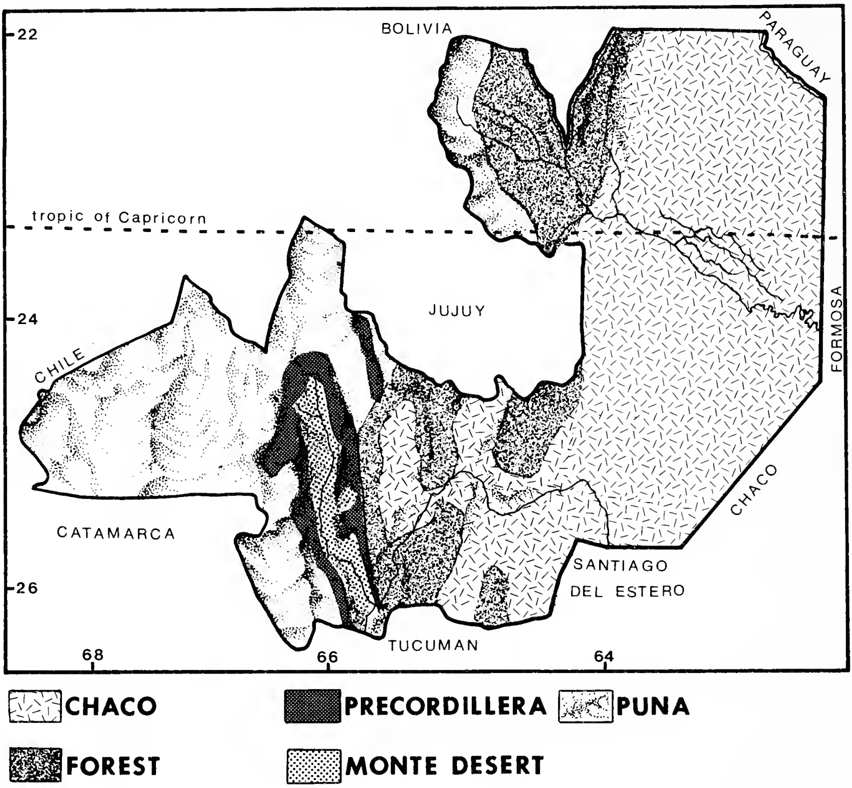

Fig. 3.—A simplified map of the vegetation of Salta Province, showing the five principal habitats: Chacoan thorn scrub; Forest (including both transitional and moist forests); Precordillera, which is found along montane slopes; Monte Desert, in the intermontane valleys of the west; and Puna, or high desert.

and Abalos, 1950; Olrog, 1958, 1959, 1976; Fornes and Massoia, 1967; Villa-R. and Cornejo, 1969), broad faunal surveys or taxonomic treatises (for example, Cabrera and Yepes, 1940; Cabrera, 1957, 1961; Pearson, 1958; Hershkovitz, 1962; Olrog, 1973), or studies dealing with the fauna of specific habitats which form major portions of the vegetation of Salta (for example, Mares, 1973, 1976).

We feel that it is particularly important to begin a survey of this ecologically complex region because, like most of South America, the flora and fauna of Salta are currently threatened by increasing industrialization and habitat modification (for example, Morello and Toledo, 1959*a*, 1959*b*; Aguerre and Quevedo, 1968). Indeed, it is precisely this

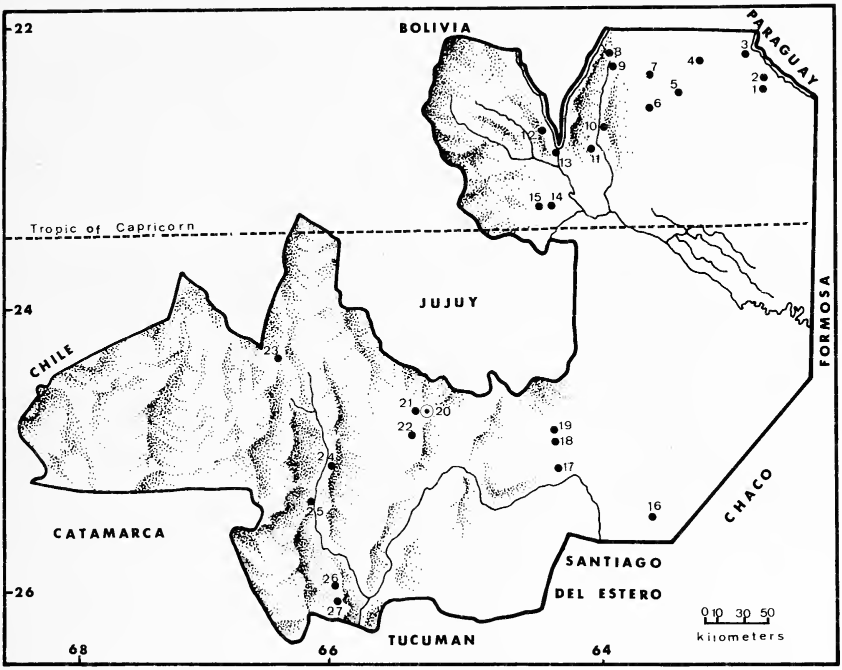

Fig. 4.—Map of the principal collecting localities within Salta Province. Often, more than one area was sampled at any major site. 1) 6 km SW of Santa Victoria, at "El Breal"; 2) Santa Victoria; 3) Santa María; 4) 5 km W of Jollin; 5) Yacimiento Tonono (Tonono Dos); 6) 27 km E Tartagal, along Tonono Rd.; 7) 8.4 km E Campo Durán; 8) Quebrada de Acambuco, 5 km W Dique Itiyuro; 9) 17 km SW beyond Dique Itiyuro; 10) 4 km S Pocoy; 11) 20 km W of General Ballivián, on Puerto Baules Rd.; 12) 24 km NW of Aguas Blancas; 13) Juntas de San Antonio; 14) 15 km S Orán, along Río Santa María; 15) 32 km SW Orán, along Río Santa María; 16) 5 km S of Tolloche, on La Viñita Rd.; 17) 3.7 km N of Ceibalito, and jct. of Anta Rd and Hwy 16; 18) 11 km N of Anta, on El Piquete Rd.; 19) 21 km N of Anta, on El Piquete Rd.; 20) Capital: Salta; 21) 12 km NW Salta, Quebrada de San Lorenzo; 22) INTA Station, Cerrillos; 23) 14 km S jct. Hwys 40 and 51, along Hwy 40 (4100 m); 24) Cachi; 25) 30 km S of Cachi, along Hwy 40; 26) 8 km N La Viñita, along Hwy 40; 27) Cafayate.

rapid encroachment of modern civilization throughout the province that has prompted this preliminary report and a more extensive report which will follow (Mares et al., in preparation). We hope to provide some baseline data on distribution and ecology of the mammals of Salta so that the inevitable changes in faunal distribution patterns that will occur in the near future will be discernible. We also hope to provide some information on a very poorly known fauna.

Fig. 5.—A natural lagoon at "El Breal" in extreme northeastern Salta Province (photograph taken at the end of the dry season). Species occurring in this area include *Molossops temminckii, Holochilus brasiliensis, Oryzomys nigripes, Akodon varius toba, Graomys griseoflavus, Pediolagus salinicola,* and *Lagostomus maximus.* The lagoon is heavily used by domestic livestock.

METHODS

General

Our research in Salta began when the senior author was engaged in an ecological study of the Monte Desert in early 1971. Trapping and survey work in the Monte led to explorations of adjacent mesic habitats. Field work in 1972 was sporadic and occurred principally in the Monte and in the subtropical forest north of Orán. In 1974, additional field work was done in the Monte and Puna of western Salta. Our most extensive period of field work was in 1976 (August–December), when we attempted to sample all major habitats of the province. In 1978 research was concentrated along the upper Río Tarija. Animals were collected by shooting or in traps (cage traps, museum special snap traps, 4-way rat-traps, gopher traps, and Sherman live traps). Bats were collected by mist netting over water or in forested areas. A total of 6130 trap nights was recorded during the course of this study, while 492 animals were collected.

Specimens were examined for reproductive condition in the field, or preserved in formalin for later laboratory analyses. Molting patterns were discerned by either examining flat skins for underlying melanin patterns (Barlow, 1969), or by utilizing a flow of compressed air to make new hair growth visible (Martin, 1973).

Fig. 6.—Part of the Chacoan Forest of extreme northeastern Salta near Santa Victoria. The characteristic "peladar" is evident, which is the area of hard-packed clay devoid of vegetation. A goat track is visible across the area, as is the browse line of the livestock. *Pediolagus salinicola* and *Lagostomus maximus* are common in this area.

Collecting Localities

An annotated list of our principal collecting localities is given below. Location of each collecting site is given in Fig. 4 and the accompanying Gazeteer; numbers below refer to sites listed in Fig. 4 and in the Gazeteer.

1. *El Breal.*—This site was located 6 km southwest of Santa Victoria along a small natural lagoon (Fig. 5). Vegetation is similar to site 2, but extensive areas of sand hummocks supporting xerophytic shrubs were present. The laguna is a center for bird aggregations including *Ajaia ajaja, Egretta thula, Ardea cocoi, Botaurus pinnatus, Jabiru mycteria, Chauna torquata,* and other species. During the dry season, which is the only time these sites are readily accessible due to flooding of primitive roads during the rainy season, domestic animals browse heavily on most natural vegetation.

2. *Santa Victoria* (Fig. 6).—This site is in extreme northeastern Salta near the border of Bolivia, Paraguay, and Argentina, and included the edges of the Río Pilcomayo. The area supports dry Chaco thorn forest with widely-spaced trees (*Acacia, Prosopis, Geoffroea*) on hard-packed soils (the "peladar" of Aguerre and Quevado, 1968). The area is heavily used for cattle and goat foraging. Human influences in the area are pronounced because of ranching activities and the activities of native Mataco and Toba Indians whose villages are situated along the river.

12–15. *Orán, Aguas Blancas-Juntas de San Antonio.*—These sites were all located

Fig. 7.—The Río Pescado in north-central Salta in the Moist Forest (photograph taken near the end of the dry season). Tapirs (*Tapirus terrestris*) occur in and along the river, and many mesic forest mammals (for example, *Lutreolina crassicaudata, Oxymycterus paramensis, Oryzomys legatus,* and *Leo onca*) are common in this area.

in the lower subtropical Moist Forest (Fig. 7). Forestry activities were being initiated in some sites in 1971, and by 1976 large areas of forest had been adversely affected. Banana plantations are common in the area, although most trapping was done in largely undisturbed forest, or in natural second growth areas along rivers or streams. At Juntas de San Antonio, the area sampled was impoverished and consisted of river floodplain supporting dense stands of willows (*Salix*).

16. *Tolloche*.—This site is in the extreme southwest of the province along the border with Santiago del Estero. The area is extremely dry and supports fairly dense Chaco forest. During the dry season, when we collected in the area, understory vegetation was practically nonexistent. Starving cattle were common in the area.

17–19. *Anta*.—This site was in central Salta. Various sites were trapped within this general area extending almost to the limits of the Parque Nacional El Rey and the Río Juramento. Most sites support transitional forest which has been greatly altered by cutting and ranching. Grazing activities of domestic animals have caused grassland portions of the Chaco in this region to be replaced by woody shrubs (Morello and Toledo, 1959*a*, 1959*b*).

23. *San Antonio de Los Cobres*.—The principal locality was situated at 3775 m elevation in the Puna. The high plateau is enclosed by Andean and pre-Andean ranges and is part of a fairly continuous region extending from Mendoza Province in Argentina to southern Peru. The climate is cold, with a mean annual temperature of 7.5°C; precipitation is low (103 mm annually at San Antonio de Los Cobres, A. L. Cabrera, 1976).

Fig. 8.—The puna above San Antonio de los Cobres, with the Nevado de Chañi (peak elevation 6200 m) in the background. The elevation of the plain in the foreground is approximately 4000 m. *Ctenomys opimus* and *Eligmodontia typus* occur in the shrubby areas.

The habitat is sandy in the flats with low scrub vegetation (Fig. 8). Common plants include *Adesmia horridiuscula* (Leguminosae), *Psila boliviensis* (Compositae), and *Fabiana densa* (Solanaceae) (A. L. Cabrera, 1957). One collecting site was at about 4500 m elevation.

24. *Cachi.*—This site is at 2280 m elevation in the southwestern portion of Salta Province and lies at the northernmost limit of the Monte Desert (Morello, 1958). *Prosopis, Larrea,* and *Acacia* comprise the dominant shrubs, while large cacti (*Trichocereus*) are also common.

27. *Cafayate.*—These sites were at 1660 m elevation in the Monte Desert in the valley of the Río Santa María (Fig. 9). Extensive *Prosopis* forests predominate in mesic localities, whereas *Larrea* forms the major vegetation on the bajadas. Tall cacti (*Trichocereus*) are common. The Cafayate area is one of the few Monte areas containing fairly extensive sand dunes. Annual rainfall is 228.3 mm (Morello, 1958); summers are wet and there is a winter drought.

CHECKLIST OF SALTA MAMMALS

The following list includes species comprising genera, families, and orders known or expected in Salta Province. The present status of each species is indicated as being: (i) introduced; (*) collected or seen by us in surveys; (c) common; (u) uncommon; (r) rare; (e) possibly in

Fig. 9.—The Monte Desert near Cafayate in Salta Province. Vegetation in this area consists primarily of *Cercidium praecox, Prosopis, Acacia,* and *Larrea cuneifolia.* This site is along the Río Calchaquies. *Microcavia australis, Eligmodontia typus,* and *Chaetophractus vellerosus* occur in flats, while *Phyllotis darwini* and *Graomys griseoflavus* are found on the slopes.

danger of extirpation; (+) probably extirpated; (p) possibly occurs in the province.

Order Marsupialia	
Family Didelphidae	
Monodelphis fosteri	(r)
Marmosa constanciae	(r)
**Marmosa elegans*	(u)
**Marmosa pusilla*	(u)
**Lutreolina crassicaudata*	(u)
**Didelphis albiventris*	(c)
Order Chiroptera	
Family Noctilionidae	
Noctilio labialis	(u)
Noctilio leporinus	(r)
Family Phyllostomidae	
Tonatia sylvicola	(r)

Glossophaga soricina	(p)
Phyllostomus discolor	(p)
Chrotopterus auritus	(r)
Anoura geoffroyi	(r)
*_Sturnira lilium_	(c)
*_Artibeus jamaicensis_	(c)
Artibeus lituratus	(u)
Pygoderma bilabiatum	(r)
*_Desmodus rotundus_	(u)
Family Vespertilionidae	
*_Myotis levis_	(c)
*_Myotis nigricans_	(u)
*_Myotis albescens_	(u)
Eptesicus brasiliensis	(u)
Eptesicus diminutus	(u)
*_Eptesicus furinalis_	(u)
*_Histiotus macrotus_	(r)
Histiotus montanus	(u)
*_Lasiurus borealis_	(u)
*_Lasiurus cinereus_	(u)
Lasiurus ega	(r)
Family Molossidae	
Molossops planirostris	(r)
*_Molossops temminckii_	(c)
Molossops abrasus	(p)
Tadarida brasiliensis	(c)
Tadarida molossus	(p)
*_Tadarida laticaudata_	(r)
Eumops auripendulus	(p)
*_Eumops bonariensis_	(u)
Eumops glaucinus	(u)
Eumops perotis	(c)
Promops nasutus	(r)
Molossus ater	(u)
*_Molossus molossus_	(u)
Order Primates	
Family Cebidae	
Alouatta caraya	(r)
Cebus apella	(r)
Order Edentata	
Family Myrmecophagidae	
Myrmecophaga tridactyla	(e)
*_Tamandua tetradactyla_	(e)

Family Bradypodidae	
Bradypus boliviensis	(p)
Family Dasypodidae	
Chaetophractus nationi	(p)
**Chaetophractus vellerosus*	(c)
Chaetophractus villosus	(p)
**Euphractus sexcinctus*	(u)
Priodontes giganteus	(e)
Cabassous chacoensis	(p)
**Tolypeutes matacus*	(c)
**Dasypus novemcinctus*	(c)
Dasypus septemcinctus	(r)
Dasypus hybridus	(p)
Burmeisteria retusa	(e)
Order Lagomorpha	
Family Leporidae	
Lepus capensis	(i)
Sylvilagus brasiliensis	(u)
Order Rodentia	
Family Sciuridae	
Sciurus ignitus	(c)
Family Muridae	
**Oryzomys legatus*	(r)
Oryzomys concolor	(p)
**Oryzomys nigripes*	(c)
Rhipidomys leucodactylus	(r)
**Akodon andinus*	(r)
**Akodon boliviensis*	(c)
Akodon caenosus	(p)
**Akodon varius*	(c)
**Akodon albiventer*	(c)
Akodon jelskii	(p)
Bolomys lenguarum	(p)
**Oxymycterus paramensis*	(u)
Calomys lepidus	(r)
**Calomys laucha*	(r)
**Calomys callosus*	(c)
**Eligmodontia typus*	(u)
Phyllotis caprinus	(p)
**Phyllotis darwini*	(c)
Phyllotis osilae	(p)
**Auliscomys sublimis*	(r)

**Graomys domorum*	(r)
**Graomys griseoflavus*	(c)
Andinomys edax	(p)
Chinchillula sahamae	(p)
Euneomys fossor	(r)
Neotomys ebriosus	(r)
**Holochilus brasiliensis*	(c)
Rattus norvegicus	(i)
Rattus rattus	(i)
Mus musculus	(i)
Family Erethizontidae	
Coendou prehensilis	(r)
Family Caviidae	
**Microcavia australis*	(c)
Microcavia shiptoni	(r)
**Galea musteloides*	(c)
Cavia tschudi	(p)
**Pediolagus salinicola*	(c)
Family Hydrochoeridae	
**Hydrochoerus hydrochaeris*	(u)
Family Dasyproctidae	
**Dasyprocta punctata*	(u)
Family Chinchillidae	
**Lagostomus maximus*	(c)
**Lagidium viscacia*	(c)
Chinchilla lanigera	(+)
Family Myocastoridae	
Myocastor coypus	(r)
Family Octodontidae	
Octodontomys gliroides	(p)
Family Ctenomyidae	
**Ctenomys frater*	(u)
**Ctenomys mendocinus*	(c)
**Ctenomys opimus*	(c)
**Ctenomys saltarius*	(c)
Family Abrocomidae	
Abrocoma cinerea	(e)
Order Carnivora	
Family Canidae	
Canis culpaeus	(r-e)
Canis griseus	(p)
Canis gymnocercus	(c)
**Cerdocyon thous*	(c)

Family Procyonidae	
Procyon cancrivorus	(r)
*_Nasua nasua_	(u)
Family Mustelidae	
Lyncodon patagonicus	(r)
Galictis cuja	(u)
*_Eira barbara_	(r-e)
Conepatus chinga	(p)
Conepatus rex	(p)
Lutra platensis	(r-e)
Family Felidae	
Felis colocolo	(r-e)
Felis geoffroyi	(u)
Felis tigrina	(r-e)
Felis wiedii	(r-e)
Felis jacobita	(p)
*_Felis yagouaroundi_	(u)
Felis pardalis	(p)
Felis concolor	(u)
*_Leo onca_	(u)
Order Perissodactyla	
Family Tapiridae	
*_Tapirus terrestris_	(r-e)
Order Artiodactyla	
Family Tayassuidae	
Tayassu pecari	(r)
*_Tayassu tajacu_	(c)
Catagonus wagneri	(r)
Family Cervidae	
Mazama americana	(r-e)
*_Mazama gouazoubira_	(c)
Hippocamelus antisensis	(r-e)
Blastoceros dichotomus	(+)
Ozotoceros bezoarticus	(+)
Family Camelidae	
*_Lama guanicoe_	(r-e)
*_Lama glama_	(c)
Vicugna vicugna	(r-e)

The species Accounts which follow include the order and family of each species, as well as its scientific name followed by the authority and literature citation for the binomial. The Spanish common name (after Olrog, in press) and the English common name follow. In some cases, we were unable to find acceptable English common names, so we have either translated the Spanish name directly, or included a descriptive English common name which we have coined for this report. All measurements are in mm, while weight is given in grams. Specimens from the Quebrada de Acambuco are housed in the collection of mammals at the Instituto Miguel Lillo in San Miguel de Tucumán, Argentina. All other specimens are in the collection of mammals of the Carnegie Museum of Natural History in Pittsburgh. Two localities to which we commonly refer are the Río Pescado, which is located about 24 km NW of Aguas Blancas in the Departamento de Orán, and the INTA (Instituto Nacional de Tecnología Agropecuaria) station in Cerrillos, near the capital city of Salta. We visited 27 principal collecting localities, but at times traps were set at more than one site within each principal locality. Thus we trapped at a total of 45 locations across the province.

ACCOUNTS OF SPECIES

Order Marsupialia

Family Didelphidae

Marmosa elegans (Waterhouse)

marmosa elegante — elegant mouse opossum

1839. *Didelphis elegans* Waterhouse, Zool. Beagle, Mamm.:95.
1894. *Marmosa elegans* Thomas, Ann. and Mag. Nat. Hist., ser. 6, 14:188.

Specimens examined (5).—CAPITAL: Quebrada de San Lorenzo, 12 km NW Salta, 1. GENERAL SAN MARTIN: 27 km E Tartagal, along Tonono Rd., 1. ORAN: Juntas de San Antonio, 1; 24 km NW of Aguas Blancas, 2.

Measurements.—One ♂: total length, 251; tail, 142; hind foot, 14.5; ear, 24.6; weight, 41. Cranial measurements (1 ♂): greatest length of the skull, 29.9; condylobasal length, 29.9; zygomatic breadth, 16.2; breadth of braincase, 11.1; least interorbital breadth, 5.3; palatal length, 15.8; length of maxillary toothrow, 9.8; length of mandibular toothrow, 10.7.

Remarks.—Mouse opossums are not common anywhere in Salta, though they are easiest to catch in the moist forest of the north. Specimens in northern Salta were taken under clumps of bamboo (*Chusquea*) from burrows located within the dense cane patches. Other animals were taken under logs near streams, and on the littered floor of second growth forest. One individual was caught from a burrow in the rocky embankment of the Río Pescado.

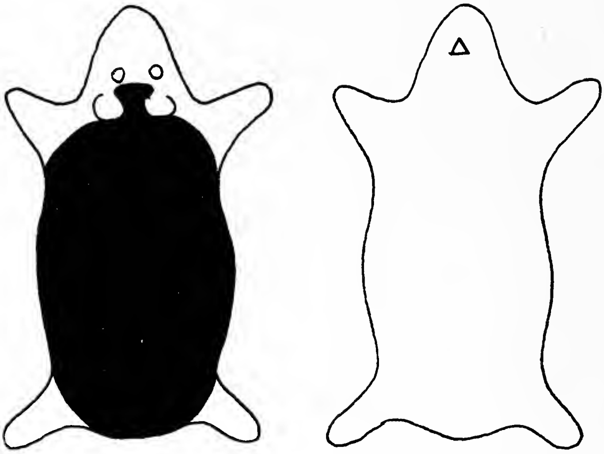

Fig. 10.—Diagram of the full dorsal molt of a *Marmosa pusilla* taken near Cachi in April, during the late autumn. No melanin deposits were evident ventrally.

Marmosa pusilla (Desmarest)
marmosa común — common mouse opossum

1804. *Didelphis pusilla* Desmarest, Nouv. Dict. d'Hist. Nat., 24:19.
1914. *Marmosa pusilla* Bertoni, Fauna Parag., p. 69.

Specimens examined (3).—ANTA: 5 km S of Tolloche, on La Viñita Rd., 1. CACHI: 30 km E of Cachi, 2.

Measurements.—One ♂ and two ♀♀, respectively: total length, 170, 170, 187; tail, 90, 90, 99; hind foot, 11.5, 13.2, 12.3; ear, 24.1, 23.0, 22.0; weight, 13.3, 15.3, 18. Cranial measurements of 1 ♂: greatest length of the skull, 24.4; condylobasal length, 23.9; zygomatic breadth, 12.5; least interorbital breadth, 3.9; breadth of braincase, 10.2; length of maxillary toothrow, 8.6; length of mandibular toothrow, 8.9; breadth across canines, 2.2; breadth across last molars, 4.8.

Remarks.—This species is less common than *M. elegans* and inhabits much drier localities. The specimens near Cachi were taken from a steep, rocky xeric hillside, whereas the specimen from Tolloche was collected in very dry thorn scrub. *Marmosa pusilla* is widespread throughout the arid parts of Salta but is never common, nor is its presence easy to predict. The Cachi specimens were in full molt dorsally (Fig. 10).

Lutreolina crassicaudata (Desmarest)
comadreja colorada — little water opossum

1804. *Didelphis crassicaudata* Desmarest, Nouv. Dict. d'Hist. Nat., 24:19.
1923. *Lutreolina crassicaudata* Thomas, Ann. and Mag. Nat. Hist., ser. 9, 11:584.

Fig. 11.—The little water opossum, *Lutreolina crassicaudata,* captured along the Río Pescado in north-central Salta. The weasel-like body form is evident.

Specimens examined (2).—ORAN: 24 km NW of Aguas Blancas, 2.

Measurements.—One ♂ and one ♀, respectively: total length, 501, 452; tail 262, 255; hind foot, 40.4, 35.8; ear, 25.6, 24.8; weight, 260, 176. Cranial measurements of the female: greatest length of the skull, 55.5; condylobasal length, 56.0; zygomatic breadth, 27.5; least interorbital breadth, 7.7; breadth of braincase, 16.8; palatal length, 31.1; length of maxillary toothrow, 19.3; length of mandibular toothrow, 17.6; breadth across canines, 5.3; breadth across last molars, 9.7.

Remarks.—This weasel-like opossum (Fig. 11) is probably widespread throughout the mesic forests of Salta and occurs as far south as San Miguel de Tucumán, Tucumán Province. The animals are most common along small quiet brooks in dense forest.

Didelphis albiventris Lund
comadreja común — opossum

1841. *Didelphis albiventris* Lund, Kongl. Dansk. Vid. Selsk. Afhand., 8:236.

Specimen examined (1).—RIVADAVIA: 6 km SW Santa Victoria, at "El Breal," 1.

Measurements.—One ♀: total length, 617; tail, 322; hind foot, 48.5; ear, 56.8; weight, 1900. Cranial measurements: greatest length of the skull, 83.8; condylobasal length, 83.0; zygomatic breadth, 40.8; least interorbital breadth, 10.1; breadth of braincase, 23.1; palatal length, 50.6; length of maxillary toothrow, 29.7; length of mandibular toothrow, 32.2; breadth across canines, 10.4; breadth across last molars, 5.6.

Remarks.—Opossums are common throughout Salta Province in forests, along river valleys, and in agricultural areas. They do not frequent areas which are very dry or which are at high elevations. The animals are heavily hunted throughout the province for their skins; they are not eaten.

Order Chiroptera

Family Phyllostomatidae

Sturnira lilium (Geoffroy)
falso vampiro flor de lis — yellow-shouldered bat

1810. *Phyllostoma lilium* Geoffroy, Ann. Mus. Paris, 15:181.
1855(1856) *Sturnira lilium* Gervais, Exped. Castelnau. Zool.:39.

Specimens examined (34).—GENERAL SAN MARTIN: Quebrada de Acambuco, 5 km W Dique Itiyuro, 1. ORAN: Juntas de San Antonio, 17; 24 km NW of Aguas Blancas, 16.

Measurements.—Mean and range of 10 ♂♂ and 10 ♀♀, respectively: total length, 60.5 (53–67), 58.1 (48–65); hind foot, 11.9 (10.5–14.3), 11.8 (10.5–17.7); ear, 18.2 (16.3–19.5), 17.9 (16.8–18.6); forearm, 42.8 (40.3–46.1), 43 (39.4–47.2); weight, 22.5 (15.3–26), 19.8 (14.1–25).

Remarks.—This is one of the most common bats in mesic areas of Salta. All specimens taken near Aguas Blancas in July (dry season) were reproductively active with testes length averaging 3.8 mm in length (range 2.5–5.3 mm). Two of 10 females were lactating. The male taken in November in Acambuco had testes measuring 4.2 mm in length.

Artibeus jamaicensis Leach
falso vampiro grande — Jamaican fruit bat

1821. *Artibeus jamaicensis* Leach, Trans. Linn. Soc., 13:75.

Specimens examined (16).—ORAN: Juntas de San Antonio, 13; 15 km S Orán, along Río Santa María, 3; 22 km SW Orán, along Río Santa María, 1.

Measurements.—Mean and range for six individuals (all adults; three ♂♂ and three ♀♀): head and body length, 86.8 (83–90); tail, 0; hind foot, 16.9 (15.9–18.1); ear, 24.4 (22.9–25.6); forearm, 66.6 (63.6–68.6); weight, 53.3 (45–60). Cranial measurements (two ♀♀): greatest length of the skull, 29.0, 29.9; condylobasal length, 26.3, 28.0; zygomatic breadth, 18.5, 19.4; breadth of braincase, 15.7, 15.6; least interorbital breadth, 7.2, 7.7; palatal length, 14.7, 15.1; length of mandibular toothrow, 10.8, 11.5; length of maxillary toothrow, 7.8, 9.5; breadth across canines, 3.8, 4.5; breadth across last molars, 6.5, 7.2.

Remarks.—This is another very common bat in mesic portions of Salta and is the most common large fruit-eating bat.

Desmodus rotundus (Geoffroy)
vampiro de Azara — vampire

1810. *Phyllostoma rotundum* Geoffroy, Ann. Mus. Paris, 15:181.
1901. *Desmodus rotundus* Thomas, Ann. and Mag. Nat. Hist., ser. 7, 8:194.

Specimen examined (1).—GENERAL SAN MARTIN: Quebrada de Acambuco, 5 km W Dique Itiyuro, 1.

Measurements.—One ♂: total length, 95; hind foot, 16.2; ear, 20.2; forearm, 62; weight, 35.

Remarks.—Vampires are not common anywhere within the province of Salta, although they may occur with some frequency in the southeastern parts of the province in areas where many cattle and goats are kept. The reproductively active male taken in November had testes measuring 9.7 mm in length.

Family Vespertilionidae

Myotis nigricans (Schinz)
murciélago castaño — black Myotis

1821. *Vespertilio nigricans* Schinz, Thierr., 1:179.
1897. *Myotis nigricans* Miller, North American Fauna, 13:74.

Specimen examined (1).—ORAN: 15 km S Orán, along Río Santa María, 1.

Measurements.—One ♂: total length, 78; tail, 35; hind foot, 7.1; ear, 13.7; forearm, 34.5. Cranial measurements: greatest length of the skull, 12.9; condylobasal length, 12.7; zygomatic breadth, 8.2; least interorbital breadth, 3.6; breadth of braincase, 6.2; palatal length, 7.0; length of maxillary toothrow, 4.1; length of mandibular toothrow, 4.9; breadth across canines, 2.2; breadth across last molars, 2.7.

Remarks.—This small bat probably occurs uncommonly throughout the province, although it is most common in mesic areas of the central forested region.

Myotis albescens (Geoffroy)
murciélago blancuzco — hoary Myotis

1806. *Vespertilio albescens* Geoffroy, Ann. Mus. Paris, 8:204.
1900. *Myotis albescens* Thomas, Ann. Mus. Civ. Genova, 40:546.

Specimens examined (2).—ORAN: 22 km SW Orán, along Río Santa María, 1. RIVADAVIA: 6 km SW Santa Victoria, at "El Breal," 1.

Measurements.—One ♂ and one ♀, respectively: total length, 85, 82; tail, 35, 37; hind foot, 8.7, 7.6; ear, 14.6, 13.1; forearm, 34.9, 35.7; weight, 7.5, 6.2. Cranial measurements (one ♂): greatest length of the skull, 13.3; condylobasal length, 12.6; breadth of braincase, 7.0; least interorbital breadth, 4.0; palatal length, 5.2; length of maxillary toothrow, 4.5; length of mandibular toothrow, 4.8; breadth across canines, 2.6; breadth across last molars, 2.7.

Remarks.—This is an uncommon *Myotis* in Salta and probably occurs primarily in the northern lowlands.

Eptesicus furinalis (D'Orbigny)
murciélago parduzco — brown bat

1847. *Vespertilio furinalis* D'Orbigny, Voy. Amer. Merid., 4:13.
1920. *Eptesicus furinalis* Thomas, Ann. and Mag. Nat. Hist., ser. 9, 5:365.

Specimens examined (5).—General San Martin: Quebrada de Acambuco, 5 km W Dique Itiyuro, 5.

Measurements.—Mean and range for five individuals (three ♂♂ and 2 ♀♀): total length, 95.3 (86–103); tail, 38.6 (32–43); hind foot, 7.3 (7.0–8.0); ear, 15.6 (15.1–16.0); forearm, 39.9 (37.4–40.8); weight, 9.3 (8–11).

Remarks.—This is an uncommon bat in Salta and probably occurs throughout the province in the lowlands and low mountains supporting forest vegetation. The five specimens taken in November (the rainy season) were all molting and none was breeding. Male testes (abdominal) were 4.4 and 4.8 mm in length in two specimens. All specimens were molting over the entire body with melanin visible under all parts of the skin.

Histiotus montanus (Philippi and Landbeck)
murciélago orejón chico — small big-eared bat

1861. *Vespertilio montanus* Philippi and Landbeck, Arch. Naturg.:289.
1907. *Histiotus montanus* Miller, Bull. U.S. Nat. Mus., 57:214.

Specimens examined (3).—General San Martin: Quebrada de Acambuco, 5 km W Dique Itiyuro, 3.

Measurements.—One ♂ and one ♀, respectively: total length, 117, 117; tail, 57, 55; hind foot, 8.3, 8.8; ear, 34.7, 34.8; forearm, 47.5, 47.2; weight, 11, 13.

Remarks.—This uncommon big-eared insectivorous bat is probably widely distributed throughout the province. A female taken in November was lactating, whereas a male taken at the same time had abdominal testes measuring 4.4 mm in length. One specimen was molting over 60% of its body.

Lasiurus borealis (Müller)
murciélago peludo rojizo — red bat

1776. *Vespertilio borealis* Müller, Natursyst. Suppl.:20.
1901. *Lasiurus borealis* Thomas, Ann. and Mag. Nat. Hist., ser. 7, 8:435.

Specimens examined (2).—General San Martin: Quebrada de Acambuco, 5 km W Dique Itiyuro, 1. Oran: 15 km S Orán, along Río Santa María, 1.

Measurements.—One ♂ and one ♀, respectively: total length, 106, 102; tail, 47, 54; hind foot, 8.9, 7.8; ear, 11.3, 14.7; forearm, 37.8, 41.1; weight, 8.5, 10.

Remarks.—Red bats are regular, but uncommon, throughout Salta Province, particularly in the central low mountain areas. One of the specimens evidenced molting on the head.

Lasiurus cinereus Beauvois
murciélago blancuzco — hoary bat

1796. *Lasiurus cinereus* Beauvois, Cat. Rais. Mus. Mr. C. W. Peale, Philadelphia-Paris:18.

Specimen examined (1).—GENERAL SAN MARTIN: Quebrada de Acambuco, 5 km W Dique Itiyuro, 1.

Measurements.—One ♂: total length, 130; tail, 63; hind foot, 9.4; ear, 17.1; forearm, 54.5; weight, 20.5.

Remarks.—This is an uncommon species in Salta but probably resembles the red bat in its pattern of occurrence. The specimen was molting (internal melanin deposits) over 60% of its body (captured in November).

Family Molossidae

Molossops temminickii (Burmeister)
moloso pigméo — Temminck's free-tailed bat

1854. *Dysopes temminickii* Burmeister, Sys. Uebers. Thiere Brasil:72.
1907. *Molossops temminckii* Miller, Bull. U.S. Nat. Mus., 57:248.

Specimens examined (21).—GENERAL SAN MARTIN: Quebrada de Acambuco, 5 km W Dique Itiyuro, 1. RIVADAVIA: 6 km SW of Santa Victoria, at "El Breal," 21.

Measurements.—Mean and range for five ♂♂ and five ♀♀, respectively: total length, 72.8 (70–76), 73.2 (68–75); tail, 24.6 (21–27), 25.6 (22–28); hind foot, 6.2 (5–6.9), 6.6 (6.4–6.7); ear, 12.1 (7.8–13.6), 12.8 (11.5–13.6); forearm, 30.6 (29.6–31.3), 30.5 (29.6–31.8); weight, 5.6 (5.2–6.5), 5.4 (5–5.6). Cranial measurements (two ♀♀): greatest length of the skull, 13.3, 13.6; condylobasal length, 13.0, 13.0; least interorbital breadth, 3.6, 3.5; breadth of braincase, 6.8, 6.7; palatal length, 6.4, 6.7; length of maxillary toothrow, 3.9, 4.5; length of mandibular toothrow, 4.3, 4.6; breadth across canines, 2.0, 1.9; breadth across last molars, 3.6, 3.4.

Remarks.—This is a common bat in the eastern lowlands of the province in Chaco vegetation, particularly if free water is nearby. The specimens taken at Santa Victoria were caught just before sunset and many bats were flying at least one hour prior to sunset. They appeared to fly in groups and were apparently foraging for insects along the edge of a saline lake. One specimen taken in November in Acambuco (the rainy season) was molting and carried one embryo.

Tadarida laticaudata Geoffroy
moloso colilargo — broad-tailed molossid

1805. *Tadarida laticaudata* Geoffroy, Ann. Mus. Paris, 6:156.

Specimen examined (1).—ORAN: 22 km SW Orán, along Río Santa María, 1.

Measurements.—One ♂: total length, 116; tail, 53; hind foot, 9.8; ear, 20.6; forearm, 46.7; weight, 14.

Remarks.—This is a very uncommon free-tail bat that probably occurs sporadically over most of the lower elevation habitats of central Salta. The only specimen we captured was taken over water in a lush area of mixed forest and orchards. This also represents an extension of its known range within Argentina (see Barquez and Ojeda, 1975).

Eumops bonariensis (Peters)
moloso orejiancho — small mastiff bat

1874. *Promops bonariensis* Peters, Monatsb. Preuss. Akad. Wiss. Berlin:232–234.
1916. *Eumops bonariensis* Osgood, Field Mus. Publ., Zool., 10:214.

Specimens examined (2).—GENERAL SAN MARTIN: Quebrada de Acambuco, 5 km W Dique Itiyuro, 1; ORAN: 15 km S Orán, along Río Santa Mariá, 1.

Measurements.—One ♂ and one ♀, respectively: total length, 99, 122; tail, 35, 51; hind foot, 8.0, 9.1; ear, 19.8, 15.1; forearm, 43.8, 47.2; weight, 11.5, 19. Cranial measurements (one ♂): greatest length of the skull, 17.7; condylobasal length, 16.3; zygomatic breadth, 10.5; least interorbital breadth, 4.0; breadth of braincase, 9.1; palatal length, 6.5; length of maxillary toothrow, 4.9; length of mandibular toothrow, 6.0.

Remarks.—The female taken in November was pregnant with a 3 g fetus. Neither specimen was molting. This species probably occurs over much of central Salta, though it is uncommon in all areas.

Molossus molossus (Pallas)
moloso coludo — velvety free-tailed bat

1766. *Vespertilio molossus* Pallas, Misc. Zool. Hagae Comitum., 12:49.
1805. *Molossus molossus* Geoffroy, Ann. Mus. Hist. Nat. Paris, 6:151.

Specimens examined (2).—GENERAL SAN MARTIN: Quebrada de Acambuco, 5 km W Dique Itiyuro, 2.

Measurements.—One ♂ and one ♀, respectively: total length, 103, 101; tail, 36, 37; hind foot, 9.0, 7.8; ear, 15.1, 14.7; forearm, 38.0, 38.4; weight, 13, 15.

Remarks.—The female was pregnant and lactating at the same time (captured in November). This is an uncommon bat throughout the province, but probably occurs over much of the central lowlands and valleys, although there is always a good possibility that this and several other "uncommon" species are actually rather widespread and common, but are difficult to catch.

Order Edentata

Family Myrmecophagidae

Tamandua tetradactyla (Linné)
oso melero — tamandua

1758. *Myrmecophaga tetradactyla* Linné, Syst. Nat.:35.
1825. *Tamandua tetradactyla* Gray, Annal. Philos., 10:343.

Specimen examined (1, skin only).—Santa María (extreme NE Salta), 1.

Measurements.—No measurements available.

Remarks.—This anteater is fairly common over the eastern half of Salta where it is heavily hunted for its hide. The single specimen we examined had been taken in very dry thorn scrub along the northeastern border of Salta. The coloration of our specimen is golden yellow with black stripes extending from the anterior portion of the forelimbs to the back.

Family Dasypodidae

Chaetophractus vellerosus Gray
quirquincho chico — little hairy armadillo

1865. *Dasypus vellerosus* Gray, Proc. Zool. Soc. London:376.
1928. *Chaetophractus vellerosus* Yepes, Rev. Univers. Buenos Aires, ser. 2, 1:500.

Specimens examined (1 complete and 2 shells).—GENERAL SAN MARTIN: 8.4 km E Campo Durán, 1. RIVADAVIA: near Santa Victoria (extreme NE Salta), 2.

Measurements.—One ♂: total length, 328; tail, 106; hind foot, 49.0; ear, 31.5; weight, 760.

Remarks.—This is a very common armadillo in Salta in the eastern thorn scrub lowlands. It is also common in some of the high mountains as well as the valleys of the Monte Desert and is most frequently noted by its numerous burrows. It probably occurs in all major habitats of Salta with the possible exception of the highest Puna. It is not common in moist forests. Individuals are heavily hunted with dogs for their shells, which are used in making small guitars, or *charangos,* as well as for food. They are regarded as a delicacy.

Euphractus sexcinctus (Linné)
gualacate — six-banded armadillo

1758. *Dasypus sexcinctus* Linné, Syst. Nat.:51.
1911. *Euphractus sexcinctus* Thomas, Proc. Zool. Soc. London:141.

Specimens examined (2, shells only).—GENERAL SAN MARTIN: Yacimiento Tonono (Tonono 2), E of Tartagal, 1. RIVADAVIA: near Santa Victoria (extreme NE of Salta), 1.

Measurements.—No measurements available.

Remarks.—Like other armadillos, *Euphractus* are heavily hunted for food. In eastern Salta, the Mataco and Toba Indians use *Euphractus* tails to carry fibers which are easily ignited after striking the shells of the tail with a flint, thus serving as a "cigarette lighter." *Euphractus* are regular, but uncommon, over the eastern half of the province.

Tolypeutes matacus (Desmarest)
quirquincho bola — three-banded armadillo

1804. *Loricatus matacus* Desmarest, Nouv. Dict. Hist. Nat.:28.
1919. *Tolypeutes matacus* Osgood, J. Mamm., 1:33.

Specimens examined (5, shells only).—GENERAL SAN MARTIN: 4 km S Pocoy, 2; Yacimiento Tonono (Tonono 2), E of Tartagal, 2. RIVADAVIA: 5 km W of Jollin, 1.

Measurements.—No measurements available.

Remarks.—This may be the most common armadillo in the eastern lowlands of Salta where it coexists with *Chaetophractus, Euphractus,* and *Priodontes*. Like the other armadillos, *Tolypeutes* is hunted for food. Its shells are also used as regional artifacts throughout the northwest.

Dasypus novemcinctus Linné
mulita grande — nine-banded armadillo

1758. *Dasypus novemcinctus* Linné, Syst. Nat.:51.

Specimen examined (1, shell only).—ORAN: 15 km S Orán, along Río Santa María, 1.

Measurements.—No measurements available.

Remarks.—This armadillo is commonly found in heavily forested areas of Salta, particularly in lowland mesic areas. It is hunted and eaten.

Order Rodentia

Family Cricetidae

Oryzomys legatus Thomas
colilargo acanelado — large-headed rice rat

1925. *Oryzomys legatus* Thomas, Ann. and Mag. Nat. Hist., ser. 9, 15:575.

Specimens examined (6).—GENERAL SAN MARTIN: 17 km SW beyond Dique Itiyuro, 1. ORAN: 24 km NW Aguas Blancas, 5.

Measurements.—Mean and range for one ♂ and four ♀♀: total length, 273.6 (255–286); tail, 148.8 (140–155); hind foot, 33.3 (32.7–34.0); ear, 24.9 (24.1–25.8); weight, 55.2 (43–80). Cranial measurements: greatest length of the skull, 34.0 (33.4–35.2); condylobasal length, 33.4 (32.6–34.7); zygomatic breadth, 17.6 (17.3–18.4); least interorbital breadth, 5.9 (5.7–6.3); breadth of braincase, 13.0 (12.8–13.4); palatal length, 16.6 (16.4–16.9); length of maxillary toothrow, 5.2 (5.0–5.3); length of mandibular toothrow, 5.5 (5.4–5.5); diastema length, 8.5 (8.2–8.7).

Remarks.—This is the largest *Oryzomys* in Salta and occurs only in mesic forests and transitional forests in the north-central portion of the province. They are not abundant in any area but are most common in littered forested areas supporting little undergrowth where they inhabit burrows in the forest floor. Some specimens were also taken in dense second growth vegetation along streams and roads, as well as from the rocky banks of the Río Pescado. The species reaches its southern limit in Salta.

The testes of a specimen taken in northern Salta at Itiyuro in September were inguinal and measured 8.6 mm in length. We follow Massoia (1974) in the specific classification of these populations. See also Gardner and Patton (1976) for the synonymy of this species with *O. nitidus*.

Oryzomys nigripes (Olfers)
colilargo común — common rice rat

1818. *Mus nigripes* Olfers, Eschwege Neue Bibl. Reisenbr., 51:209.
1959. *Oryzomys nigripes* Hershkovitz, Jour. Mamm., 40, 3:339.

Specimens examined (26).—ANTA: 21 km N Anta, on El Piquete Rd. along Río del Valle, 2. CERRILLOS: INTA Station, 9. GENERAL SAN MARTIN: 17 km SW, beyond Dique Itiyuro, 2; 20 km W General Ballivián, on Puerto Baulés Rd., 1. ORAN: Juntas de San Antonio, 3; 24 km NW Aguas Blancas, 1. RIVADAVIA: 6 km SW Santa Victoria, at "El Breal" (extreme NE Salta), 8.

Measurements.—Mean and range for three ♂♂ and four ♀♀: total length, 213.7 (181–242); tail, 128.4 (113–150); hind foot, 24.7 (22.9–26.2); ear, 18.9 (17.0–21.6); weight, 21.4 (13.5–29.5). Cranial measurements: greatest length of the skull, 24.9 (23.0–27.8); condylobasal length, 22.2 (20.4–24.5); zygomatic breadth, 13.1 (12.3–15.0); least interorbital breadth, 3.7 (3.3–4.2); breadth of braincase, 11.0 (10.5–11.6); palatal length, 11.7 (10.8–12.7); length of maxillary toothrow, 3.6 (3.3–3.9); length of mandibular toothrow, 3.7 (3.4–4.0); diastema length, 5.9 (5.2–6.4).

Remarks.—This is one of the most common small mammals in forested areas of Salta. Its habitats include mesic forests, gallery forests and old fields in fairly mesic areas. Animals were captured from burrows under rocks and logs or in trees. In northern Salta, specimens were captured in dense cane (*Chusquea*) thickets. These mice are also common along permanent rivers supporting gallery forest in the Monte Desert of the southwestern parts of the province.

A male captured in September in Itiyuro had inguinal testes measuring 7.2 mm in length. Another captured near General Ballivián in late September had scrotal testes measuring 7.7 mm in length, whereas a male captured near Pocoy at about the same time had scrotal testes with a length of 6.9 mm. A female captured with the latter individual evidenced a copulatory plug. In October in far eastern Salta ("El Breal") a pregnant female (five embryos) was captured, whereas a male with large scrotal testes was taken at the same time and a second male with large scrotal testes (9.3 mm in length) was also taken. Two other females captured at about the same time in that locality had embryos (1 embryo equals 12.9 mm crown-rump length; 4 embryos equal 21.6, 19.1, 19.0 mm crown-rump length). Two males taken near Anta in mid-October had scrotal testes of 7.3 mm and 8.0 mm in length, respectively.

Molt in *O. nigripes* is from ventral to dorsal and proceeds caudally (Fig. 12). Of four individuals captured in July, none was molting. One of nine individuals taken in September was molting over 25% of its body, while four of seven animals taken in October were molting over less than 50% of their body. Ojeda (1980) discusses molt in this species in Tucumán, while Mares (1977*a*) reports on water balance for two populations.

Our designation of this species as *O. nigripes* rather than *O. longicaudatus* follows Hershkovitz (1959) and Wetzel and Lovett (1974).

Akodon andinus (Philippi)
ratón andino — Andean grass mouse

1858. *Mus andinus* Philippi, Arch. Naturg., 23, I:77.
1898. *Akodon andinus* Trouessart, Catal. Mammal., 2:535.

Specimens examined (2).—LA POMA: 18 km S jct Hwys 40 and 51, along Hwy 40, 4500 m, 2.

Measurements.—One ♂ and one ♀, respectively: total length, 133, 125; tail, 54, 49; hind foot, 20.2, 19.5; ear, 16.0, 13.8; weight, 18, 13. Cranial measurements: greatest length of the skull, 22.9, 22.2; condylobasal length, 22.5, 20.9; least interorbital breadth, 4.0, 4.1; breadth of braincase, 10.8, 11.3; palatal length, 11.0, 10.1; length of maxillary toothrow, 3.4, 3.3; length of mandibular toothrow, 3.2, 3.8; diastema length, 5.9, 5.3.

Remarks.—This small buffy *Akodon* was only taken at out highest collecting locality at approximately 4500 m. The species is largely diurnal, at least in April (autumn) at this altitude. Both animals were captured on fairly steep rocky hillsides. The male had large scrotal testes (10.7 mm in length), while the female was not breeding. The male was molting primarily on the dorsum (Fig. 13), although we were unable to discern the pattern of molt.

Akodon boliviensis Meyen
ratón plomizo — Bolivian grass mouse

1833. *Akodon boliviensis* Meyen, Verhandl. Kais. Leop. Carol. Akad. Wiss., 16, II:600.

Specimens examined (23).—CAPITAL: Quebrada de San Lorenzo, 12 km NW Salta, 2. CERRILLOS: INTA Station, 11. ORAN: 24 km NW Aguas Blancas, 10.

Measurements.—Mean and range for 10 individuals: total length, 162.9 (153–183); tail, 76.3 (71–83); hind foot, 22.3 (20.3–24.0); ear, 17.4 (15.5–20.3); weight, 19.4 (14.3–25.5). Cranial measurements of four individuals: greatest length of the skull (N = 1), 25.1; condylobasal length (N = 1), 23.2; zygomatic breadth (N = 2), 12.5, 15.0; least interorbital breadth (N = 2), 4.6, 5.0; breadth of braincase (N = 2), 12.5, 11.0; palatal length, 14.6, 12.2, 12.4, 12.1; length of maxillary toothrow, 4.6, 3.8, 3.7, 4.0; length of mandibular toothrow, 4.9, 4.0, 4.0, 4.1; diastema length (N = 3), 7.9, 7.2, 6.3.

Remarks.—This small dark *Akodon* is one of the commonest rodent species found in Salta, particularly in second growth areas in mesic forest localities. Specimens were taken under rocks and logs, and along streams and road cuts. They are also common in agricultural areas. This species is found throughout the central, low-elevational, moist forested regions of the province, where it co-occurs with the larger *Akodon varius,* and probably with the slightly smaller, buffier *A. caenosus* as well (see Barquez et al., 1980).

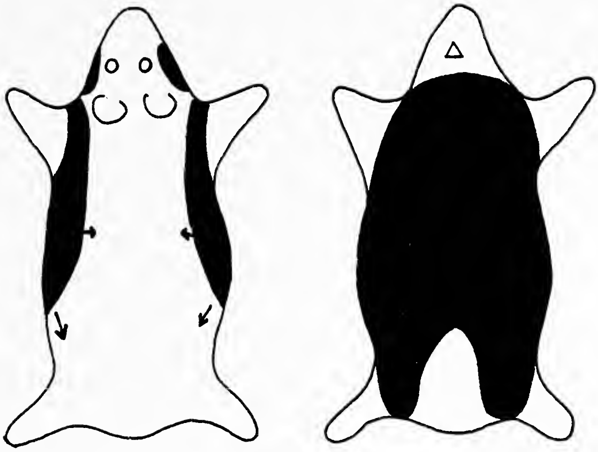

Fig. 12.—Molting pattern in *Oryzomys nigripes*—the venter is completely pigmented with melanin, while molt proceeds dorsally and posteriorly.

Akodon varius Thomas
ratón variado — variable grass mouse

1902. *Akodon varius* Thomas, Ann. and Mag. Nat. Hist., ser. 9, 1:190.

Specimens examined (66).—CAFAYATE: 6 km NE Cafayate, along Hwy 68, 1; 5 km W Cafayate, Yacochuya, 1. CERRILLOS: INTA Station, 13. GENERAL SAN MARTIN: 4 km S Pocoy, 3; 17 km SW, beyond Dique Itiyuro, 17; 20 km W General Ballivián on Puerto Baulés Rd., 13. GUACHIPAS: 20 km S Pampa Grande, along Hwy 9, 3. ORAN: Juntas de San Antonio, 1; 22 km SW Orán, along Río Santa María, 6; 24 km NW Aguas Blancas, 18. RIVADAVIA: 6 km SW of Santa Victoria, at "El Breal," 1.

Measurements.—Mean and range for three ♂♂ and five ♀♀ (from Orán): total length, 190.1 (160–222); tail, 89 (81–103); hind foot, 25.2 (20.8–26.7); ear, 21.5 (20.6–23.2); weight, 39.2 (20–60). Cranial measurements: greatest length of the skull, 28.7 (26.3–30.8); condylobasal length, 26.8 (24.5–28.5); zygomatic breadth, 14.4 (13.7–15.2); least interorbital breadth, 5.2 (5.0–5.8); breadth of braincase, 12.5 (12.1–12.8); palatal length, 13.4 (11.7–15.1); length of maxillary toothrow, 4.8 (4.3–5.3); length of mandibular toothrow, 4.7 (4.2–5.2); diastema length, 7.3 (6.6–8.2).

Remarks.—This species and *O. nigripes* are the most common small mammals over mesic parts of Salta. *Akodon varius* is abundant in second growth portions of forested areas, river banks, stream banks, sugarcane fields, old fields, orchards and grasslands. This is the largest *Akodon* in Salta and co-occurs frequently with *A. boliviensis, O. nigripes,* and *C. callosus* (Ojeda, 1979). Individuals are often captured from burrows under logs or rocks or in forest litter. The species is nocturnal. There is much morphological and karyological variation in individuals within and among populations (Barquez et al., 1980).

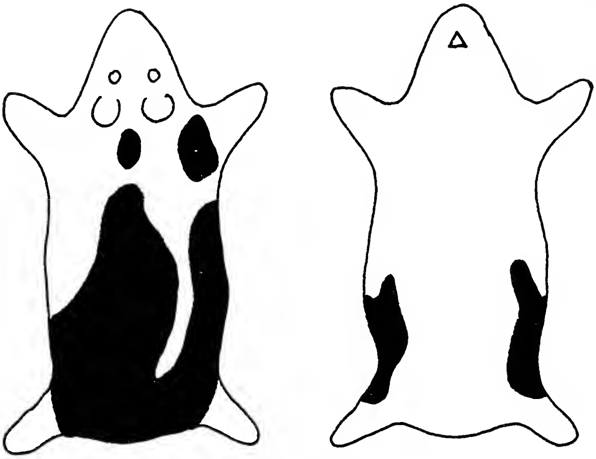

Fig. 13.—Pattern of melanin deposition in a male *Akodon andinus* captured in April at 4500 m elevation.

Of two males taken in April, one had scrotal testes (10.8 mm in length), while the other had abdominal testes (5.1 mm in length). Two females captured at this time were not breeding. One male taken in August had inguinal testes. Of eight males captured in September, five had scrotal testes with lengths of 8.0, 8.7, 9.0, 9.6 and 11.4 mm, respectively, while the other three had inguinal testes of lengths 7.3 and 8.7 mm. In October, of six females, three had closed vaginas, one had a plugged vagina, and one had an open vagina. Of 11 males captured at this time, 10 had scrotal testes with lengths (N = 4) of 5.7, 8.8, 9.3, and 14.6 mm, whereas one had inguinal testes. In November, two females were lactating, one with an open and one with a plugged vagina. Three males taken in this month had scrotal testes and one had inguinal testes.

Molt in *A. varius* proceeds from anterior to posterior and from dorsal to ventral (Fig. 14). Of 10 individuals taken in July, none was molting. Nine of 30 animals were molting in September, with eight having melanin over less than 10% of their surface, while one was molting over more than 10% of its body. Five of 13 animals taken in October were molting: two at a level below 10%, two at about a 25% level, and one at more than 50%. All six specimens examined in November were molting–three at less than 10% and three at greater than 50% levels. One of four animals taken in April, a young individual, was molting over 10% of its body (Fig. 15).

Mares (1975*a*) discusses water balance in this species.

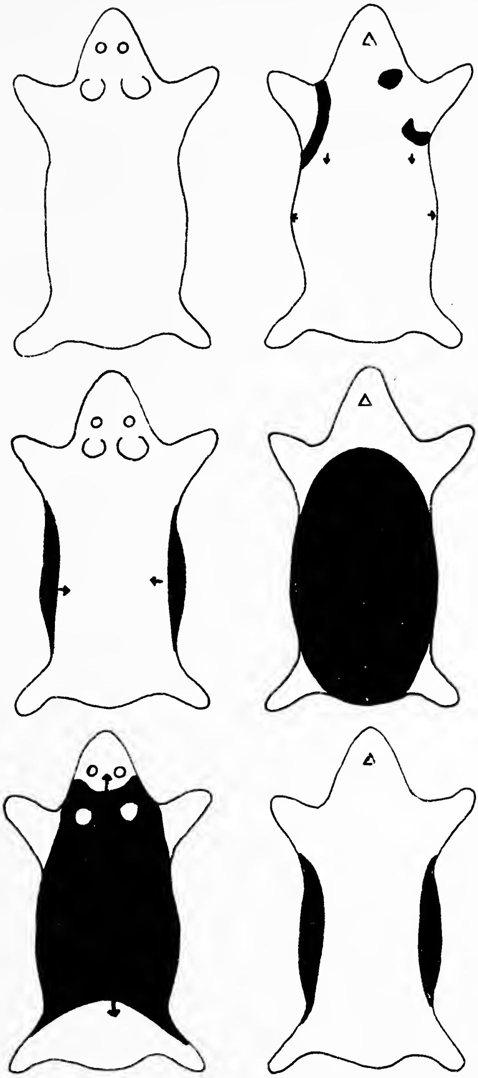

Fig. 14.—Molt pattern in a series of adult *Akodon varius* taken between October and November. Molt begins anteroventrally, proceeds posteriorly, then dorsally and toward the head and tail.

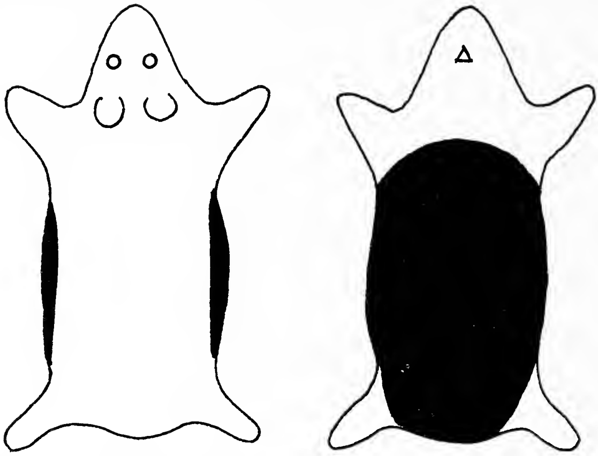

Fig. 15.—Melanin deposits in a young male *Akodon varius* captured near Orán in November. No pattern was discernible, but hair growth may be as in the adults, with our specimen representing the stage of molt immediately preceeding hair growth on the dorsum, as in the middle of Fig. 14.

Akodon albiventer Thomas
ratón ventriblanco — white-bellied grass mouse

1897. *Akodon albiventer* Thomas, Ann. Mag. Nat. Hist., ser. 6, 20:217.

Specimens examined (10).—LA POMA: 14 km S jct Hwys 40 and 51, along Hwy 40, 4100 m, 10.

Measurements.—Mean and range of five ♂♂ and three ♀♀: total length, 159.6 (153–170); tail, 71.1 (66–78); hind foot, 21.7 (21.0–22.4); ear, 15.2 (14.0–16.1); weight, 21.4 (16.5–29.5). Cranial measurements: greatest length of the skull, 24.1 (23.2–25.3); condylobasal length, 23.3 (22.6–24.8); zygomatic breadth (N = 3), 14.4 (11.6–13.1); least interorbital breadth, 4.6 (4.4–4.8); breadth of braincase, 11.1 (10.7–11.6); palatal length, 11.5 (10.8–12.2); length of maxillary toothrow, 3.9 (3.8–4.0); length of mandibular toothrow, 4.3 (3.8–5.0); diastema length, 6.2 (5.8–6.6).

Remarks.—This handsome *Akodon* with a white venter occurs at high elevations (>4000 m) in mesic areas. It is not common and is probably limited to the pre-Andean and Andean mountain chains. Individuals were taken in and near a small marsh with very lush vegetation (Fig. 16) in April 1976.

Four females were not in reproductive condition; two males had abdominal testes with lengths of 2.6 and 2.9 mm, respectively; one had inguinal testes with a length of 6.0 mm, and two had scrotal testes with lengths of 5.3 and 7.5, respectively.

Eight of 10 individuals were molting; five had melanin deposits over

Fig. 16.—A marsh located in the Puna at 4000 m elevation near San Antonio de los Cobres. This site contained *Phyllotis darwini, Galea musteloides* and *Auliscomys sublimis.*

25–50% of the skin's inner surface. Molt on all was primarily or totally limited to the dorsum, with only occasional patches of melanin deposited on the venter. Molt proceeds from posterodorsal to anterodorsal (Fig. 17).

Oxymycterus paramensis Thomas
hocicudo parameño — burrowing mouse

1902. *Oxmycterus paramensis* Thomas, Ann. Mag. Nat. Hist., ser. 7, 9:139.

Specimens examined (6).—GENERAL SAN MARTIN: 17 km SW beyond Dique Itiyuro, 500 m, 2. ORAN: 22 km SW Orán, along Río Santa María, 1; 24 km NW of Aguas Blancas, 3.

Measurements.—Mean and range for three ♂♂: total length, 215.3 (192–243); tail, 100 (87–113); hind foot, 29 (28.4–29.6); ear, 20.8 (20.6–21.0); weight, 42 (36.7–52). Cranial measurements: greatest length of the skull, 32.4 (31.4–34.1); condylobasal length, 28.5 (27.7–30.1); zygomatic breadth, 13.9 (13.5–14.4); least interorbital breadth, 6.0 (5.8–6.2); breadth of braincase, 13.5 (13.4–13.5); palatal length, 14.2 (13.4–15.3); length of maxillary toothrow, 5.1 (5.0–5.2); length of mandibular toothrow, 5.4 (5.2–5.6); diastema length, 7.2 (6.9–7.5).

Remarks.—This is one of the most shrew-like of the akodont rodents and inhabits the forest floor in mesic areas of north-central Salta. Some

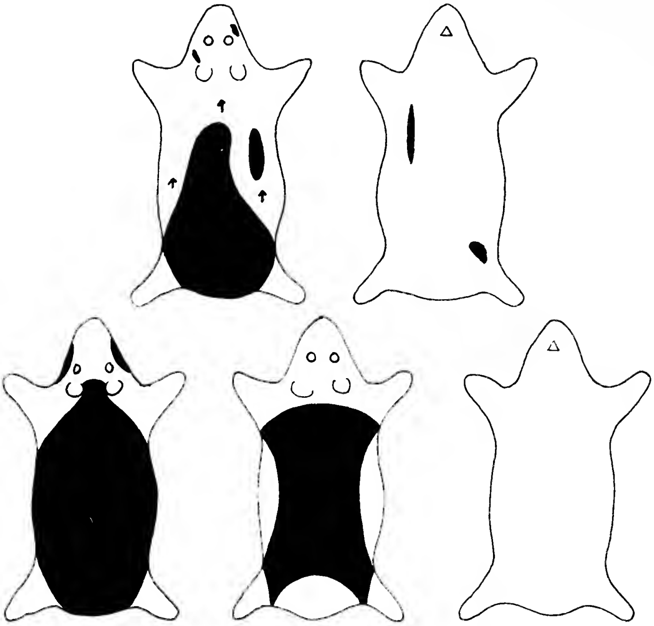

Fig. 17.—Molt in *Akodon albiventer*. Small patches of melanin were visible on the venter, but molt in a series of eight specimens was noted primarily on the dorsum, moving from posterior to anterior (above) and eventually covering the entire animal, with new hair growth occurring in the mid-dorsal region at the end of the molting sequence (bottom).

specimens were taken under logs in dense verdant second growth. One was taken from the sand-rock embankment of the Río Pescado. This is an uncommon species in northwest Argentina and appears to be nocturnal. It probably is limited to the northern wet forests, although it possibly will be found in mesic forest enclosures in central, or even south-central Salta.

Two individuals captured in September were not breeding—one had small abdominal testes, whereas the other had large (10.4 mm length) inguinal testes.

Calomys laucha (Olfers)
laucha chica — vesper mouse

1818. *Mus laucha* Olfers, Eschwege Neue Bibl. Reisenbr., 51:209.
1959. *Calomys laucha* Hershkovitz, J. Mamm., 40:339.

Specimens examined (3).—CAFAYATE: 5 km NE Cafayate, 1. RIVADAVIA: 4 km NE Santa Victoria, 2.

Measurements.—Two ♂♂ and 1 ♀, respectively: total length, 150, 134, 125; tail, 83, 60, 56; hind foot, 19.5, 14.5, 14.8; ear, 16.8, 13.9, 15.6; weight, 10, 18, 18. Cranial measurements of one ♂ and one ♀, respectively: greatest length of the skull, 20.8, 20.3; condylobasal length, 18.9, 18.3; zygomatic breadth, —, 10.9; breadth of braincase, 9.4, 9.6; least interorbital breadth, 3.4, 3.6; palatal length, 10.2, —; length of maxillary toothrow, 2.9, 2.7; length of mandibular toothrow, 3.0, 3.0; diastema length, 5.0, 4.9.

Remarks.—This very small *Mus*-like mouse with a white venter is uncommon, although occurring over much of Salta Province, particularly in dry areas. One specimen was taken in a sandy area of the Monte Desert near Cafayate (see Fig. 9), whereas two were taken in the xeric thorn scrub of far eastern Salta under sparse bushes.

The specimens taken in eastern Salta were caught in October—the female was lactating, and the male had large scrotal testes.

Calomys callosus (Rengger)
laucha grande — large vesper mouse

1830. *Mus callosus* Rengger, Naturg. Saeugeth. Paraguay:231.
1960. *Calomys callosus* Cabrera, Rev. Mus. Argent. Cienc. Natur., Zool., 4, 2: 477.

Specimens examined (22).—ANTA: 21 km N Anta, on El Piquete Rd along Río del Valle, 7. CERRILLOS: INTA Station, 2. GENERAL SAN MARTIN: 4 km S Pocoy, 5; 20 km W General Ballivián, on Puerto Baules Rd., 2. ORAN: 2 km S Juntas de San Antonio, 2; 15 km S Orán, along Río Santa María, 1; 22 km SW Orán, along Río Santa María, 3.

Measurements.—Mean and range for five individuals: total length, 182.8 (175–192); tail, 87.2 (82–92); hind foot, 21.1 (18.8–22.5); ear, 19.5 (18.5–20.5); weight, 30.9 (20–40.9). Cranial measurements (mean and range): greatest length of the skull (N = 4), 26.4 (25.3–29.3); condylobasal length (N = 6), 24.8 (22.8–27.7); zygomatic breadth (N = 3), 14.3 (13.4–15.0); least interorbital breadth (N = 6), 4.4 (4.0–5.2); breadth of braincase (N = 5), 11.4 (10.7–11.7); palatal length (N = 6), 13.6 (13.0–14.8); length of maxillary toothrow (N = 6), 4.1 (3.5–4.7); length of mandibular toothrow (N = 6), 4.2 (3.9–5.0); diastema length (N = 6), 6.6 (6.4–7.4).

Remarks.—This is one of the common rodents in second growth habitats in mesic forested areas, such as stream edges, road cuts, old fields, grassy areas, sugar cane fields, and river banks. Individuals are often captured from burrows under rocks or logs, or from tangled roots. The species does not appear to climb and is nocturnal.

Two females captured in March were pregnant with 8 and 6 embryos, respectively. Three females taken in September were not in breeding condition, whereas, of four males taken at the same time, three had inguinal testes measuring 8.0, 9.1, and 13.5 mm, and one had scrotal testes measuring 9.1 mm in length.

Molt in *C. callosus* begins as isolated patches on the dorsum and venter that move medially in dorsal parts and posteriorly in ventral parts (Fig. 18). In February, nine of 10 individuals had melanin deposits over less than 20% of the surface, whereas one had more than 40% of the surface covered by melanin. Two individuals captured in

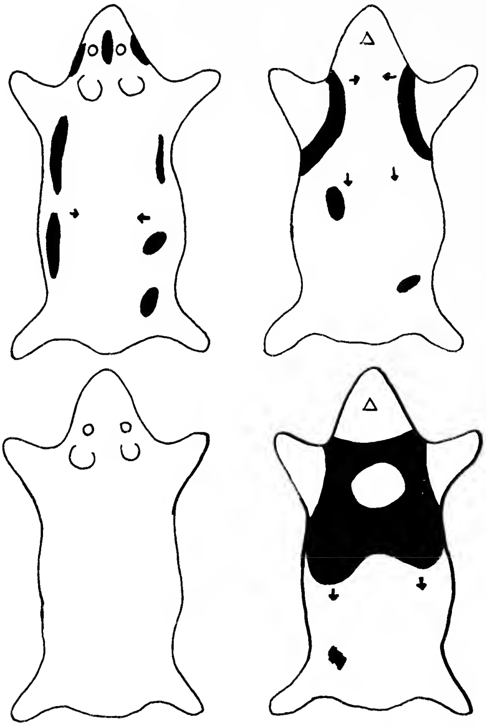

Fig. 18.—Molting pattern in *Calomys callosus*. Isolated patches of melanin indicate molt initiation on both the dorsum and ventrum (above). Hair growth proceeds medially and posteriorly (below).

March were molting over less than 20% of their body, whereas two individuals captured in September were molting over less than 10% of their body.

Eligmodontia typus Cuvier
laucha colilarga bayo — Gerbil mouse

1837. *Eligmodontia typus* Cuvier, Ann. Scienc. Natur., ser. 2, 7:169.

Specimens examined (5).—CAFAYATE: 14 km NE Cafayate, along Hwy 68, 1; 8.2 km NE Cafayate, along Hwy 68, 1; 1 km W Río Santa María, along Hwy 68, 1. LA POMA: 3 km S jct Hwys 40 and 51, along Hwy 40, 4000 m, 2.

Measurements.—Mean and range for one ♂ and two ♀♀ (lowland), followed by those of two ♀♀ (highland): total length, 185 (178–190), 163, 168; tail, 104.3 (104–105), 69, 79; hind foot, 23.2 (22–25), 22.6, 23.4; ear, 20.7 (19.6–22.0), 20.0, 20.8; weight, 18.6 (14.5–22.9), 26.0, 31.1. Cranial measurements of one ♀ (lowland) followed by those of two ♀♀ (highland): greatest length of skull, 25.5, 24.9, 24.9; condylobasal length, 24.8, 22.5, 23.9; least interorbital breadth, 4.3, 4.1, 4.0; breadth of braincase, 11.7, 11.9, 11.9; palatal length, 12.4, 12.4, 11.9; length of maxillary toothrow, 3.8, 3.9, 3.8; length of mandibular toothrow, 3.9, 3.9, 3.8; bullar length (less tubes), 5.7, 4.6, 4.9; diastema length, 5.7, 6.3, 6.1.

Remarks.—This species is limited to the western portions of Salta in the valleys of the Monte Desert and in the high plateau of the Puna. Lowland individuals occur primarily in rolling sand hummocks with halophytic vegetation (for example, Fig. 9), or in creosote bush flats. They are not common in any area of Salta, although they occur regularly in Monte localities. The highland animals are much larger than the lowland form and have shorter tails and longer, laxer pelage. Indeed, the highland form may well be a separate species, although a decision will await larger series of specimens for comparison. *E. typus* probably does not dig its own burrows—it inhabits abandoned tuco-tuco (*Ctenomys*) burrows and those of other rodents as well. This species is one of the most desert-adapted small mammals in Argentina (Mares, 1975*a,* 1975*b,* 1977*b*; Mares, Blair et al., 1977).

A female taken in April 1974 near Cachi had 8 embryos averaging 10.4 mm in crown-rump length, while a second female carried 6 embryos which averaged 5.1 mm in crown-rump length. The species is nocturnal and adapts easily to a laboratory environment (Mares and Mares, in preparation).

Phyllotis darwini (Waterhouse)
pericote panza gris — Darwin's leaf-eared mouse

1837. *Mus darwini* Waterhouse, Proc. Zool. Soc. London:28.
1896. *Phyllotis darwini* Thomas, Proc. Zool. Soc. London:1020.

Specimens examined (10).—CACHI: 35 km E Cachi, approx. 3000 m, 4. LA POMA: 14 km S jct Hwys 40 and 51, along Hwy 40, 4000 m, 1; 14 km S jct Hwys 40 and 51, along Hwy 40, 4100 m, 4; 8 km N La Viñita, along Hwy 40, 1.

Measurements.—Mean and range for four ♀♀: total length, 219.2 (186–251); tail, 106.7 (91–125); hind foot, 25.3 (24.1–26.5); ear, 26.8 (24.6–27.5); weight, 40.7 (25.5–61). Cranial measurements: greatest length of the skull, 29.4 (26.2–31.1); condylobasal length, 28.3 (25.5–30.2); zygomatic breadth, 15.3 (14.5–16.1); least interorbital breadth 4.4 (4.1–4.6); breadth of braincase, 13.3 (13.0–13.7); palatal length, 15.4 (13.9–15.9); length of maxillary toothrow, 5.3 (4.8–6.0); length of mandibular toothrow, 5.3 (4.9–5.8); bullar length, 5.0 (5.0–5.1); diastema length, 7.8 (6.3–8.3).

Remarks.—This well-haired phyllotine is distributed through the hilly and mountainous areas of Salta, particularly in the central and western portions of the province. It inhabits riparian areas in mesic forests as well as gallery forests in lowland deserts when these are along permanent rivers. High desert areas are also frequented, even on the steepest hillsides, as are high Puna localities. The species is always associated with rocks and is probably the most common mammal on the dry bouldery slopes of xeric mountains.

All of our specimens were taken in April. None of five females was breeding, although one had a swollen uterus. One male had small abdominal testes measuring 3.2 mm in length.

Water balance and habitat of this species are described in Mares (1975*b*, 1977*c*).

Auliscomys sublimis (Thomas)
pericote andino — Andean leaf-eared mouse

1900. *Phyllotis sublimis* Thomas, Ann. Mag. Nat. Hist., ser. 7, 6:467.
1932. *Auliscomys sublimis* Gyldenstolpe, Kungl. Sv. Vetensk. Handl., vol. 11, 3:95.

Specimen examined (1).—LA POMA: 14 km S jct Hwys 40 and 51, along Hwy 40, 4100 m, 1.

Measurements.—One ♂: total length, 173; tail 55; hind foot, 23.4; ear, 24.0; weight, 38.5. Cranial measurements: greatest length of the skull, 28.3; condylobasal length, 26.8; zygomatic breadth, 15.1; least interorbital breadth, 4.2; breadth of braincase, 12.8; palatal length, 15.3; length of maxillary toothrow, 5.2; length of mandibular toothrow, 5.6; bullar length (less tubes), 4.7; diastema length, 7.7.

Remarks.—This is the most vole-like of the phyllotines found in Salta, having lax pelage and a short tail. The single specimen was taken at night in a mesic seepage area of the Puna (Fig. 18) in a grassy-rocky area. It had scrotal testes of medium length, 9.5 mm. This species has not been reported for Salta before, although Pearson (1958) and Hershkovitz (1962) list specimens from Jujuy Province. See Pearson and Patton (1976) concerning the generic status of this species. See also Reig (1978).

Graomys domorum (Thomas)
pericote pálido — pale leaf-eared mouse

1902. *Eligmodontia domorum* Thomas, Ann. Mag. Nat. Hist., ser. 7, 9:132.
1916. *Graomys domorum* Thomas, Ann. Mag. Nat. Hist., ser. 8, 17:142.

Specimens examined (5).—ANTA: 11 km N Anta, on El Piquete Rd, 1. GENERAL SAN MARTIN: Approx. 4 km S Pocoy, NE Salta, 2; 20 km W General Ballivián, on Puerto Baules Rd, 2.

Measurements.—Mean and range for one ♂ and two ♀♀: total length, 323 (310–337); tail, 175.7 (170–178); hind foot, 31.1 (30.0–31.8); ear, 27.3 (25.5–28.5); weight, 102 (100–104). Cranial measurements: greatest length of the skull (N = 2), 38.5 (37.8–39.3); condylobasal length (N = 3), 35.7 (35.1–37.2); zygomatic breadth (N = 4), 18.3 (17.9–19.1); least interorbital breadth (N = 4), 6.6 (5.9–7.5); breadth of braincase (N = 3), 14.9 (14.1–15.5); palatal length (N = 4), 19.3 (18.4–20.2); length of maxillary toothrow (N = 4), 5.6 (5.2–5.9); length of mandibular toothrow (N = 4), 5.7 (5.4–5.9); bullar length (N = 4), 6.5 (6.0–6.9); diastema length (N = 4), 9.5 (9.0–10.2).

Remarks.—This is the largest phyllotine occurring in Salta, although *Andinomys* may ultimately be found in the province. *Graomys domorum* appears to be limited to the transitional forest occurring on very low mountains in central Salta (Fig. 19), but it may occur in drier

Fig. 19.—The Transitional Forest (site 10) of north-central Salta during the dry season (September). *Graomys domorum* and *Nasua nasua* were captured in this type of habitat.

portions of the subtropical forest that bisects Salta from north to south. Animals were taken in thick grass along road cuts and from second growth areas. Although large rocks were often present, *Graomys* does not seem to be as intimately associated with boulders as is *P. darwini*.

Two females captured in September were not breeding, whereas a male captured at that time had large scrotal testes. A male taken in October had scrotal testes 9.7 mm in length.

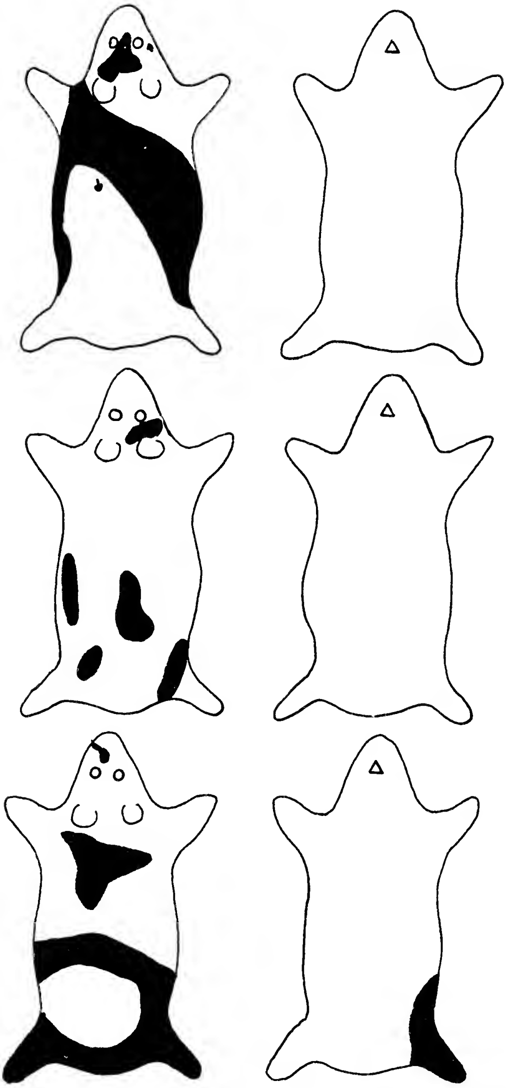

Fig. 20.—Melanin patterns evident on several *Graomys griseoflavus*. Little molting was detected on the ventrum, with broad bands or isolated patches of hair growth being noted on the dorsum.

Graomys griseoflavus (Waterhouse)
pericote común — gray leaf-eared mouse

1837. *Mus griseoflavus* Waterhouse, Proc. Zool. Soc. London:28.
1916. *Graomys griseoflavus* Thomas, Ann. Mag. Nat. Hist., ser. 8, 17:142.

Specimens examined (30).—ANTA: 3 km N of Ceibalito, on jct of Anta Rd. and Hwy 16, 1; 21 km N of Anta, 1. CACHI: 5 km S (by rd.) of jct of Seclantás Rd. and Hwy 59 (about 30 km E Cachi), 2600 m, 2; 30 km S Cachi, 4. GENERAL SAN MARTIN: 27 km E Tartagal, 3. RIVADAVIA: 4 km NE Santa Victoria, 6; 2 km W Santa María, 5; 6 km SW Santa Victoria, at "El Breal" (extreme NE Salta), 7. SAN CARLOS: 8 km N La Viñita, along Hwy 40, 1.

Measurements.—Mean and range for two ♂♂ and six ♀♀: total length 271.7 (213–320); tail, 153.1 (125–177); hind foot, 28.0 (25.5–29.5); ear, 25.0 (21.6–29.5); weight, 62.5 (38–72). Cranial measurements: greatest length of the skull, 32.8 (31.5–35.1); condylobasal length, 29.9 (27.3–31.7); zygomatic breadth, 16.3 (13.6–19.0); least interorbital breadth, 5.3 (4.7–5.9); breadth of braincase, 14.2 (13.2–15.2); palatal length, 16.7 (14.3–18.4); length of maxillary toothrow, 5.5 (5.1–6.0); length of mandibular toothrow, 5.3 (4.8–6.0); bullar length, 6.2 (5.6–7.0); diastema length, 8.2 (7.7–8.8).

Remarks.—This aggressive, strong phyllotine occurs widely throughout the drier middle and lower portions of Salta. It is regular in *Prosopis* areas (Mares, Enders et al., 1977) where it feeds on the leaves and pods of the tree and occasionally takes insects as well. We have never taken this species in very mesic localities, nor at the highest localities. It may be associated with boulders on hillsides or along flowing rivers with associated gallery forests, but it also may spend most of its time in trees. The animals also frequent cultivated areas such as vineyards and orchards.

All specimens were captured in April, September, or October. One April female was not breeding, whereas two were lactating. Both males examined in April had inguinal testes of lengths 5.2 and 8.1 mm, respectively. Four September males had large scrotal testes. One October female was not breeding; three had vaginas with copulatory plugs; and two had open vaginas. Two October males had large scrotal testes.

Two of seven April animals were molting at less than the 10% level. Two of six September specimens were molting over 10–15% of their body, whereas all 11 October specimens were molting over 10–50% of their body. We were unable to discern a pattern in hair replacement and it appears quite variable (Fig. 20), although it seems to begin dorsally.

Water balance, habits, and habitat of this species are discussed by Mares (1975*a*, 1975*b*, 1976, 1977*c*; Mares, Blair et al., 1977, Mares and Hulse, 1977, and Mares, Enders et al., 1977).

Fig. 21.—The shrub in the center of the photograph is about 2 m high and contained nests of *Holochilus brasilensis*. The animals were seen climbing throughout this and similar shrubs and were captured in traps set at the base of the bushes. These shrubs were located near the lagoon shown in Fig. 5, being found perhaps 30 m from the water's edge.

Holochilus brasiliensis (Desmarest)
rata nutria o rata colorada — marsh rat

1819. *Mus brasiliensis* Desmarest, Nov. Dict. Hist. Nat., 2nd ed., 29:62.
1897. *Holochilus brasiliensis* Thomas, Ann. Mag. Nat. Hist., ser. 6, 19:496.

Specimens examined (31).—ORAN: Juntas de San Antonio, 1. RIVADAVIA: 6 km SW Santa Victoria, at "El Breal" (extreme NE Salta), 30.

Measurements.—Mean and range for 10 individuals (five ♂♂ and five ♀♀): total length, 329.8 (284–381); tail, 161.2 (140–192); hind foot, 39.6 (35.2–42.7); ear, 21.8 (20.8–23); weight, 146.9 (81–230). Cranial measurements (mean and range for three ♂♂ and four ♀♀, respectively): greatest length of the skull, 35.9 (34.0–38.6), 36.1 (35.3–37.1); condylobasal length, 34.3 (32.2–37.2), 34.0 (33.7–34.5); zygomatic breadth, 20.2 (19.4–21.2), 20.2 (19.9–20.7); least interorbital breadth, 4.7 (4.5–4.9), 4.8 (4.4–5.2); breadth of braincase, 14.2 (13.6–14.7), 14.1 (13.4–14.9); palatal length, 20.9 (20.0–22.3), 20.5 (19.8–21.1); length of maxillary toothrow, 6.9 (6.5–7.2), 7.0 (6.7–7.1); length of mandibular toothrow, 7.2 (7.1–7.3), 7.0 (6.7–7.3); diastema length, 10.4 (9.5–11.5), 10.5 (10.3–10.8).

Remarks.—This large sigmodont rodent is common throughout the lower mesic elevations of Salta Province, particularly in cultivated sugar cane fields. The species is usually at least semiaquatic and pos-

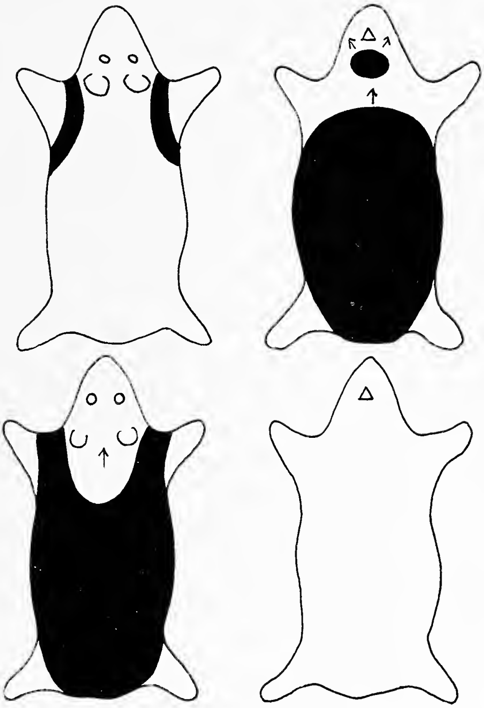

Fig. 22.—Molting pattern in *Holochilus brasilensis* captured in October. Molt proceeded from ventrum to dorsum (above), with the hair of the head being replaced last, after ventral growth was completed (below).

sesses some webbing on the hind feet. It is common along canals and rivers in agricultural areas. Curiously, almost all of our specimens were taken from the dry chaco of eastern Salta near a stagnant salty lake. The *Holochilus* were nesting in low (2 m) shrubs and were very common in the area (Fig. 21). They probably arrived at the site from the Rio Pilcomayo during periods of general inundation.

The series from eastern Salta was taken in October 1976, at the end of the dry season in that area. All of the adult males examined (eight) had scrotal testes; one had testes measuring 18.6 mm in length, whereas most of the others had scrotal testes varying from small to medium. All but one of the females examined (20 in total) had vaginas that were either open or sealed with a copulatory plug. One female had a closed vagina. Two were pregnant with 3 and 4 embryos, respectively. The latter's embryos measured 3.0 mm in crown-rump length.

Eight individuals were examined for molt, three ♂♂ and five ♀♀.

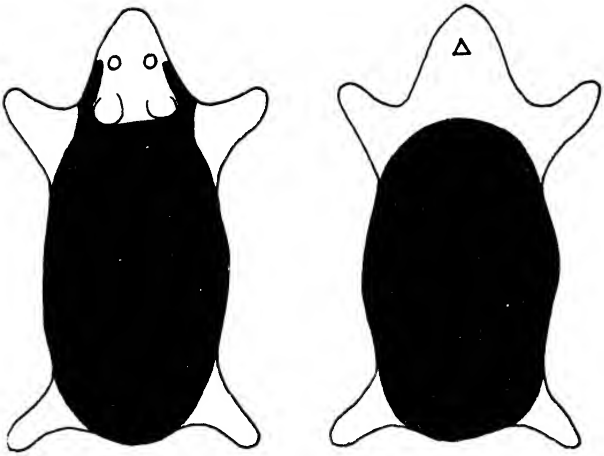

Fig. 23.—Melanin deposition pattern in a female *Microcavia australis* captured in April. Hair growth was occurring over the entire body.

All males were molting between 30–80% of their body, whereas the females showed only small patches of melanin deposited behind the ears and eyes (Fig. 22).

Family Caviidae

Microcavia australis (Geoffroy and D'Orbigny)
cuis chico — southern cavy

1833. *Cavia australis* Geoffroy & D'Orbigny, Magas. de Zool., 3.
1907. *Microcavia australis* Kraglievich, Physis, 8:578.

Specimens examined (2).—CACHI: 10 km E of Cachi, 1; 25 km E of Cachi, 1.

Measurements.—One ♂ and two ♀, respectively: total length, 210, 104; tail, 0, 0; hind foot, 47.5, 35.2; ear, 22.4, 17.4; weight, 326, 66. Cranial measurements: greatest length of the skull, 49.1, 34.1; condylobasal length, 46.4, 30.1; zygomatic breadth, 30.4, 19.8; least interorbital breadth, 11.1, 9.6; palatal length, 24.0, 14.5; length of maxillary toothrow, 11.8, 7.9; length of mandibular toothrow, 12.1, 9.2; diastema length, 13.1, 7.8.

Remarks.—This tail-less, medium-sized caviid is common in the western lowlands of Salta in the valleys of the Monte Desert (Fig. 9). We doubt that *Microcavia* occurs with any frequency outside of the arid valleys of western Salta. Two specimens of *Microcavia* are listed in The Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" as being taken from El Quebrachal and from Dragones. Both of these localities are in the westerly portion of the Chaco thorn forest of Salta. The site located further east (Dragones) is near the Río Bermejo and it is possible that populations may exist within the corresponding gallery forest. Nevertheless, in travelling widely throughout eastern Salta, we did not see any individuals in the thorn scrub. Specimens in western Salta were taken from burrows under low shrubs (for example, *Larrea, Plectrocarpa*), as well as from burrows placed under fallen trees (especially *Prosopis*). These rodents are agile climbers and spend a great part of their time climbing in *Prosopis* trees where they feed on the leaves. When startled, they will leap or fall clumsily to the ground and scurry away to their burrows. Many animals inhabit a single burrow system. They are most common in sandy areas, or in areas of clayey soil; they are particularly common along gallery forests of desert gullies, or in *Prosopis* forests in areas with a high water table. The species has been studied in detail by Rood (1970, 1972). Additional information is available in Mares (1973, 1975*a*), Mares, Blair et al. (1977), and Mares, Enders et al. (1977).

The male taken in April 1974 (autumn, dry season) had large scrotal testes (26.5 mm in length), whereas the female captured at this time was not breeding.

The female was molting over the entire body (Fig. 23).

Galea musteloides Meyen
cuis común — common cavy

1832. *Galea musteloides* Meyen, Nova Acta Ac. Gaes, Leop. Car., 16:597.

Specimens examined (2).—CERRILLOS: INTA Station, 1. LA POMA: 14 km S jct Hwys 40 and 51, along Hwy 40, 4100 m, 1.

Measurements.—One ♂ and one ♀, respectively: total length, 198, 170; tail, 0, 0; hind foot, 38.9, 42.0; ear, 21.4, 22.7; weight, 243, 192. Cranial measurements: greatest length of the skull, 51.1, 47.3; condylobasal length, 48.1, 43.3; zygomatic breadth, 29.4, 25.7; least interorbital breadth, 10.7, 10.5; breadth of braincase, 19.8, 20.3; palatal length, 25.3, 21.9; length of maxillary toothrow, 11.8, 10.5; length of mandibular toothrow, 11.3, 10.1; diastema length, 14.0, 12.1.

Remarks.—This medium-sized caviid inhabits the far western thorn scrub of Salta, particularly in the foothills supporting Transitional Forest, the mesic subtropical forest, and in the high Puna. In Salta it seldom coexists with *Microcavia,* although these species do coexist in other localities (see, for example, Contreras, 1965, 1966; Rood, 1970, 1972). Generally, *Galea* in Salta is most common in moist microhabitats, such as croplands, stream edges, forest edges, road cuts, and orchards. Burrows are similar to *Microcavia,* although *Galea* does not seem to climb trees as does *Microcavia.*

The female taken at 4100 m in April of 1974 was lactating, whereas a male taken in October near the town of Cerrillos had large scrotal testes.

Pediolagus salinicola (Burmeister)
conejo del palo — Chacoan cavy

1875. *Dolichotis salinicola* Burmeister, Proc. Zool. Soc. London:634.
1935. *Pediolagus salinicola* Yepes, Rev. Inst. Bacteriol., 7:245.

Specimens examined (6).—Rivadavia: 5 km W Santa María, 1; 5 km SE Santa María, 1; 4 km NE Santa Victoria, 3; 1 km W Santa María, 1.

Measurements.—Mean and range for three ♂♂ and two ♀♀: total length, 443.3 (420–470); tail, 23.6 (19–30); hind foot, 97.1 (91–100.2); ear, 60.5 (56.7–64.6); weight, 1890 (1500–2200). Cranial measurements (N = 4): greatest length of the skull, 86.7 (81.7–90.7); condylobasal length, 79.3 (77.4–81.7); zygomatic breadth, 43.3 (40.2–45.0); least interorbital breadth, 25.1 (25.5–24.8); breadth of braincase, 34.0 (33.0–34.6); palatal length, 37.5 (34.4–40.7); length of maxillary toothrow, 16.7 (14.8–19.2); length of mandibular toothrow, 16.9 (15.6–19.0); diastema length, 24.6 (23.7–25.6).

Remarks.—This is the largest caviid in Salta and inhabits the most arid sections of the low, flat thorn scrub of the eastern part of the province. They are very rabbit-like in external appearance and in the overall aspect of the cranium. Animals are often found in pairs; they dig large burrows throughout the thorn scrub and are particularly common in areas supporting tall *Prosopis* (Fig. 6).

Four of the specimens taken in October 1976 were breeding. Two females were pregnant with 2 embryos each, one in each uterine horn. Two males had large scrotal testes measuring 39.6 and 45.6 mm, respectively.

None of the animals was molting.

Family Hydrochoeridae

Hydrochoerus hydrochaeris (Linné)
carpincho — capybara

1766. *Sus hydrochaeris* Linné, Syst. Nat., 12th ed.:103.
1904. *Hydrochoerus hydrochaeris* J. A. Allen, Bull. Amer. Mus. Nat. Hist., 20:444.

Remarks.—Capybaras are the largest rodents in the world. They are largely aquatic and inhabit the larger rivers in mesic portions of northern Salta. Capybara tracks were seen in the Río Tarija near the confluence of the Ríos Tarija and Pilcomayo.

Family Dasyproctidae

Dasyprocta punctata Gray
aguti rojizo — agouti

1842. *Dasyprocta punctata* Gray, Ann. Mag. Nat. Hist., ser. 1, 10:264.

Remarks.—Agoutis inhabit the moist forest of central Salta, where they extend from the low river valleys to the forested hillsides. Several individuals were seen near the Río Pescado, 24 km NW of Aguas Blancas.

Fig. 24.—Burrow of *Lagostomus maximus* near Tolloche in southeastern Salta. Large areas are cleared of vegetation by these rodents, which subsequently must forage over a larger area. The burrow in the center of the photograph measures over 50 cm across the opening. *Prosopis* and *Acacia* trees surround the mound system.

Family Chinchillidae

Lagostomus maximus (Desmarest)
vizcacha — plains viscacha

1817. *Dipus maximus* Desmarest, Nouv. Dict. Hist. Nat., 2nd ed., 13:117.
1914. *Lagostomus maximus* Hollister, Proc. Biol. Soc. Washington, 27:58.

Specimens examined (2).—RIVADAVIA: 5 or 6 km SW of Santa Victoria, at "El Breal" (extreme NE of Salta), 2.

Measurements.—Two ♀♀: total length, 591, 595; tail, 170, 140; hind foot, 121.8, 118.4; ear, 58.3, 52.7; weight, 3450, 3150. Cranial measurements: greatest length of the skull, 107.4, 86.7; condylobasal length, 95.8, 79.4; zygomatic breadth, 61.2, 52.9; least interorbital breadth, 28.8, 24.4; breadth of braincase, 38.3, 35.5; palatal length, 58.2, 45.1; length of maxillary toothrow, 24.8, 21.2; length of mandibular toothrow, 25.3, 21.9; diastema length, 33.3, 25.4.

Remarks.—This is the largest non-aquatic rodent occurring in Salta. It is common throughout the eastern half of the province in the arid and semiarid lowlands of the Chaco. *Lagostomus* are colonial, burrowing animals and excavate an extensive system in the thorn scrub from which they forage for green vegetation (Fig. 24). As they consume more and more plants in the immediate vicinity, the animals must travel further to obtain food, until they are travelling 100 m or more. They are nocturnal and extremely wary, taking refuge in their burrow at the slightest disturbance. They will hurry back to the burrow openings and peer outward over the area until they feel free to re-emerge to resume foraging. They issue deep grunts when alarmed. Llanos and Crespo (1952) provide much information on *Lagostomus*.

A female captured in October 1976 was pregnant with 2 embryos.

Lagidium viscacia (Molina)
vizcacha serrana — mountain viscacha

1782. *Lepus viscacia* Molina, Sagg. Stor. Nat. Chili:307.
1919. *Lagidium viscaccia* Thomas, Ann. Mag. Nat. Hist., ser. 9, 3:500.

Remarks.—These rabbit-like diurnal rodents inhabit the boulder strewn slopes and ridges of the arid mountains of western Salta. We observed *Lagidium* at 4000 m near San Antonio de Los Cobres.

Family Ctenomyidae

Ctenomys frater Thomas
tucu-tuco colorado — forest tucu-tuco

1919. *Ctenomys frater* Thomas, Ann. Mag. Nat. Hist., ser. 7, 9:228.

Specimens examined (2).—ORAN: 22 km SW Orán, along Río Santa María, 1; 24 km NW of Aguas Blancas, 1.

Measurements.—Two ♀♀: total length, 244, 251; tail, 72, 77; hind foot, 38.0, 38.5; ear, 11.3, 9.4; weight, 204, 234. Cranial measurements: greatest length of the skull, 43.4, 42.1; condylobasal length, 43.2, 41.1; zygomatic breadth, 28.8, 26.7; least interorbital breadth, 10.8, 9.5; breadth of braincase, 17.7, 18.5; palatal length, 22.9, 22.4; length of maxillary toothrow, 12.0, 9.7; length of mandibular toothrow, 12.2, 10.1; diastema length, 11.4, 12.4.

Remarks.—This is an uncommon tucu-tuco limited to the most mesic forests in north-central Salta Province. The species inhabits flat areas with deep soil, often near small creeks. They do not appear to burrow as extensively as some of the desert species of *Ctenomys,* nor do they appear to be as vocal.

Ctenomys opimus Wagner
tucu-tuco tojo — highland tucu-tuco

1848. *Ctenomys opimus* Wagner, Arch. Naturg., 1:75.

Specimens examined (1).—LA POMA: 12 km S jct Hwys 40 and 51, along Hwy 40, (4000 m), 1.

Measurements.—One ♂: total length, 280; tail, 82; hind foot, 41.0; ear, 9.8; weight, 404. Cranial measurements: greatest length of the skull, 49.1; condylobasal length, 49.4; zygomatic breadth, 32.7; least interorbital breadth, 11.7; breadth of braincase, 19.7; palatal length, 27.7; length of maxillary toothrow, 9.8; length of mandibular toothrow, 10.5; diastema length, 15.8.

Remarks.—This large gopher-like rodent is only found in the high Andean steppe, or Puna (Fig. 8). The animals are very common in the low shrubs that are characteristic of the puna of about 4000 m altitude, such as *Parastrephia, Fabiana, Psila,* and *Adesmia.* Pearson (1959) discusses various aspects of the biology of this species in Peru.

Ctenomys saltarius Thomas
tucu-tuco salteño — Salta tucu-tuco

1912. *Ctenomys saltarius* Thomas, Ann. Mag. Nat. Hist., ser. 8, 10:639.

Specimen examined (1).—SAN CARLOS: 8 km N La Viñita, along Hwy 40, 1.

Measurements.—One ♀: total length, 283; tail, 80; hind foot, 37.5; ear, 10.3; weight, 230. Cranial measurements: greatest length of the skull, 42.7; condylobasal length, 42.2; zygomatic breadth, 28.1; least interorbital breadth, 9.4; breadth of braincase, 18.5; palatal length, 21.6; length of maxillary toothrow, 11.3; length of mandicular toothrow, 11.3; diastema length, 11.0.

Remarks.—This medium-sized burrowing rodent inhabits the hillsides and valleys of the northern Monte Desert. They are especially common in creosote bush (*Larrea cuneifolia*) flats and in areas with *Prosopis* on soft, friable soil. *Ctenomys* feeds on creosote bush and other small shrubs (see Mares and Hulse, 1977) by opening its burrows at the base of the shrub and cutting stems just above ground level. This species vocalizes readily and its thumping calls can be heard throughout the northern Monte, day or night.

One female captured in April was molting on the dorsum (Fig. 25), although we could not discern a pattern.

Ctenomys sp.

Remarks.—We observed burrows and mounds of a tucu-tuco near Estación Tonono in eastern Salta. This level thornscrub habitat is characteristic of *C. mendocinus* in the Chaco Forest of north-central Argentina. Although we did not capture any individuals, we surmise that *C. mendocinus* is the only tucu-tuco in that area.

Order Carnivora

Family Canidae

Cerdocyon thous (Linné)
zorro de monte — crab-eating fox

1766. *Canis thous* Linné, Syst. Nat. 12th ed.:60.
1914. *Cerdocyon thous* Thomas, Ann. Mag. Nat. Hist., ser. 8, 13:356.

Remarks.—This small dark fox is common throughout much of the forested portions of Salta. We have seen individuals in the region of Orán, as well as in the dry Chaco near Joaquín V. Gonzalez.

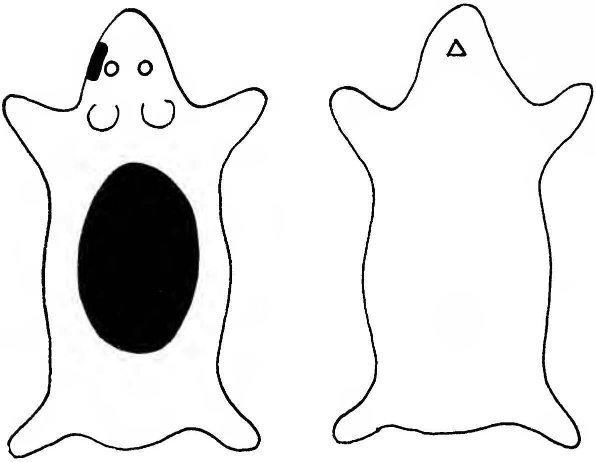

Fig. 25.—Melanin deposits in a *Ctenomys saltarius* captured in April (late autumn). No pattern of hair replacement was evident and melanin was found primarily in the mid-dorsal region.

Family Procyonidae

Nasua nasua (Linné)
coatí — coati

1766. *Viverra nasua* Linné, Syst. Nat., 12th ed.:64.
1900. *Nasua nasua* Berg, Comunic. Mus. Nac. Buenos Aires, 1:219.

Specimen examined (1).—GENERAL SAN MARTIN: 15 km W General Ballivián, on Puerto Baules Rd., 1.

Measurements.—One ♀: total length, 780; tail, 385; hind foot, 87.3; ear, 42.5; weight, 1.400. Cranial measurements: greatest length of the skull, 107.7; condylobasal length, 101.7; zygomatic breadth, 48.5; least interorbital breadth, 20.4; breadth of braincase, 42.3; palatal length, 66.6; length of maxillary toothrow, 29.0; length of mandibular toothrow, 37.6; breadth across canines, 13.0; breadth across last molars, 16.3.

Remarks.—This procyonid is limited to the Transitional Forest and the Moist Forest in north-central Salta, where it is uncommon. The specimen we collected was moving along a dry riverbed in the daytime.

Family Mustelidae

Eira barbara (Linné)
hurón mayor — tayra

1758. *Mustela barbara* Linné, Syst. Nat.:46.
1940. *Eira barbara* Cabrera y Yepes, Mamif. Sud-Americ.:144.

Remarks.—Only one of these large mustelids was seen in Salta as it ran across a road near the confluence of the Ríos Tarija and Bermejo.

Family Felidae

Felis yagouaroundi Geoffroy
gato eyra — jaguarundi

1803. *Felis yagouaroundi* Geoffroy, Catal. Mammif. Mus. d'Hist. Nat.:124.

Remarks.—One of these small cats (a black color phase) was seen along the Río Pescado, 24 km NW of Aguas Blancas in the Moist Forest.

Leo onca (Linné)
yaguareté — jaguar

1758. *Felis onca* Linné, Syst. Nat.:42.
1957. *Leo onca* Cabrera, Rev. Mus. Argent. Cienc. Natur., Zool., 4:299.

Remarks.—Tracks of a jaguar were seen along the Río Pescado, 24 km NW of Aguas Blancas in the Moist Forest, where the animal had killed a tapir.

Order Perissodactyla

Family Tapiridae

Tapirus terrestris (Linné)
tapir — tapir

1758. *Hippopotamus terrestris* Linné, Syst. Nat.:74.
1867(1868). *Tapirus terrestris* Gray, Proc. Zool. Soc. London:879.

Remarks.—Tracks of tapirs were seen along the Río Pescado, 24 km NW of Aguas Blancas. The tapir is the largest mammal in Salta and inhabits major rivers in the mesic northern portion of the province.

Order Artiodactyla

Family Tayassuidae

Tayassu tajacu (Linné)
pecarí de collar — collared peccary

1758. *Sus tajacu* Linné. Syst. Nat.:50.
1903 (1904). *Tayassu tajacu* Thomas, Proc. Zool. Soc. London:242.

Specimens examined (4, skulls only).—GENERAL SAN MARTIN: 4 km S Pocoy, 4.
Measurements.—No external measurements available.

Remarks.—Collared peccaries are common in the low mountains and flatlands of the eastern portion of Salta where they occur in sympatry with *Catagonus wagneri* (Olrog et al., 1976; Wetzel, 1977). They occur in Chaco Forest, Transitional Forest, and Moist Forest. They are heavily hunted for food and for their hide. In 1977, 3000 peccary hides (*D. tajacu, Tayassu pecari,* and *C. wagneri,* probably) were exported from Salta Province. Between 1972 and 1979, 310,372 peccary hides were exported from Argentina (Ojeda, unpublished manuscript).

Family Cervidae

Mazama gouazoubira (G. Fischer)
corzuela parda — brownish brocket deer

1814. *Cervus gouazoupira* G. Fischer, Zoognosia, 3:465.
1951. *Mazama gouazoubira* Hershkovitz, Fieldiana Zool., 31:567.

Remarks.—This medium-sized deer is a very common inhabitant of the Chaco thorn forest. We saw many individuals throughout the lowland Chaco of northeastern Salta and near the edge of the Transitional Forest in the northeast.

Family Camelidae

Lama glama (Linné)
llama — llama

1758. *Camelus glama* Linné, Syst. Nat.:65.
1891. *Lama glama* Thomas, Proc. Zool. Soc. London:387.

Remarks.—Domestic llamas are common in all of the highlands of Salta, and are also found in some parts of the Monte Desert. They are used for their wool and as beasts of burden.

Lama guanicoe (Muller)
guanaco — guanaco

1776. *Camelus guanicoe* Muller, Linné, Natursyst., Suppl.:50.
1921. *Lama guanicoe* Osgood, Jour. Mamm., 2:39.

Remarks.—Guanacos are common only in the highest Puna elevations, usually above 3500 m. They are heavily hunted for their fur and are also eaten. We saw guanacos above Cachi and near San Antonio de Los Cobres.

DISCUSSION

Salta Province possesses a complex mammal fauna primarily because of its relatively tropical location and the confluence of various major habitats within its provincial boundaries. Nine orders, 29 families, 89 genera, and about 142 species of mammals occur within the borders of Salta. In this report we have emphasized the broad diversity of the mammals of Salta, as well as their habitat selection. Our very limited field time was spent in such a manner that we were able to garner some indication of the overall makeup of the mammal fauna of the province. Obviously much more extensive work must be done in order to arrive at a better approximation of the actual faunal composition of Salta's mammals. Nevertheless, it is apparent that this region is faunistically important, particularly since many species reach their southern limits within the province. *Tonatia sylvicola, Phyllostomus discolor, Glossophaga soricina, Alouatta caraya, Bradypus boliviensis, Sciurus ignitus, Oryzomys legatus, Coendu prehensilis, Dasyprocta punctata,* and several other species occurring in the moist forest reach their current southern limits in central Salta. In historic times, it is likely that some of these extended southward as far as Tucumán, or even Catamarca, provinces, but habitat modification to the south of Salta has extirpated many forest species.

The distributional patterns of the species discussed in this report are summarized in Table 1. Few species are limited to one major habitat (13 of 58), although each of our five macrohabitats contains at least one species whose range within Salta is limited to that particular habitat type. Most species occur within two habitat types, although a few may be found in three, or even four, of the five macrohabitats. None occurs in all five habitat types, which is an illustration of the great habitat diversity within the province and the distinctiveness of the macrohabitats one from the other. The two most physiognomically similar habitats, that is the Chaco Transitional Forest and the Moist Forest, share the greatest number of species. The Transitional Forest and the Chacoan Thorn Scrub support the greatest number of species (35 and 32, respectively), while the Puna (13 species) and the Precordillera (15 species) support the fewest. The Moist Forest supports an intermediate number of species (29).

The most common mammals within the province are rodents, bats, marsupials, and edentates. Wtihin any of the principal macrohabitats, individuals from these groups predominate as far as frequency of occurrence, and probably also from the standpoint of biomass. This is particularly true because of the abundance of large caviomorph rodents in most habitats, and the abundance of edentates in most portions of the province.

Our determinations of commonness or rareness are entirely subjective, but we list these impressions because of the pronounced effects of commercial and sport hunting pressures and habitat modification upon the mammals of Salta. A large segment of the mammal fauna of the province is in danger of being extirpated, and no effective conservation measures are currently underway. No detailed ecological investigation of any species has ever been conducted within the provinces of Salta, Jujuy, Tucumán, Santiago del Estero, Chaco, San Juan, or La Rioja. Without a basis in ecological studies, effective management practices, should these be attempted, will be greatly impeded. There are few places on earth where one can travel from lush tropical

Table 1.—*Habitat affinities within Salta Province of the 58 species of mammals discussed in this report. "X" indicates that a species occurs within a particular habitat, while "(X)" denotes probable occurrence within a particular habitat. "X'" indicates a species which occurs only within one particular macrohabitat.*

	Major habitat type				
Species	Puna	Pre-cordillera Monte Desert	Humid forest	Transitional forest	Chacoan thorn scrub
Marmosa pusilla		X			X
Marmosa elegans			X	X	X
Lutreolina crassicaudata			X		
Didelphis albiventris		X	X	X	X
Artibeus jamaicensis			X	X	
Sturnira lilium			X	X	
Desmodus rotundus		(X)	X	X	X
Myotis albescens					X
Myotis nigricans			X	X	
Myotis levis		X		X	(X)
Eptesicus furinalis				X	
Histiotus montanus	(X)			X	X
Lasiurus borealis	(X)	X	X	X	X
Tadarida laticaudata			X	X	
Eumops bonariensis			X	X	X
Molossops temminckii				X	X
Molossus molossus				X	X
Tamandua tetradactyla				X	X
Chaetophractus vellerosus	X	X			X
Euphractus sexcinctus					X'
Tolypeutes matacus					X'
Dasypus novemicinctus			X	X	
Oryzomys nigripes			X	X	X
Oryzomys legatus			X	X	
Akodon albiventer	X'				
Akodon andinus	X'				
Akodon boliviensis			X	X	
Akodon varius		X	X	X	X
Oxymycterus paramensis			X	X	
Calomys callosus		X	X	X	X
Calomys laucha		X			X
Eligmodontia typus	X	X			
Graomys griseoflavus		X			X
Graomys domorum				X'	
Phyllotis darwini	X	X			
Auliscomys sublimis	X'				
Holochilus brasiliensis			X		X
Ctenomys sp.				X	
Ctenomys frater			X'		
Ctenomys opimus	X'				
Ctenomys saltarius		X'			
Lagostomus maximus					X'
Lagidium viscacia	X'				

Table 1.—*Continued.*

Species	Major habitat type Puna	Pre-cordillera Monte Desert	Humid forest	Transitional forest	Chacoan thorn scrub
Microcavia australis		X			X
Galea musteloides	X		X	X	X
Pediolagus salinicola					X′
Hydrochoerus hydrochaeris			X	X	X
Dasyprocta punctata			X	X	
Nasua nasua			X	X	
Eira barbara			X	X	
Cerdocyon thous			X	X	X
Felis yagouaroundi			X	X	X
Leo onca			X	X	X
Tapirus terrestris			X	X	
Tayassu tajacu			X	X	X
Lama glama	X′				
Lama guanicoe	X	X			
Mazama gouazoubira				X	X

forest supporting tapirs, primates, toucans, and jaguars and, within less than 100 air miles, be in a desert with columnar cacti, xeric-adapted mice, and Andean condors. Salta Province is such a place, and the further deterioration of the marvelous environmental complexity of the province will be an immeasurable loss.

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A REVIEW OF THE CUBAN MEMBERS OF THE GENUS *ARRHYTON* (REPTILIA, SERPENTES, COLUBRIDAE)

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Abstract

Cuban colubrid snakes of the genus *Arrhyton* are shown to belong to six species, of which two (*A. ainictum* from Camagüey Province and *A. tanyplectum* from Pinar del Rió Province) are named herein. A phyletic sequence among the species is suggested, and data are presented on the characteristics and ecology (insofar as known) of all species.

Introduction

The last reviser (Schwartz, 1965) recognized three Cuban species—*Arrhyton taeniatum* Günther, *A. dolichurum* Werner, *A. vittatum* Gundlach and Peters—of the (then considered) endemic colubrid genus *Arrhyton*. He also named *A. v. landoi* as a new subspecies. Two more recent works have changed the nomenclatural situation as far as *Arrhyton* is concerned—1) Maglio (1970) included Jamaican and Puerto Rico taxa in his expanded definition of the genus, although we are not convinced that his inclusion of extra-Cuban species within *Arrhyton* is correct, that biological and nomenclatural problem does not concern us directly

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in the present context; 2) Lando and Williams (1969) raised *landoi* to specific (rather than subspecific) rank, based primarily on the lower tooth counts of *A. landoi* in respect to *A. vittatum.* Schwartz and Thomas (1975) continued, however, to consider *landoi* as a subspecies of *A. vittatum.* They also reported a specimen of *A. v. landoi* from Francisco in Camagüey Province; all previous records had been from the southern coastal regions of Oriente Province, and the Camagüey record stood alone geographically. It was also significant in another context—the specific or subspecific status of *landoi* is in part contingent upon whether it is sympatric with *A. vittatum.* The Francisco specimen suggests that this is the case, although there are no *A. vittatum* from intermediate localities nor have the two taxa been taken syntopically.

The present review stems from the facts that the junior author has collected many additional *Arrhyton,* and that material, deposited in other Cuban collections, has been gathered together in the Instituto de Zoología. These specimens were in turn sent to the senior author who had assembled most of the specimens in North American collections. Thus we have had available for study (or scale counts and measurements) a total of 158 specimens of Cuban *Arrhyton.* Schwartz (1965) studied a total of 75 specimens; the number available to us has more than doubled. Although there are still puzzles remaining within Cuban *Arrhyton,* and there are huge hiatuses in the known distributions of several of the species, the added material has clarified certain problems. We discuss the taxa in the order proposed by Lando and Williams (1969), who suggested that *vittatum* is the most primitive, *taeniatum* the most specialized, and that *landoi* and *dolichurum* are intermediate. This sequence does not violate our own concepts; even though we have named new taxa in the present paper, they fall naturally into this sequence. In fact, the Cuban members of the genus would seem to fall naturally into three groups; this division will be discussed later in this paper.

TAXONOMIC ACCOUNTS

Arrhyton vittatum Gundlach and Peters

Cryptodacus vittatus Gundlach and Peters, 1862, Monatsb. Akad. wiss. Berlin, p. 1003. *Type-locality:* Cárdenas, Matanzas Province, Cuba. *Holotype:* ZMB (Museum für Naturkunde, Humboldt-Universität, Berlin, D.D.R.) 4096 (not examined by authors).

Arrhyton bivittatum Cope, 1863, Proc. Acad. Nat. Sci. Philadelphia, 14:82. *Type-locality:* Cuba. *Holotype:* USNM 5784 (examined by authors).

Arrhyton vittatum: Boulenger, 1894, Cat. Snakes British Mus., 2:252.

Carpodacus vittatus Schwartz, 1965, Proc. Biol. Soc. Washington, 78:105 (*in errore*).

Definition.—A small (males to 194 mm, females to 207 mm snout-vent lengths), usually distinctly lined, non-glossy or iridescent, snake without a distinctly upturned rostral, ventrals 107 to 123 in males, 108 to 122 in females; subcaudals paired, 52 to 76 in males, 52 to 81 in females; head neither conspicuously flattened nor broad; dorsal pattern a series of three dark brown longitudinal lines, the most lateral of which lie on scale rows 3 and 4 (occasionally on 2 to 5) and are much darker than the median line (see Fig. 3 for all dorsal body pattern); lined pattern not less pronounced in juveniles than in adults; ventral color dull cream in preservative and white to pale pinkish in life; ratio of tail/total length × 100, 28.3 to 36.6 in all males (regardless of size), 28.8 to 38.4 in all females; loreal present, usually single bilaterally, occasionally 1/2 or 2/2; prefrontals usually two, occasionally one; dorsal cephalic pattern a dark (brown) blotch whose margins are ill-defined and not outlined distinctly with white (see Fig. 2 for all dorsal head patterns), involving the scutes posterior to the prefrontals and extending to the edges of the parietals, or beyond onto the anteriormost body scales; median brown dorsal line (which usually involves the median and two paramedian dorsal scale rows) begins at the posterior edge of the cap and is usually joined to it; a brown loreal line extends from the naris through the eye and temporals, and thence along scale rows 3 and 4 (usually), the temporal portion of this line distinct and separate from the brown cap by a pale line which extends from the posterior margin of the eye more or less along the outer edges of the parietals; of the three dorsal lines, the lateral pair is often much darker than the median line, which may be very faint or even barely discernible; in smaller individuals, the first two rows of dorsal scales may be almost as dark as the lateral line, so that its lower margin is less distinct than in adults; some brown stippling or suffusion on the infralabials and the chin in general; scale rows usually 17-17-17, supralabials usually 7/7, infralabials usually 9/9 (but see Variation below); one preocular and two postoculars on each side.

Variation.—We have grouped together the series of *A. vittatum* into four geographic samples from west to east as follow: 1) I-PR—Isla de Pinos, Pinar del Río (12 specimens); 2) H-M—Habana-Matanzas (30); 3) V-C—Las Villas-Camagüey (18); 4) NO—northern Oriente (5). Some scale data on these samples are given in Table 1. The largest male (IZ 5595) has a snout-vent length of 194 (all measurements in millimeters) and is from Pinar del Río Province; a male from Matanzas Province (MFP 534) is only very slightly smaller with a snout-vent length of 193. The longest female (ASFS V50459) has a snout-vent length of 207 and is from Habana Province; no other female approaches this one in length. Taking the entire lot into consideration, western specimens seem to be longer than eastern snakes; the sample from NO, however, contains only five specimens. Still, the much larger V-C series (18 specimens) does not include any extremely large individuals. Ventral scales in males have means between 112.9 (H-M) and 117.7 (NO), with a range of 107 to 123 (both H-M sample). Ventral means in females range between 111.6 (H-M) and 116.8 (V-C), with a range of 108 (H-M) to 120 (H-M, V-C). Male subcaudal means vary between 64.6 (V-C) and 70.4 (I-PR), with a range of 52 (V-C) to 76 (I-PR). Female subcaudal means vary between 59.0 (V-C) to 76.0 (I-PR), with a range of 52 (V-C) to 81 (I-PR). Means of total underbody scales

Table 1.—*Scale counts and ratios of six species of Cuban* Arrhyton; *means and extremes by sex are shown.*

Taxon	Sex	N	Ventrals	Subcaudals	Total underbody scales	Tail/total length × 100
Arrhyton vittatum						
Isla de Pinos-Pinar del Río	♂	7	116.3 (111–122)	70.4 (62–76)	186.6 (173–198)	33.7 (32.1–35.3)
	♀	4	112.3 (111–115)	76.0 (70–81)	188.3 (181–195)	36.6 (34.2–38.4)
Habana-Matanzas	♂	14	112.9 (107–123)	65.8 (61–73)	174.8 (171–193)	32.7 (29.0–35.7)
	♀	7	111.6 (108–120)	60.2 (55–67)	172.4 (165–187)	30.9 (29.2–33.0)
Las Villas-Camagüey	♂	12	117.1 (110–122)	64.6 (52–71)	180.8 (155–192)	32.0 (28.3–34.6)
	♀	4	116.8 (112–120)	59.0 (52–66)	175.8 (166–184)	30.4 (28.8–32.1)
Northern Oriente	♂	3	117.7 (116–119)	69.0 (64–75)	186.7 (182–191)	33.5 (30.3–36.6)
	♀	2	116.0 (115–117)	66.5 (64–69)	182.5 (179–186)	32.4 (31.9–32.9)
Arrhyton landoi	♂	20	127.6 (118–150)	83.9 (71–111)	211.8 (191–252)	35.0 (30.7–40.1)
	♀	12	127.9 (115–141)	83.0 (69–96)	210.1 (184–237)	34.1 (32.4–36.3)
Arrhyton ainictum	♂	1	137	108	245	32.7
Arrhyton dolichura	♂	7	128.9 (127–132)	116.4 (101–127)	245.0 (232–254)	42.7 (40.4–45.8)
	♀	5	126.6 (123–132)	111.8 (104–127)	238.0 (229–252)	41.2 (39.6–44.4)
Arrhyton tanyplectum	♂	2	145.5 (145–146)	132.5 (132–133)	278.0 (277–279)	42.7 (41.9–43.5)
	♀	1	141	121	262	41.4
Arrhyton taeniatum	♂	19	178.0 (168–187)	87.1 (73–99)	264.8 (249–278)	25.7 (22.0–28.3)
	♀	19	180.2 (173–189)	89.6 (76–105)	284.6 (251–292)	24.9 (18.4–29.5)

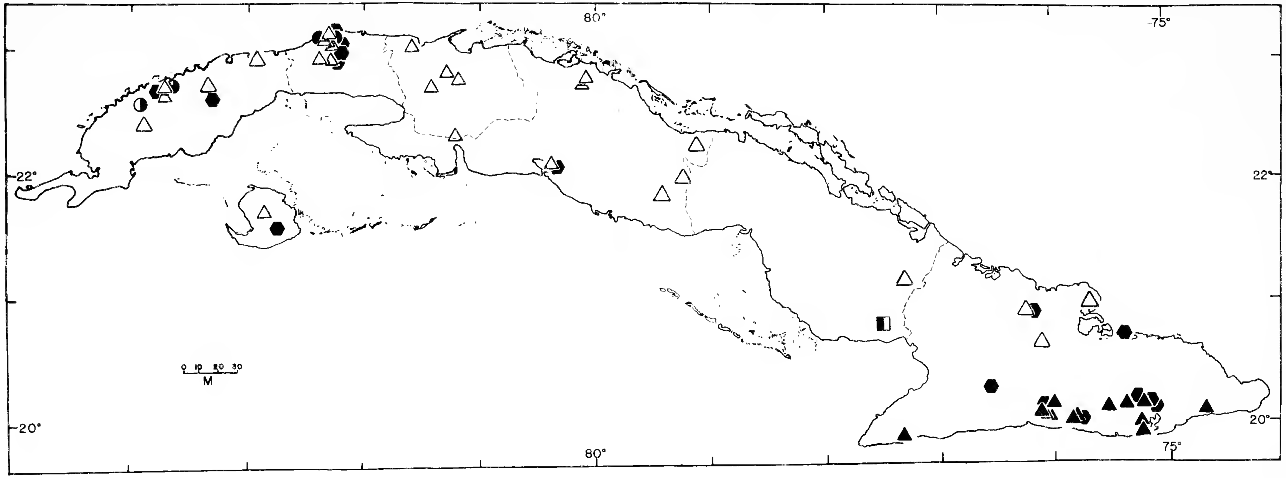

Fig. 1.—Map of Cuba, showing the known distributions of six species of *Arrhyton*, as follow: *vittatum*, hollow triangles; *landoi*, solid triangles; *ainictum*, semi-solid square; *dolichura*, solid circles; *tanyplectum*, semisolid circles; *taeniatum*, solid hexagons. In some cases, adjacent localities have been combined for greater clarity.

(ventrals + subcaudals) in males vary between 174.8 (H-M) and 186.7 (NO), with a range of 155 (V-C) to 198 (I-PR). Total underbody scales in females have means between 172.4 (H-M) and 188.3 (I-PR); the range is 165 (H-M) to 195 (I-PR). Tail/total length ratios × 100 means in males vary between 32.0 (V-C) and 33.7 (I-PR), with a range of 28.3 (V-C) to 36.6 (NO). The same ratio means in females vary between 30.4 (V-C) and 36.6 (I-PR), with a total range of 28.8 to 32.1 (both V-C). In general, western (I-PR) specimens have somewhat higher scale counts; the trend is most obvious in subcaudal scales. Central specimens (H-M) in general have low counts, whereas specimens from Las Villas eastward have higher counts once again. There are no significant differences in tail/total length ratios from west to east.

Supralabials are usually 7/7, with only one of 61 specimens with a count of 7/8. Infralabials are modally 9/9 (22 specimens), with other counts of 8/8 (19), 6/7 (one), 7/8 (four), and 8/9 (10). The incidence of 9/9 is highest in NO (three of five specimens = 60%) and in H-M (12 of 25 specimens = 48%); no I-PR specimen has a count of 9/9. Prefrontals are usually two, but two specimens from H-M and one from NO have one prefrontal. One loreal is usually present on each side, but one specimen from H-M has 2/2 and another from V-C has 1/2. Preoculars are 1/1 in all but one specimen (V-C) with 1/2. Postoculars are usually 2/2 except for one specimen (H-M) with a count of 1/2. The lateral stripe is usually on scale rows 3 and 4, but one specimen (H-M) has the lateral stripes on rows 2–5. Most specimens have a dorsal scale row formula of 17-17-17, but other counts include 18-17-17 (four specimens), 19-17-17 (four), 15-17-17 (two), and 18-18-17 (one).

Lando and Williams (1969) gave the following tooth counts for seven *A. vittatum*: dentary, 15–17; maxilla, 12–15 + 2; pterygoid, 9–10; palatine, 10–15.

Distribution.—Islandwide on Cuba and the Isla de Pinos, except for the southern coast (south of the Sierra Maestra and the Sierra de Purial and its affiliates) in Oriente Province (see Fig. 1 for distributions of all species).

Remarks.—Very little information is available upon the habits or habitats of *A. vittatum*. One specimen (AMNH 77780) was taken crossing a dry road through semi-xeric forest during the day, and another (IZ 5108) was found under a rock. We assume that the species is cryptic, but may be active during the day as well as at night.

Specimens examined.—ISLA DE PINOS: no further locality (MCZ 12446–47. PINAR DEL RIO PROV.: Valle de Pica Pica, Sumidero (IZ 5596); mountains N San Vicente (AMNH 77780); Viñales (MFP 263); Loma de Taburete, Sierra del Rosario (not mapped) (IZ 5108); Sierra del Rosario (IZ 5716); Cabañas (IZ 5580–83); Cafetal El Liberal, Cabañas (IZ 5595). HABANA PROV.: La Habana (USNM 93929); Vedado, La Habana (MCZ 44404); Reparto El Moro, La Habana (IZ 5605); Atabey, Marianao (ASFS V50456–60, IZ 4709); El Cotorro (AMNH 46723–28 + 1 unnumbered MFP); Jacomino (not mapped) (MFP 527); Valle de Lawton (not mapped) (IZ 5576); Chávez (IZ 5624); Santiago de la Vegas (IZ 3631, IZ 4648–49); Cojímar (MCZ 12362); no locality other than "Cuba" (USNM 5784—holotype of *bivittatum*). MATANZAS PROV.: Matanzas (USNM 103627); Finca S. Matías, 9.5 km from Matanzas (MFP 534); J. G. Gómez, Bolondrón (IZ 5607); Finca Rueda, Jovellanos (IZ 1994); San Miguel de los Baños (IZ 3724); Río Harábana, Ciénaga de Zapata (MCZ 10846). LAS VILLAS PROV.: San Felipe, Arroyo Blanco (IZ 3045); Soledad, Cienfuegos (MCZ 7925, MCZ 12358, MCZ 22712, MCZ 32676, MCZ 34259–60); Sancti Spíritus (ANSP 15909); Sierra de Jatibonico (MCZ 7951); Sagua la Grande (IZ 1074); Sitiecito, Sagua la Grande (MFP 184). CAMAGÜEY PROV.: Martí (UMMZ 70889–93, UMMZ 72404–05). ORIENTE PROV.: Banes (UMMZ 139742–44); San Germán (MFP 212); Holguín (IZ 5578).

Arrhyton landoi Schwartz

Arrhyton vittatum landoi Schwartz, 1965, Proc. Biol. Soc. Washington, 78:109. *Type-locality:* mountains north of Imías, Oriente Province, Cuba. *Holotype:* MCZ 42505 (examined by authors).

Arrhyton landoi: Lando and Williams, 1969, Stud. Fauna Curaçao and Carib. Is., 31:194.

Definition.—A moderate-sized (males to 238 mm, females to 250 mm snout-vent lengths), boldly to faintly longitudinally lined, non-glossy or iridescent snake without a distinctly upturned rostral, ventrals 118 to 150 in males, 115 to 141 in females; subcaudals paired, 71 to 111 in males, 69 to 96 in females (one female with an incomplete tail has 117 subcaudals); head neither conspicuously flattened nor broad; dorsal pattern a series of three dark (in juveniles) to rather faint (in adults) brownish longitudinal lines, the most lateral of which lie on scale rows 3 and 4 (occasionally on 4 only); venter dull cream in preservative and pink to grayish or cream in life; ratio of tail/total length × 100, 30.7 to 40.1 in all males, 32.4 to 36.3 in all females; loreal present, usually bilaterally single, two specimens with 1/2 loreals; prefrontals one or two; dorsal cephalic pattern a clearly defined and delimited dark brown cap, its center lighter than its periphery, surrounded by a pale tan figure from the posterior border of the parietals through and above the eye onto the prefrontals; a brown (but paler centrally) stripe across the lores and through the eye and across the temporals and continuing as the lateral stripe on the body; infralabials (and often supralabials) and chin rather heavily stippled with brown; scale rows usually 17-17-17; supralabials usually 7/7, infralabials usually 9/9 (see Variation below); usually one preocular and two postoculars on each side.

Variation.—We have examined 33 specimens of *A. landoi* from the southern Oriente coast. The longest male (ASFS V6233) has a snout-vent length of 238, the longest female (ASFS V6234) 250; both are from the United States Naval Base. Scale data are presented in Table 1. Supralabials are usually 7/7 (28 specimens), but other counts include 7/8 (three), 8/8 (one), and 6/9 (one); infralabials are usually 9/9 (26), but other counts include 8/8 (three), 9/10 (two), and 8/10 (one). Prefrontals are two in 20 specimens, single in 11. Loreals are bilaterally one, with two specimens having 1/2 loreals. Preoculars are 1/1 in all specimens. Postoculars are 2/2 in 31 specimens, 1/2 in one specimen. The lateral stripe is usually on scale rows 3 and 4 (28 specimens) but two individuals have a narrow lateral line on scale row 4 only. Dorsal scale rows are usually 17-17-17 (28 specimens), with other counts of 16-17-17 (one), 18-17-17 (one), and 19-17-17 (one).

The distinctive dark brown cap, clearly outlined anteriorly and laterally with pale tan, is characteristic of all young and most adult specimens; however, there is a tendency for older individuals to have the edges of the cap more fragmented and less distinct than in young individuals. The intensity of the three body stripes, as well as the width of the middorsal stripe, are also variable. In general, the clarity of the stripes decreases with increasing size. The middorsal stripe may be broad and conspicuous or quite narrow and relatively inconspicuous. In some specimens (IZ 5592) the cephalic cap is followed by a pair of (presently) very pale spots, almost forming a pale nuchal band, bisected by the connection of the dark middorsal stripe with the dark head figure. Some other smaller specimens have a pair of pale blotches in this same area, whereas others lack it. Lando and Williams (1969) recorded the dorsum of a specimen in life of *A. landoi* as reddish brown with black middorsal stripe; lower surface cream, chin white (U.S. Naval Base specimen).

Lando and Williams (1969) gave the following tooth counts for three specimens of *A. landoi*: dentary, 14–15; maxilla, 10–11 + 2; pterygoid, 9; palatine, 9.

Comparisons.—The fact that *A. landoi* was first named as a subspecies of *A. vittatum* suggests that these two taxa are indeed similar. They are also geographic replacements, because *A. vittatum* is unknown from within the southern Oriente range of *A. landoi*. The single presumed *A. landoi* from Francisco, Camagüey Province, reported by Thomas and Schwartz (1975), we now feel represents another taxon, so that *A. landoi* is not known to occur within the range of *A. vittatum* to the north and west.

Aside from the dental differences noted by Lando and Williams (1969), the two species differ in size and scutellation. *Arrhyton landoi* is much the larger snake, with maximum snout-vent lengths in males of 238 and in females of 250, in contrast to a male maximum of 194 and female maximum of 207 in *A. vittatum* (both large specimens are from western Cuba in Pinar de Río and Habana provinces); most *A. vittatum* are much smaller than these two maximally sized individuals. Ventrals in male *A. landoi* are 118 to 150 (mean = 127.6), in females 115 to 140 (127.9); male *A. vittatum* have 107 to 123 ventrals (means by sample between 112.9 and 117.7) and females have 108 to 120 ventrals (means by sample between 111.6 and 116.8). Although there is some overlap between these counts in *A. landoi* and *A. vittatum,* it is minimal, and *A. landoi* have more ventrals than do *A. vittatum*.

Subcaudal scales show the same situation. In *A. landoi* males, subcaudals vary between 71 and 111 (mean = 83.9), in females between 69 and 96 (83.0); one female has an incomplete tail with 117+ subcaudals. In *A. vittatum,* males have subcaudals between 52 and 76 (means by sample between 64.6 and 70.4, the high mean from the Isla de Pinos-Pinar del Río sample), and females between 52 and 81 (means by sample between 59.0 and 76.0, the high mean again from western specimens).

Total underbody scales repeat the same phenomenon. Male *A. landoi* have 191 to 252 underbody scales, females 184 to 237 (the female with an incomplete tail has 239+). Male *A. vittatum* have between 155 and 198 underbody scales (means by sample between 174.8 and 186.7) and females between 165 and 195 (means by sample between 172.4 and 188.3). Tail/total length ratios × 100 in male *A. landoi* are 30.7 to 40.1 (mean = 35.0), in females 32.4 to 36.3 (34.1). This ratio in male *A. vittatum* varies between 28.3 and 36.6 (means by sample between 32.0 and 33.7), in females between 28.8 and 38.4 (means by sample between 30.4 and 36.6).

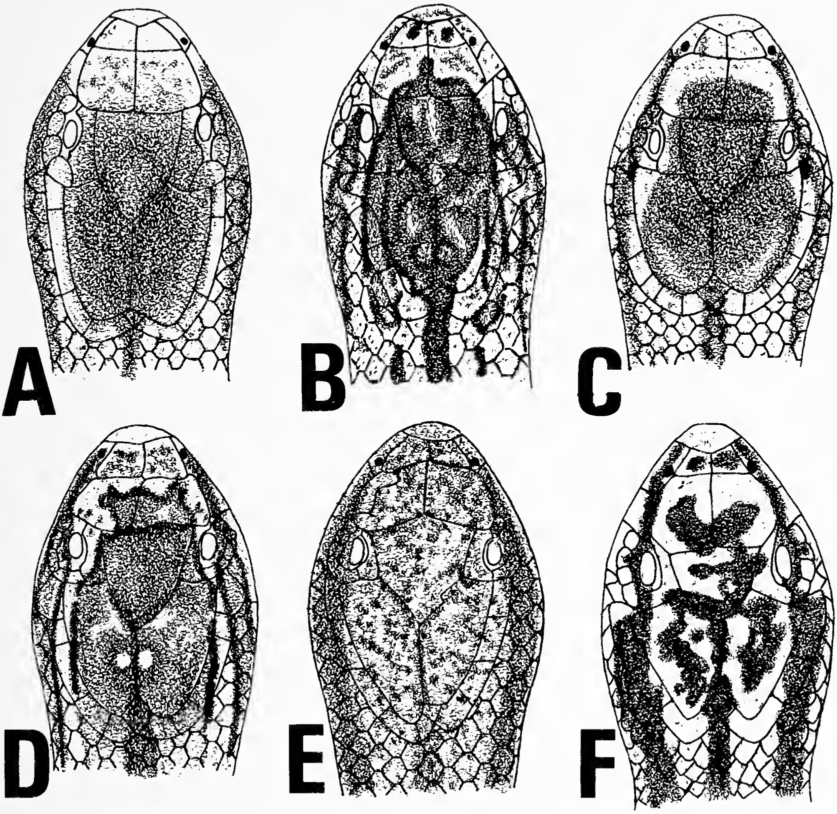

Fig. 2.—Dorsal views of heads of six species of *Arrhyton*, as follow: A, *vittatum* (AMNH 46727); B, *landoi* (USNM 139743); C, *ainictum* (IZ 4256—holotype); D, *dolichura* (IZ 1046); E, *tanyplectum* (AMNH 77782—holotype); F, *taeniatum* (IZ 5575).

The high incidence of one prefrontal in *A. landoi* (12 of 32 specimens, 38%) is noteworthy in comparison with *A. vittatum* (four of 52, 8%). All other scale counts are comparable.

Distribution.—The southern coast of Oriente Province and associated mountain ranges, from the Ensenada de Mora in the west to the mountains north of Imías in the east.

Remarks.—Schwartz (1965) noted the collection by Richard Thomas of a pair (ASFS V6233–34) of *A. landoi* on the U.S. Naval Base; they were secured in a rotting mat of palm fibers about the base of a fan palm in a palm thicket on a xeric scrubby hillside. Lando and Williams (1969) recorded one snake (MCZ 68728) as found under a stone about 6 inches below the ground surface; when exposed, the snake burrowed actively into the loose soil and rocks. A second specimen (MCZ 68943) was found on soil (under a rock?) and used the same escape tactics. Tolson took an adult male (ASFS V15036) in a wooded area under a large sheet of plywood almost completely concealed under leaf mold and debris.

Specimens examined.—ORIENTE PROV.: Ensenada de Mora, Pilón (AMNH 36703–04); 6.5 km S Palma Soriano (AMNH 83584); Cobre Range, Sierra Maestra (MCZ 42547); Río Frío, El Cobre (IZ 5628, IZ 5638); near Loma del Gato, Hongolosongo (IZ 5625); Santiago de Cuba (AMNH 2949, IZ 5577); Colonia España, Santiago de Cuba (UIMNH 49303); Cueva de Mamoncillo, Santiago de Cuba (IZ 5134); Playa Damajayabo, 2 km from Santiago de Cuba (IZ 5636); Vista Alegre (IZ 5600–01, IZ 5626, IZ 5635, IZ 5638); Santa María de Loreto, Ti Arriba (IZ 5629); Guantánamo (IZ 5602, IZ 5606); Soledad Estate, Guantánamo (IZ 5592); Río Guantánamo (IZ 5627); Tiguabos (IZ 5662); Las Pailas (IZ 5593); United States Naval Base, Guantanamo Bay—various localities (ASFS V6233–34, ASFS V15036, MCZ 141580, MCZ 58724, MCZ 68943, UIMNH 49301–02); mountains N Imías (MCZ 42505—holotype).

Arrhyton ainictum, new species

Holotype.—IZ 4256, an adult male, from Cueva del 18, Francisco, Camagüey Province, Cuba, taken 30 July 1974 by Lorenzo Zayas.

Definition.—A large (male holotype and only known specimen 363 mm snout-vent length), rather faintly longitudinally lined snake without a distinctly upturned rostral, ventrals 137, subcaudals paired, 108; head neither conspicuously flattened nor broad; basic dorsal pattern a series of three longitudinal lines, the lateral pair faint, the median dorsal line even fainter and diffuse, the lateral lines on scale rows 3 and 4; venter cream in preservative, presumably white in life; ratio of tail/total length × 100, 32.7; loreals asymmetrical, 1/2; prefrontals two; dorsal cephalic pattern a brown cap, not appreciably lighter centrally, sharply defined marginally and extending from the prefrontals onto the parietals and joining the extreme dark anterior portion of the median body line which within a short distance becomes faint and diffuse; a pair of paramedian tan blotches, darker than the central pale tan dorsal ground color, separated from the cap; a dark brown loreal line from the nares anteriorly around the snout and posteriorly to the eye, thence posteriorly to form the anterior portion of the lateral stripes which become faint a short distance posteriorly; between the median dorsal and lateral stripes on each side is another faintly indicated longitudinal stripe on scale rows 6 and 7, so that the net effect is a quinquelineate (rather than trilineate) snake; dorsum (as preserved) pale tan, dorsal scale rows (1 to lower half of 3 below lateral lines) white and concolor with venter; dorsal scales generally with dark bases, this dark pigment more extensive posteriorly, giving the tail a "braided" look.

Variation.—Other than the measurements and counts given in the definition, counts on the holotype are: supralabials, 7/7; infralabials, 8/8; 1/1 preoculars; 2/3 postoculars; total length, 589, tail length, 176; scale rows, 17-17-17; total underbody scales, 245.

Comparisons.—*Arrhyton ainictum* is easily distinguished from *A. vittatum* by its much larger size (maximally sized male *A. vittatum* 194 mm snout-vent length), greater number of ventrals (137 versus a maximum of 122 in *A. vittatum* males), the clearly defined cephalic cap, and the quinquelineate pattern.

Because the holotype of *A. ainictum* has previously been reported (Schwartz and Thomas, 1975) as *A. v. landoi* (=*A. landoi* in our present usage), it is obvious that the most pertinent comparisons are with that taxon. The two species differ from each other in a number of ways, although we admit to a close relationship between them. *Arrhyton ainictum* is the larger snake (largest male *A. landoi* 250 snout-vent length); ventral and subcaudal counts in *A. ainictum* fall within the ranges of these counts in *A. landoi* but near the upper extremes. Total underbody counts show the same situation (245 in *A. ainictum*, 191 to 252 in *A. landoi* males); ratio of tail/total length (32.7) likewise falls within the range of *A. landoi* males (30.7 to 40.1), but toward the lower extreme. Although 2/3 postoculars is likely a peculiar aberration in the holotype, it is not known to occur in *A. landoi*, which modally has 2/2 postoculars. However, no *A. landoi* has a quinquelineate pattern as does *A. ainictum*, and the cephalic patterns, although similar, are not identical. In large adult *A. landoi* (which are invariably smaller than the holotype of *A. ainictum*), the cephalic cap tends to become less sharply defined, whereas in *A. ainictum* the cap is quite sharply delimited and is not strikingly paler centrally as is the case in *A. landoi*.

Distribution.—Known only from the type-locality.

Remarks.—Considering the history of the nomenclature of Cuban *Arrhyton*, we may seem foolhardy to name a new species of the genus on the basis of one specimen. We have little doubt that *A. ainictum* is distinct but its level of distinctness is in dispute. It might indeed more properly be regarded as a western subspecies of *A. landoi* (in which case its locality is removed some 125 airline km and across the large Golfo de Guacanayabo) from the nearest *A. landoi* locality (Ensenada de Mora, Pilón). The intervening land area includes the low-lying and mesic Valle Central, through which the large Río Cauto flows westward into the Golfo de Guacanayabo. Most of western Oriente and all of Camagüey provinces are unknown as far as *Arrhyton* are concerned; specimens from this region are from areas far removed (Holguín, San Germán, Banes), with the exception of a series of unquestioned *A. vittatum* from Martí, 45 km N of Fran-

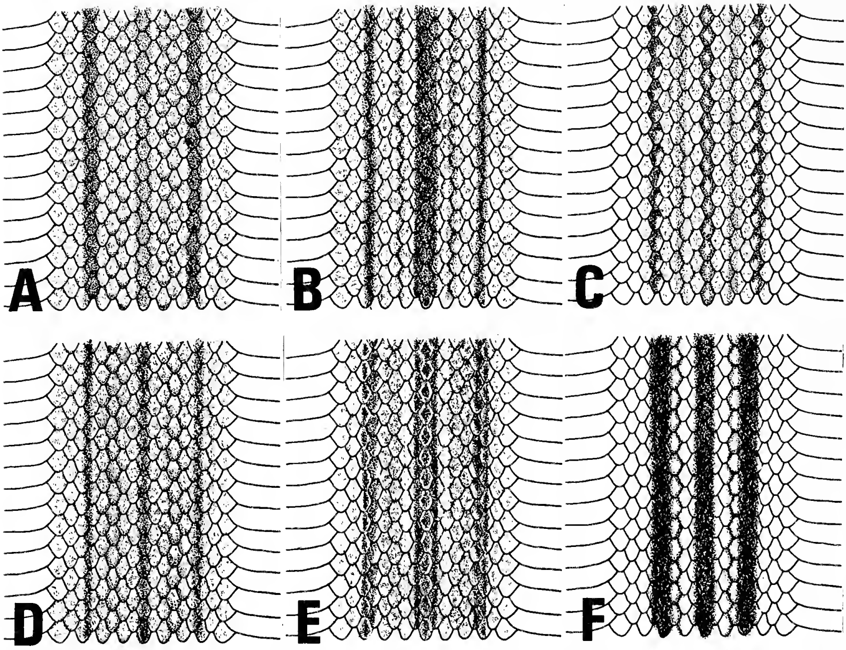

Fig. 3.—Midbody patterns of six species of *Arrhyton*; same specimens as in Fig. 2. A, *vittatum*; B, *landoi*; C, *ainictum*; D, *dolichura*; E, *tanyplectum*; F, *taeniatum*.

cisco. There are no other *Arrhyton* of any species known from Camagüey[1] (in which province the type-locality lies in the southeastern part) or from the adjacent portion of Oriente. All these facts have swayed us in naming this single specimen as a new species. In many ways *A. ainictum* may seem to be related to far-western *A. dolichura,* which it resembles to some extent.

Etymology.—The name *ainictum* is from the Greek, meaning "expressed in riddles," in allusion to the puzzle which this specimen and species presents.

Arrhyton dolichura Werner

Arrhyton dolichurum Werner, 1909, Mitt. Naturh. Mus. Hamburg, 26:224. *Type-locality:* "Alabama (?)"; restricted by Grant, Smith, and Alayo, 1959, Herpetologica, 15:130, to La Habana, Habana Province, Cuba. *Holotype:* now destroyed; formerly in the Universität Hamburg, Zoologische Museum.

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[1] Since this manuscript was completed, a specimen of *A. vittatum* has been collected by Lorenzo Zayas at Loma de San Martín, Sierra de Najasa, in southeastern Camagüey Province; the snake (sex undetermined) has 119 ventrals and 84 subcaudals, and a total length of 285, tail 95. The locality is about 38 km north-northwest of the type-locality of *A. ainictum.*

Definition.—A moderate (males to 233 mm, females to 249 mm snouth-vent lengths) trilineate, neither glossy nor iridescent snake, with a slightly upturned rostral, ventrals 127 to 132 in males, 123 to 132 in females; subcaudals paired, 101 to 127 in males, 104 to 127 in females; head neither conspicuously flattened nor broad; dorsal pattern a series of three brown lines, the most lateral of which lie on scale rows 3 and 4; lined pattern not less pronounced in juveniles than in adults; ventral color cream in preservative and probably white in living individuals; ratio of tail length/total length × 100, 40.4 to 45.8 in males, 39.6 to 44.4 in females; loreal present, bilaterally single; prefrontals two; dorsal cephalic pattern a dark brown cap of uniform intensty, vividly outlined with white, the white pigment involving the snout and the lateral margins of the brown cap from the prefrontals to the parietals, where the cap joins the median dark middorsal line which is prominent and contrasting with the brown dorsal color; a dark loreal line from the nares to the eye, and thence posteriorly across the temporals to form the dark lateral body stripes; rostral and first few supralabials flecked with dark brown on a pale to white ground; a minute but very conspicuous pair of tiny white dots paramedially, one of each side of the parietal suture at about its anterior one-third; dorsal scales somewhat more darkly edged along their posterior margins; dorsal scale rows 1 and 2 and lower portion of 3 (that is, all rows ventral to the lateral lines) white and concolor with the venter.

Variation.—The series of *A. dolichura* consists of seven males and five females. Maximum snout-vent length in males is 233 (IZ 1202) and in females 249 (IZ 1044). Scale counts are given in Table 1. Other counts are as follows: supralabials, always 7/7; infralabials, 8/8 (eight specimens), 8/9 (two), and 9/9 (two). Prefrontals are always two, loreals always 1/1, preoculars always 1/1, postoculars usually 2/2 (11 specimens), occasionally 1/2 (one); dorsal scale rows are 17-17-17 in 11 specimens and 17-17-15 in one.

The coloration and pattern given in the definition apply well to the entire series. The brown cap, not paler centrally, with a crisp and distinct white outlining, the whitish or pale anterior portions of the prefrontals, the trilineate body pattern, the dark posterior margins to the dorsal scales, the white parietal dots, and the pale lower scale rows below the lateral lines—all are common to the entire series. The relatively high number of subcaudals is reflected in the tail/total length ratio × 100, which is 40.4 to 45.8 (mean = 42.7) in males, 39.6 to 44.4 (41.2) in females.

Comparisons.—*Arrhyton dolichura* is easily distinguished from *A. vittatum* by the higher scale counts, larger size, and different head pattern in the former. *Arrhyton landoi* and *A. dolichura* are similar in size and have similar means of ventrals in both sexes. The number of subcaudals in *A. dolichura* (111 to 127 in males, 104 to 129 in females) is greater than the number of subcaudals in *A. landoi* (71 to 111 in males, 69 to 117+ in females), although there is some overlap. The head patterns in these two species are similar except that in *A. landoi* the brown cap is lighter centrally than peripherally, and the pair of tiny white parietal dots is absent; the cap is not vividly outlined in white in *A. landoi* as it is in *A. dolichura*. The tail/snout-vent length ratios × 100 will easily separate the two species; in males, this ratio in *A. landoi* is 30.7 to 40.1 (mean = 35.0), in *A. dolichura* 40.4 to 45.8 (43.7); in females, this ratio in *A. landoi* is 32.4 to 36.3 (34.1), in *A. dolichura* 39.6 to 44.4 (41.2).

Comparisons indicate that *A. ainictum* reaches a much larger size (male 363 snout-vent length) than *A. dolichura* (males to 233). The ventral count of the male *A. ainictum* (137) falls above the upper limit of this count in *A. dolichura* (132). The tail/total length ratio × 100 is 32.7 in *A. ainictum* and varies between 40.4 and 45.8 in *A. dolichura*. The cephalic cap in *A. ainictum*, although distinctly outlined, is not strongly contrastingly outlined as it is in *A. dolichura*. Finally, the quinquelineate pattern in *A. ainictum* does not occur in *A. dolichura*. Furthermore, the two species are separated by a distance of 650 airline kilometers.

Distribution.—Known only from the vicinity of La Habana, Cuba.

Remarks.—Although the species name was originally spelled *dolichurum*, in an apparent effort to make it of neuter gender to agree with the neuter gender of the name *Arrhyton*, such an action is incorrect. The name *dolichurum* is used as an appositional noun, not an adjective, and the Greek word for "tail" (*oura*) is feminine and must retain its feminine status under these circumstances. Accordingly we have made the orthographic change.

Certainly no other species of *Arrhyton* has had such a checkered nomenclatural history. Originally described by Werner as possibly from the state of Alabama, the name fell into disuse until 1959, when Grant et al., studying one specimen with locality data and two others (published data from the holotype and a third specimen from "Cuba" reported by Bocourt), re-instated the name. They presented a photograph of a dorsal view of the single specimen in their possession (from La Habana), but unfortunately the head of the specimen is bent downward so that the very distinctive head pattern is just barely visible and easily overlooked. Schwartz (1965) examined four specimens (one from Habana, three from Pinar del Río provinces); the latter three specimens were collected by him and were seen in life. In misreading Grant et al.'s paper, Schwartz attributed the species to Habana, Pinar del Río, and Oriente provinces; Garrido later brought to his attention that Grant et al.'s reference in their paper to the "Oriente specimen" in actuality referred to the specimen they had examined from La Habana but which was *housed* at that time in the Universidad de Oriente collection; thus, the species is unknown from Oriente Province, and the correction was made by Schwartz and Thomas (1975).

With the acquisition of many more specimens, it now becomes equally obvious that *A. dolichura* does not occur in Pinar del Río

Province; the three snakes called *A. dolichurum* by Schwartz are, remarkably, still another species (see below). As far as now known, *A. dolichura* has been collected only in the immediate environs of La Habana, although it surely has a broader distribution in west-central Cuba. Werner (1909) gave a total length of 410 mm and a tail length of 177 mm for the female holotype (tail/total length ratio × 100, 43.1) and ventral and subcaudal counts of 131 and 114 (total underbody count 245); his color description agrees with the specimens here regarded as *A. dolichura* rather than with those to the west. Additionally, the ventral, subcaudal, and tail/total length ratio all fall within the known ranges for *A. dolichura* as we use the name.

Specimens examined.—HABANA PROV.: Reparto Atabey, La Habana (IZ 4288); Marianao, La Habana (IZ 5633); Bosque de la Habana (MLJ 2, IZ 5604, IZ 5630); El Laguito, Marianao, La Habana (IZ 1043–46, ASFS V50455); frente al Laguito, Country Club, La Habana (IZ 5633).

Arrhyton tanyplectum, new species

Holotype.—AMNH 77782, an adult male, from cliffs at San Vicente, Pinar del Río Province, Cuba, taken 9 July 1957 by Albert Schwartz. Original number ASFS 2661.

Paratypes.—AMNH 77779, Cueva de los Indios, San Vicente, Pinar del Río Province, Cuba, 18 June 1957, W. H. Gehrmann, Jr.; AMNH 81135, north base, Pan de Azúcar, 8 km E Matahambre, Pinar del Río Province, Cuba, 13 August 1958, A. García.

Definition.—A large (males to 306 mm, females to 265 mm snout-vent lengths) trilineate, glossy, and somewhat iridescent snake, with a slightly upturned rostral, ventrals 145 and 146 in two males, 141 in one female; subcaudals paired, 132 and 133 in males, 121 in female; head neither conspicuously flattened nor broad; dorsal pattern a series of three dark brown lines on a brown ground, the lateral lines on scale rows 3 and 4; lineate pattern equally prominent in both juveniles and adults; ventral color cream in preservative, pale yellow in living specimens; the median dorsal line continues boldly to the tip of the tail; dorsal scales dark-edged giving a rather "scaly" or "braided" appearance to the entire animal, most pronounced on the tail; ratio of tail/total length × 100, 41.9 and 43.5 in males, 41.4 in the female; loreal present, single bilaterally; prefrontals two; head without a distinct cap, the upper surface of the head merely suffused with darker brown, this color reaching as far laterally as the loreopostocular line which is poorly defined, not separated from the dorsal head color, and concolor with it; venter immaculate, but mental scale and the first one to four infralabials with dark stippling or a blotch.

Description of the holotype.—An adult male, snout-vent length 306, tail length 236; body relatively long and slim and rather racer-like, head slightly broader than neck; dorsal scale rows 17-17-17; ventrals 145; subcaudals paired, 132 plus conical tip; loreal relatively large, rectangular, longer than high; preoculars 1/1, postoculars 2/2; rostral slightly upturned, tilted anteriorly; supralabials 7/7; infralabials 8/8; anterior and posterior chin shields approximately the same length, but the posterior pair pointed posteriorly, and the anterior pair parallelogrammatic. Dorsum iridescent; ground color (preserved but not appreciably different from color in life) brown with three longitudinal dark brown lines; top of head completely and rather irregularly mottled with brown and tan, but mottling not prominent; median dorsal stripe from occiput to tip of tail, involving the median and less than half of each paramedian scale row to above vent, and on tail occupying the median third of the paired paramedian scales; lateral longitudinal lines beginning at naris, proceeding across lores to eye, and then posteriorly across temporals to scale rows 3 and 4 along entire length of body; just anterior to vent, lateral stripe descends to scale rows 1 and 2 and continues to tail tip on these rows. Scales between lines brownish and on body their anterior edges darker brown; on the dorsal surface of the tail, the brown anterior edges become more prominent, and form a block-like pattern involving the longitudinal lines, and giving the appearance of a "woven" or "braided" tail. Venter virtually immaculate yellow in life, except for a few brownish punctuations on the mental scale and the first four infralabials. Hemipenis partially extruded, proximally equipped with many tiny spines, and distally with a double crown of relatively long stout spines.

Variation.—Scale counts for the two males and one female are shown in Table 1. Additional scutellar data are as follows: supralabials, 6/6 (one specimen) or 7/7 (two); infralabials, 8/8 (two) or 9/9 (one); prefrontals, 2; preoculars, 1/1; postoculars, 2/2; scale rows, 17-17-17. The two paratypes are (AMNH 77779) a male, snout-vent length 176, tail length 127, and (AMNH 81135) a female, snout-vent length 265, tail length 187.

The two paratypes agree in all details of coloration and pattern with the holotype. The absence of a discrete black cap, even in the small male paratypes, is pertinent and significant. The dorsal ground color was recorded as P1.15E11 in AMNH 77779 (color designation from Maerz and Paul, 1950).

Distribution.—Pinar del Río Province, Cuba, from Pan de Azúcar (Matahambre) in the west to San Vicente in the east.

Comparisons.—*Arrhyton tanyplectum* does not require comparison with *A. vittatum, A. landoi,* or *A. ainictum.* The dorsal pattern and absence of a head cap distinguish *A. tanyplectum.* The high number of ventrals (145 to 146 in males, 141 in female) distinguishes *A. tanyplectum* from *A. vittatum* (107 to 123 in males, 108 to 120 in females). The ventral counts of *A. tanyplectum* fall at or near the upper extremes for *A. landoi* (118 to 150 in males, 115 to 141 in females) and *A. ainictum* (137 in male). Subcaudal counts in *A. tanyplectum* (males 131 to 132, female 121) are greater than in *A. vittatum* (males 52 to 76, females 52 to 81), *A. landoi* (males 71 to 111, females 69 to 117+), or *A. ainictum* (male 108). Total underbody scales likewise are distinctive in *A. tanyplectum* (males 277 to 279, female 262), whereas these counts in *A. vittatum* are (males 155 to 198, females 165 to 195), *A. landoi* (males 191 to 252, females 184 to 239+), and *A. ainictum* (male 245). Finally, tail/total length ratios × 100 have the following means:

A. tanyplectum males, 42.7, female, 41.4; *A. vittatum* males (by sample), 32.0–33.7, females, 30.4–36.6; *A. landoi* males, 35.0, females, 34.1; *A. ainictum* male, 32.7.

Arrhyton tanyplectum requires detailed comparison with *A. dolichura*. Both are relatively large trilineate snakes; however, *A. dolichura* has a distinctly and vividly outlined cephalic cap, which is absent in even the smallest *A. tanyplectum*. We stress this fact since obliteration of the cap might be considered ontogenetic, which it is not. The two species likewise differ in number of ventral scales; *A. tanyplectum* males have 145 to 146 ventrals in contrast to 127 to 132 in *A. dolichura,* and the single female *A. tanyplectum* has 141 ventrals in contrast to 123 to 132, in female *A. dolichura*. Male *A. tanyplectum* subcaudals are 132 to 133, female 121; male *A. dolichura* 101 to 127, females 104 to 127. Total underbody scales in male *A. tanyplectum* are 277 to 279, in female 238, whereas these counts in male *A. dolichura* are 232 to 254 and in females 229 to 252. Tail/total length ratios × 100 in males of the two species have the same mean (42.7), and almost the same mean in females (41.4 in *A. tanyplectum,* 41.2 in *A. dolichura*).

Lando and Williams (1969) gave dentitional counts for one "*A. dolichurum*" (AMNH 81135, now a paratype of *A. tanyplectum*). The counts are dentary, 12; maxilla, 10 + 2; pterygoid, 8; palatine, 7.

Etymology.—The name *tanyplectum* is from the Greek for "in long plaits," in reference to the braided appearance of the tail.

Remarks.—The holotype was taken at night prowling at the base of the cliffs of a *mogote* at San Vicente; the small male paratype was taken at night in a formal garden at the base of the *mogote* in which the Cueva de los Indios lies, during a rain that had been heavy and had begun in the afternoon. The female paratype was taken among rocks at the base of cliffs, again at night, along with two specimens of the small boid *Tropidophis feicki* Schwartz; the previous afternoon had been dull and rainy. All three specimens and the circumstances under which they were collected suggest that this species is cryptic diurnally and forages above ground nocturnally, especially during and after rainy weather. The presence of cliffs and their associated talus seems to be the preferred niche occupied by *A. tanyplectum*.

Presumably *A. tanyplectum* occurs in suitable situations within the Sierra de los Organos (and also the Sierra del Rosario?) in Pinar del Río Province. That it is related to *A. dolichura* seems obvious, but there is an hiatus of about 145 airline kilometers between their known ranges.

Arrhyton taeniatum Günther

Arrhyton taeniatum Günther, 1858, *Cat. Snakes Brit. Mus.*, p. 244. *Type-locality:* Cuba. *Holotype:* British Museum (Natural History) 1946.1.21.48 (not examined by authors).

Colorhogia redimita Cope, 1863, Proc. Acad. Nat. Sci. Philadelphia, 14:81. *Type-locality:* eastern Cuba. *Holotype:* USNM 29769 (examined by authors).

Arrhyton fulvum Cope, 1863, Proc. Acad. Nat. Sci. Philadelphia, 14:82. *Type-locality:* Cuba. *Holotype:* USNM 1ˆ421 (not examined by authors).

Definition.—A large (males to 396 mm, females to 448 mm snout-vent lengths) glossy snake with upturned rostral, ventrals 168 to 187 in males, 173 to 189 in females; head conspicuously flattened and broad; dorsal pattern a series of five (three dark, two paler) longitudinal lines, the median and lateral pair dark, the lateral pair on scale rows 4 to 6, or 3 to 6 (occasionally 4 and 5), this lineate pattern most conspicuous in juveniles, less so in large adults where the pale lines darken and thus render the three dark lines less distinct; ventral surface immaculate, creamy white in preserved specimens and presumably so in life; tail/total length × 100 in males 22.0 to 28.3, in females 18.4 to 29.5; loreal absent (except as in the holotype of *redimitum*); prefrontals two; dorsal cephalic pattern an irregular but symmetrical series of dark blotches involving all dorsal head scales, with a more or less distinct dark cap, separated from the postocular beginning of the dark lateral lines by a light supraocular line which expands just behind the parietals into the dorsal pale lines; supralabials usually light, but anteriormost and rostral may have dusky centers; infralabials mostly immaculate, except that mental and the first two infralabials usually have some dusky mottling or stippling, which may extend posteriorly onto the infralabials and may also involve the first pair of chin shields. Scale rows usually 17-17-17; supralabials usually 7/7, infralabials usually 8/8; one preocular and two postoculars on each side.

Variation.—Scale counts are shown in Table 1. We have examined 41 specimens of *A. taeniatum* from the Isla de Pinos (two), Pinar del Río (two), Habana (six), Las Villas (12), and Oriente (19); thus, although there are no specimens available from the provinces of Matanzas or Camagüey, the species appears to be islandwide in distribution. The largest male (AMNH 46885) has a snout-vent length of 396 and a tail length of 126 and is from Habana Province; the largest female (AMNH 77781) has a snout-vent length of 448 and a tail length of 137 and is from Pinar del Río Province. Other scale counts include the following: supralabials 7/7 (35 specimens), 6/7 (two), and 6/6 (one); infralabials 8/8 (27), 8/9 (14), 9/9 (six), 7/8 (one); prefrontals always 2; loreals absent (37 specimens), 1/0 (one), 1/1 (one); preoculars 1/1 (39), 1/2 (one); postoculars 2/2 (38), 1/2 (one). Dark lateral stripe on scale rows 4–6 (23), 3–6 (23), 4–5 (two); scale rows 17-17-17 (34), 19-17-17 (five), 17-17-15 (one).

There seems to be no significant geographic variation in scutellation on Isla de Pinos and Cuban snakes. Schwartz (1965) noted that the single Isla de Pinos snake available then (CM 1877) has an unusually high number of subcaudals (93), but fresh material shows that counts of 92 or more occur in males from Habana and Oriente provinces, with a maximum of 99 in an Oriente snake. Schwartz also noted that a Pinar del Río snake (AMNH 77781) had the highest female ventral count (189); however, a Pinar del Río male (IZ 5262) has the lowest count (168) for members of this sex. Although no other females equal the high count in the Pinar del Río female, two Oriente females have counts of 187 and others in the low 180's.

The dorsal pattern likewise seems not to vary geographically. The major ontogenetic changes are involved with the intensity of the dorsal lines; these may become increasingly obscured with age until a condition (as in IZ 5594—a male, snouth-vent length 323) where they are so blurred that the five lines are distinguished only with difficulty. Although there is some variation in the scale rows involved with the dark lateral lines as noted above, row 4 is invariably involved in the lateral lines; most specimens have either three or four scale rows involved with the lateral line.

Color data on an adult male (IZ 4790—snout-vent length 369) from the Isla de Pinos, taken by the junior author, are: "a dorsal stripe or a lateral zone very bright canary yellow, which separated the white ventral color from the chestnut of the lateral stripes. Dorsum chestnut." Direct comparison of this specimen with another collected on the same date in Habana, showed the Isla de Pinos snake paler and less terracotta in color. Although we do not have ample color notes on Cuban (versus Isla de Pinos) snakes, it is possible that they differ in details of coloration, although not in pattern.

Lando and Williams (1969) gave the following dentitional counts on two *A. taeniatum*: dentary, 12; maxilla, 10 + 2; pterygoid, 6; palatine, 7.

Distribution.—Cuba, where known from the provinces of Pinar del Río, Habana, Las Villas, and Oriente; Isla de Pinos.

Comparisons.—*Arrhyton taeniatum* is amply distinct from all other species of *Arrhyton* on Cuba. The usual absence of a loreal scale, the tail/total length ratios × 100 (males 22.0 to 28.3, females 19.4 to 29.5), and the cephalic and dorsal patterns all serve to distinguish *A. taeniatum* from other Cuban *Arrhyton*. Additionally, its large size (males to 396, females to 448 snout-vent lengths), and high number of ventrals (males 168 to 187, females 173 to 189) serve to characterize the species.

Remarks.—The broad and somewhat compressed head with an upturned rostral suggests that *A. taeniatum* is probably a burrowing snake. The latter contention has been confirmed in that the junior author found an *Amphisbaena cubana,* which is strictly fossorial, in the alimentary tract of an *A. taeniatum* from the Isla de Pinos (IZ 4790). Field notes by P. J. Darlington on MCZ 22709–10 and MCZ 22705 state that these specimens were taken under rocks in dry pasture. C. T. Ramsden recorded one specimen (IZ 5585) as collected under Guinea grass (at Santa Cecilia), and another (IZ 5591) under a clod of dry earth (San Carlos, near Guantánamo). One has the impression that *A. taeniatum* is an open (rather than forested) area snake.

Specimens examined.—ISLA DE PINOS: Cayo Potrero, Ciénaga de Lanier (IZ 4790); no other locality (CM 1877). PINAR DEL RÍO PROV.: San Vicente (AMNH 77781); San Diego de los Baños (IZ 5262). HABANA PROV.: "La Alianza," Cuatro Caminos (IZ 5594, IZ 5634); El Cotorro (AMNH 46684–85); Cojímar (MCZ 8507); Chávez (IZ 5609). LAS VILLAS PROV.: Soledad, Cienfuegos (MCZ 10916, MCZ 12356–57, MCZ 19874, MCZ 22705–11); Guayanaro (not mapped) (USNM 139734). ORIENTE PROV.: Holguín (IZ 5578); La Esperanza, Jiguaní (IZ 5607); Barrederas (MFP 475); La Rosita de Borrero, Río Frío (ASFS V50453, IZ 5591); Santiago de Cuba (AMNH 20384); Ciudamar, Santiago de Cuba (UIMNH 49304); nr. Universidad de Oriente, Santiago de Cuba (ASFS

V50452); Guamá (USNM 29768); Guantánamo (IZ 5575); "Santa Cecilia," Guantánamo (IZ 5585, ASFS V50454); San Carlos, Guantánamo (IZ 5575, IZ 5587–91); no locality other than "Cuba" (USNM 29769—holotype of *redimitum*).

DISCUSSION

As we pointed out, Lando and Williams (1969) suggested that the Cuban members of *Arrhyton* could be arranged in a series, from *A. vittatum* as the most primitive to *A. taeniatum* as the most specialized, with *A. dolichurum* and *A. landoi* between these two extremes. We agree with this contention, and the present data on the new taxa named herein confirm it. In fact, it now is possible to arrange the members of the genus in Cuba into several groups. These are, from primitive to advanced:

I. *vittatum* group (*vittatum, landoi, ainictum*)
II. *dolichura* group (*dolichura, tanyplectum*)
III. *taeniatum* group (*taeniatum*)

I. The *vittatum* group is composed of small to large species, without strong morphological adaptations for burrowing (that is, head neither flattened nor broad, no upturned rostral), relatively low number of ventrals and subcaudals, and short tail. Some sort of dark cephalic pattern present, either indistinct or distinctly outlined with pale color; body pattern trilineate or quinquelineate. The geographic distribution is islandwide, with one species (*A. vittatum*) on the Isla de Pinos. *Arrhyton landoi* and *A. ainictum* may be interpreted as species satellite to *A. vittatum*; each of the former two species occurs in areas which seem to be unoccupied by *A. vittatum* (*A. landoi* in southern Oriente, *A. ainictum* in southeastern Camagüey).

II. The *dolichura* group contains two species; these are both restricted to extreme western and west-central Cuba; they are not highly modified for fossorial activity, are moderate to large in size, both have loreals, high numbers of ventrals and subcaudals, and long tails, their patterns are similar but *dolichura* has a well defined cephalic cap and *tanyplectum* does not.

III. The sole member of the *taeniatum* group is *A. taeniatum*. In its large size, obvious adaptations for burrowing in head form and structure, absence of a loreal, and short tail, this species is extremely distinct from all other Cuban *Arrhyton*. In fact, a case might be made for separating *taeniatum* as a distinct genus (see below). The quinquelineate pattern, although roughly similar to that of *A. ainictum*, is likewise distinctive. *Arrhyton taeniatum* is islandwide in distribution and also occurs on the Isla de Pinos.

Although the extra-Cuban species of *Arrhyton* (*callilaemus* Gosse, *funereum* Cope, *polylepis* Buden on Jamaica; *exiguum* Cope on Puerto Rico and the Virgin Islands) do not directly concern us, it is perhaps pertinent to point out certain facts concerning them and to compare their characteristics with those of the six Cuban species (data from Buden, 1966; Schwartz, 1967; Maglio, 1970). The four extra-Cuban *Arrhyton* are moderate to large snakes (*A. exiguum* reaches a maximum snout-vent length of 418 in males and 438 in females, as large as or larger than *A. taeniatum*). All have 19-19-17 dorsal scale rows (in contrast to 17-17-17 in Cuban species). None shows an extreme adaptation for burrowing, although all are cryptic. All have short to moderately long tails, with subcaudals in males varying between 77 in *exiguum* and 122 in *callilaemus,* in females between 62 in *funereum* and 109 in *callilaemus.*

Considering primarily skeletal details, Maglio (1970) stated that "it is in *taeniatum* . . . that we find the greatest development of the trends observed in the series leading from *funereus* and *callilaemus* . . . to *vittatum* and *dolichurum* . . ." His proposed phylogeny (p. 44) of the species included in *Arrhyton* (and Hispaniolan *Darlingtonia*) is reasonable, with Jamaica having the more basic species, and Cuba, Hispaniola, and Puerto Rico the more specialized ones. This phylogenetic sequence is based upon presence or absence of scale pits, number of maxillary and palatine teeth, hemipenial structure, and presence or absence of a loreal scale. The resemblances in these characters between Hispaniolan *Darlingtonia* and Cuban *Arrhyton taeniatum* is striking; yet these two "terminal" snakes in the series do not superficially resemble each other, and the similarities are almost certainly convergent. To accommodate the four extra-Cuban species in our proposed sequence of Cuban *Arrhyton* is difficult, because the Cuban radiation is far greater and more divergent than that encompassed by all extra-Cuban species combined. We are not even certain that all snakes now included in *Arrhyton* by Maglio should be associated at the generic level; cryptic and (especially) fossorial habits demand modification of skull structure (and Maglio noted that *A. taeniatum* has the most peculiar skull of the entire lot). The extra-Cuban species would all seem to be as basic as or more primitive than the Cuban *vittatum* group. We suggest that at least *pro tem* they be regarded as another group of *Arrhyton,* the *callilaemus* group, which is more basal than the Cuban *vittatum* group.

The facts that 1) Maglio was willing to accept *Darlingtonia* on Hispaniola as a genus distinct from (but allied to) *Arrhyton,* 2) the absence of other members of the complex on Hispaniola, and 3) the resulting hiatus in the *callilaemus* group (that is, none on Hispaniola but occurring to the west on Jamaica and to the east on Puerto Rico) suggest that *taeniatum* should likewise be accorded full generic rank. Unfortunately, the evidence is in part circumstantial and inferential. Perhaps, to some biologists the fact that *taeniatum* is the type-species of *Arrhyton* makes the issue even more troublesome, because another name would have to be resurrected for the balance of the genus (*Cryptodacus*

Gundlach and Peters, 1862, has priority; *vittatus* is the type-species). We are unwilling to take such a radical step but suggest that it might be considered in the future.

As the above paragraphs indicate, there is still too little data to postulate a sound theoretical history of the genus on Cuba (or on Jamaica and Puerto Rico, if the species on those islands are indeed assignable to *Arrhyton*). It is intriguing that the least and the most specialized species in Cuba (*A. vittatum* and *A. taeniatum*) are the only ones that are islandwide and occur also on the Isla de Pinos. *Arrhyton vittatum* is generally unspecialized, whereas *A. taeniatum* is very specialized; if the former is cryptic but not strongly fossorial and the latter is strongly fossorial, this may account for the ability of these two species, one at each end of the *Arrhyton* spectrum, to be grossly sympatric. All other species have relatively limited distributions, with *A. landoi* having the most extensive range along the southern Oriente coast. Perhaps most surprising is the occurrence of the *dolichura* group only in western and west-central Cuba. The two species of this group are apparently relatively closely related and *A. tanyplectum* is associated with rocky talus and cliffs; as far as the records are concerned, *A. dolichura* is an edificarian (!) snake. Obviously, we once more know too little of the ecology of *A. dolichura*. However, the occurrence of one of these species in the Sierra de los Organos is not surprising, because this mountain range (as well as the adjacent Sierra del Rosario) has several endemic species of amphibians and reptiles.

To pursue this discussion further is futile. Although we have examined far more material of Cuban *Arrhyton* than any other workers, there are still huge hiatuses in the distributions of several of the species, and we know all too little of the ecology of most of them. Nor can we answer questions on habits or syntopy-sympatry to yield any fruitful answers. We feel, however, that we have greatly expanded the knowledge of the systematics of these rarely collected small snakes.

ACKNOWLEDGMENTS

The senior author's fieldwork in Cuba was under the sponsorship of two National Science Foundation grants (G-3865, G-6252). For Schwartz's previous revision of *Arrhyton,* he borrowed specimens from the following collections, to whose curators we are in debt: American Museum of Natural History (AMNH), Charles M. Bogert; Academy of Natural Sciences of Philadelphia (ANSP), James E. Bohlke; Carnegie Museum of Natural History (CM), Neil D. Richmond; Museo Felipe Poey (MFP), Universidad de la Habana, Carlos G. Aguayo; Museum of Comparative Zoology (MCZ), Ernest E. Williams and Benjamin Shreve; Museo y Biblioteca de la Habana, Miguel L. Jaume (MLJ); Museum of Zoology, University of Michigan (UMMZ), the late Norman E. Hartweg and Thomas M. Uzzell; University of Illinois Museum of Natural History (UIMNH), Hobart M. Smith; National Museum of Natural History (USNM), the late James A. Peters. Some of these same specimens have been reborrowed for the present study, and we wish additionally to thank the following for their courtesy: Richard G. Zweifel and George W. Foley (AMNH), Clarence J. McCoy (CM), José P. Rosado (MCZ), and George R. Zug and Ronald I. Crombie (USNM). Material has been collected by the junior author, and specimens from other Cuban collections have been deposited in the Instituto de Zoología, Academia de Ciencias de Cuba (IZ) and others in the collection of the senior author (Albert Schwartz Field Series—ASFS). The senior author has had assistance in the field from Armando García, William H. Gehrmann, Jr., Richard Thomas, and Peter J. Tolson, who have collected specimens now in the AMNH and ASFS. Material in Cuban collections has been increased through the efforts of Lorenzo Zayas, Luis de Armas, and L. R. Hernández. We wish also to thank Luis Moreno and Noel González for the loans of specimens under their care.

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ADDENDUM

The recent redivision of Cuban provinces into many more units than previously must be mentioned. Most American biologists concerned with Cuban geography have neither new maps nor information on the details of this division. We have, in the body of the text, used the classic political subdivisions and the map likewise shows them. However, below we give the proper and current names for the provinces; province names are in capitals, with the corresponding precise localities in lower case type, these arranged by species in the sequence discussed in the present paper.

A. vittatum.—ISLA DE LA JUVENTUD (Isla de Pinos); CIUDAD DE LA HABANA (La Habana, Vedado, Marianao, Cotorro, Jacomino, Lawton, Chávez, Santiago de las Vegas, Cojímar); SANCTI SPÍRITUS (San Felipe, Arroyo Blanco, Sancti Spíritus, Sierra de Jatibonico); CIENFUEGOS (Cienfuegos); VILLA CLARA (Sagua La Grande, Sitiecito); HOLGUÍN (Banes, Holguín, San Germán).

A. landoi.—GRANMA (Pilón); SANTIAGO DE CUBA (Palma Soriano, El Cobre, Hongolosongo, Santiago de Cuba, Damayajabo, Vista Alegre, Santa María de Loreto); GUANTÁNAMO (Guantánamo, Soledad Estate, Tiguabos, Las Pailas, U.S. Naval Base, Imías).

A. ainictum.—LAS TUNAS (Francisco).

A. dolichura.—CIUDAD DE LA HABANA (Atabey, Marianao, Bosque de la Habana, El Laguito)

A. taeniatum.—ISLA DE LA JUVENTUD (Isla de Pinos); CIUDAD DE LA HABANA (Cuatro Caminos, El Cotorro, Cojímar, Chávez); CIENFUEGOS (Cienfuegos, Guayanara); HOLGUÍN (Holguín); GRANMA (Jiguaní); SANTIAGO DE CUBA (Río Frío, Santiago de Cuba, Ciudamar, Guamá); GUANTÁNAMO (Guantánamo, San Carlos).

The provinces of all other localities cited are the same as those in current usage.

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MAMMALIAN FOSSILS OF SAMOS AND PIKERMI. PART 2. RESURRECTION OF A CLASSIC TUROLIAN FAUNA

Nikos Solounias[1]

Abstract

A brief history of the known Pikermi and Samos paleontological expeditions is presented. The quarries of Samos have been relocated. The interrelationship of local stratigraphy at Samos, radiometric samples, and quarries enabled the inference that all the bone horizons are essentially of one age (8.5–9 *Ma*). Bones accumulated primarily in overbank and paleosol deposits, they show little transport and are frequently concentrated in lenses. Bones probably accumulated either in local depressions and/or due to droughts. Although the Pikermi and Samos localities have been explored since the 1830s, this is the first modern revision and reevaluation of the entire fauna; many unreported taxa are added to the species lists. Pikermi and Samos sample species of one or two fairly similar faunas. The differences between Pikermi and Samos are at least due to sampling bias, time, and ecology. Samos represents the more diverse sample of the fauna and perhaps slightly more open country conditions.

Introduction and History of Excavations

The Late Miocene (Turolian) localities from Samos Island and Pikermi, Greece, are significant because of their key location between Europe, Asia, and Africa, the quantity of fossils, their quality of preservation, the brevity of space and geologic time represented, and especially the diversity of species. There is no other late Miocene locality in Eurasia or Africa that records, in such a narrow stratigraphic interval, as many mammalian species as Samos. A study of Samos and

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Submitted 9 May 1980.

Table 1.—*Museums housing Pikermi and Samos fossils.*

AMNH	—American Museum of Natural History, New York	(P), S
BM(NH)	—British Museum of Natural History, London	P, S
CM	—Carnegie Museum of Natural History, Pittsburgh	P, S
GPIT	—Geologisches und Paläontologisches Institute und Sammlungen, Tübingen	S
HLMD	—Hessischer Landesmuseum, Darmstadt	P, S
MGL	—Musée Géologique, Lausanne	S
MGPUP	—Musea Geologia-Paleontologia dell Università di Padova	P, S
MHNG	—Musée d'Histoire Naturelle Genève	(P), S
MHNL	—Musée d'Histoire Naturelle, Lyon	P
MHNP	—Musée National d'Histoire Naturelle, Paris	P, (S)
MNKF	—Freiburg (Brisgaw) Museum für Naturkunde	S
MPM	—Mytilinii Paleontological Museum, Samos	S
NHMBa	—Naturhistorisches Museum Basel	(P), S
NHMBe	—Naturhistorisches Museum, Bern	S
NHMW	—Naturhistorisches Staatsmuseum, Wien	P, S
NMB	—Naturhistorisches Museum, Berlin	P, (S)
NNLH	—Naturkundeabteilung des Niedersächischen Landesmuseum, Hannover	S
PIA	—Paleontological Institut, Athens	P, (S)
PIM	—Mineralogisches und Geologisches-Paläontologishes Institute, Münster	S
PIUW	—Paläontologishes Institute Universität, Wien	P, S
RMS	—Naturhistoriska Riksmuseum, Stockholm	P
RPMH	—Roemer-Pelizaeus Museum, Hildesheim	S
SMF	—Senckenbergische Naturforschende Gesellschaft, Naturhistorisches Museum, Frankfurt	S
SMNL	—Staatl Museum für Naturkunke, Ludwigsburg	S
SPGM	—Sammlung für Paläontologie und Historische Geologie, München	P, S
UCM	—University of Colorado Museum, Boulder	S
UGR	—Ungarn Geological Institute, Budapest	S
USNM	—National Museum of Natural History, Washington	(P), (S)
YPM	—Yale Peabody Museum, New Haven	(P)
ZMH	—Zoologisches Museum, Hamburg	S

P = Pikermi, S = Samos, ( ) means only few specimens.

Pikermi provides valuable evidence in solving biostratigraphic, biochronologic, and paleontological problems. Samos and the faunally similar but less species-rich Pikermi are two classic mammalian localities explored primarily during the nineteenth and early twentieth centuries. This brief study presents the first detailed stratigraphy and the first complete faunal reevaluation and revision since Forsyth Major's 1894 study.

Pikermi, 21 km northeast of Athens, was discovered by the English archeologist Georges Finlay, who excavated with Anton Lindermayer

Table 2.—*History of known paleontological excavations at Pikermi.*

Date	Collector	Exact region	Approximate number of specimens	Museum
1835	Finlay, Lindermayer	Unknown	Unknown	PIA, Athens
1838	Bavarian soldier rediscovers Pikermi			
1839–1850	Wagner	Unknown	300 500 traded to other museums or destroyed in World War II	SPGM, Munich
1853	Mitsopoulos	Unknown	Unknown	PIA, Athens
1853	Minister Baron, Fourth Rouen	Unknown	Unknown	MHNP, Paris
1854	Dr. Chaeretis	Unknown	30	MHNP, Paris
1855–1856, 1860	Gaudry	Unknown	1,000	MHNP, Paris
1860–1870	Unknown	Unknown	60	RMS, Stockholm
1882	Dames	Unknown	Unknown	NMB, E. Berlin
1885	Newmayr and Tausch	Unknown	300	PIUW, Vienna
1901	Woodward	Unknown	2,500	BM(NH), London
1910–1920*	Skoufos	Unknown	Unknown	PIA, Athens
1912–1922	Abel	Unknown	3,500	PIUW, NHMW, Vienna
1970–1974	Symeonidis, Zapfe, de Bruijn, and others	Chomateri locality	100	PIA, Athens

* Approximate.

Table 3.—*History of the known paleontological excavations at Samos.*

Date of collection	Collector	District	Approximate number of specimens	Museum
Before 1852	Italian travellers	Unknown	25	MGPUP, Padova
1887	C. I. F. Major	Andrianos, Stefana, Potamies	1,600 30 10	MGL, Lausanne MHNG, Geneva NHMBa, Basel
1889	C. I. F. Major	Stefana,* Vrysoula*	500	BM(NH), London
1893	G. Bukowski	Unknown	20	PIUW, Vienna
1889–1900	K. von dem Borne commissioned by Sturtz in Bonn	Andrianos, Potamies Vrysoula, probably others	2,100	SMNL, Ludwigsburg; SPGM, Munich; MHNP, Paris; NHMW, Vienna; BM(NH), London; probably HLMD, Darmstadt; NNLH, Hanover; MNKF, Freiburg; GPIT, Tübingen
1897	T. Stützel	4 unknown localities	100 (many destroyed in W.W. II)	SPGM, Munich**
1901–1902	A. Hentschel	Same 4 unknown localities as Stützel	100	SPGM, Munich**
1901	E. Fraas	Unknown	25	SPGM, Munich; SMNL, Ludwigsburg
1909–1920	K. Acker	All localities	2,500	NHMW, Vienna; SMF, Frankfurt, SMNL, Ludwigsburg; ZMH, Hamburg; RPMH, Hildesheim; NHMBe, Bern; NHMBa, Basel

Table 3.—*Continued.*

Date of collection	Collector	District	Approximate number of specimens	Museum
1909	T. Werner	Potamies and other localities	2,000	PIM, Münster
1911	T. Kormos	Unknown	Unknown	UGR, Budapest
1912	D. Psilovikos	Unknown	100	AMNH, New York***
1913	G. J. Weinberger	Unknown	20	NHMW, Vienna
1921–1924	B. Brown	Tholorema, Limitzis, Andrianos, Potamies, Megalos Vrahos, Vrysoula	3,000	AMNH, New York
1939*	Germans	Potamies	Unknown	Unknown
1963	J. Melentis	Andrianos	50	MPM, Mytilinii
1976	N. Solounias	Andrianos, Potamies	150	UCM, Boulder

* Uncertain.

** 51 specimens from Munich were sold to CM, Pittsburgh, by Schlosser.

*** Brown purchased these specimens for the AMNH.

in 1835. Three years later a Bavarian soldier of the Greek King Othon discovered a monkey skull filled with calcite crystals which he mistook for diamonds. It was his arrest in Munich for grave robbery that initiated the first extensive excavations by Andreas Wagner conducted from 1839 to 1850. Following Wagner, Albert Gaudry excavated in 1855–1856 and 1860, and studied the entire Pikermi fauna. In 1885, Melchor Neumayr and L. v. Tausch excavated for the PIUW, Vienna (see Table 1 for museum names). Arthur Smith Woodward collected for the BM(NH), London, in 1901; and finally, the last major excavation was made by Othenio Abel for the PIUW and NHMW, Vienna, between 1912 and 1922. At least six more minor excavations have been conducted at Pikermi by Swedes, Germans, Italians, Greeks, and others. In addition, museum trading has distributed the fossils of Pikermi throughout the world (Table 1). Table 2 briefly summarizes the traceable Pikermi excavations.

The Samos fossils, unlike those of Pikermi, were known to ancient Greeks. They were rediscovered by Italian travellers who took a small collection to the University of Padova between 1852 and 1866. The first excavations brought to scientific attention were conducted by Charles Immanual Forsyth Major in 1887 and 1889. He was also the only worker who studied the entire Samos fauna. Following Major's work, the beds (Table 3) were repeatedly excavated by several German parties and, later, by Barnum Brown (1921–1924) for the AMNH, New York (Table 4).

Primarily, most of the Samos and Pikermi collections were made to enrich museums rather than to collect the fossils for systematic research. In general, more paleontologists worked at Pikermi than at Samos which was excavated almost exclusively by museum personnel and businessmen (Solounias, 1979; 1981). The significance of the Samos fauna was not apparent, because the fossils were dispersed to so many museums. Samos may also have been overlooked because it was similar to Pikermi and because it could have been considered an isolated island fauna.

Because workers neglected to reveal the specific locations of their excavations, the exact position of the Pikermi bone beds is not accurately known. For example, despite Gaudry's 1862–1867 detailed Pikermi monograph, no locality map was included. A similar problem existed at Samos. Forsyth Major reported the general location of his 1887 quarries (Solounias, 1979; 1981). With the help of Dimetrios Psilovikos, who worked for the earlier German parties, Brown discovered all the sites excavated prior to 1921. The Samos bone beds were located by using old museum labels indicating geographic landmarks, old photographs, letters, notes, careful mapping of bone fragments in the field, and interviewing old farmers who worked for Barnum Brown.

Table 4.—*Information on the Samos bone beds.*

Bone bed	District	Land owner	Excavated by**	Date
Q6	Tholorema	Wasteland	Brown	1921–1924
L	Limitzis	Emmanuel Nikolaou Leondidis, 1915	Acker	1909–1920
Q5	Limitzis	Soumas, 1924–1978 (east of Papamoschatos' farm in 1978)	Brown	1921–1924
A	Andrianos	Aristarchos Sofoulis, 1924	Major Acker	1887 1909–1920
Q1	Andrianos	Aristarchos Sofoulis, 1924	Brown Melentis Solunias	1921–1924 1963 1976
Q2	Potamies	Efstathios Validakis, 1924; George Papaemmanuel, 1980	?Werner Brown	1909 1921–1924
Q4	Potamies	Trifon Validakis, 1924; Christos Validakis, 1980	Brown	1921–1924
S2	Potamies	Efstathios Validakis, 1924; George Papaemmanuel, 1980	Solounias	1976, 1979
S3	Potamies	George Papaemmanuel, 1980	Solounias	1976, 1979
S4	Potamies	Wasteland	Solounias	1976
Q3	Megalos Vrahos	Gliarmis, 1924; Lefteris Efthimiou, 1980	Brown	1921–1924
S	Stefana	Unknown	Major	1887, 1889*
G	Smakia	Kostas Konstantinidis, 1890; Stefanos Papaioannou, 1980; next to land of Kostas Fregadiotis, 1980	German collectors	
QX	Vrysoula in Mytilinii	Army base	?Major Brown	1889* 1921–1924
AG	Agiadhes	Unknown	No one	

* Date uncertain.

** These excavators are definitely known, but most sites were probably prospected and/or excavated by others. This is especially true for bone beds L, A, and Q2.

LOCAL STRATIGRAPHY AND AGE

The local stratigraphy of the Pikermi horizons has not been studied thoroughly. Previous work on the geology has been general (Gaudry 1862–1867; Lepsius, 1893; Abel, 1927) as has been the recent research (von Freyberg, 1951; Symeonidis et al., 1973; Symeonidis and Marcopoulou-Diacantoni, 1977). The sediments cannot be radiometrically dated.

The five to seven bone beds of Pikermi occur in a 0.5 by 3.0 km area along the Megalo Remma ravine. They are confined to no more than 50 m of section and thus are not greatly different in age from each other. Although no formation has been formally recognized (I propose the use of Pikermi Formation as in Abel, 1927:83) for the bone bearing deposits, and although there is no information as to the exact locality of each fossiliferous horizon, the following lithologies occur at Megalo Remma ravine: (a) massive reddish mudstones, 60 to 150 cm thick; (b) dark maroon, laterally discontinuous mudstones no more than 3 to 15 cm thick; (c) lenticular conglomerates, 20 cm to 6 m thick, of well rounded gravels. Some of these conglomerates are as much as 100 m broad and 6 meters deep in cross section; generally most are 3 to 15 m broad and 60–120 cm thick. The clasts are well sorted marbles and originated from the surrounding basement; (d) massive algal limestones.

Recent geologic research at Samos has revealed a tectonically complex basin with many lithologies (Van Couvering and Miller, 1971; Meissner, 1976*a*, 1976*b*; Angelier, 1976; Solounias, 1979).

The 15 bone beds of Samos are confined to the Mytilini Formation with the exception of three minor fossiliferous horizons, and span no more than 100 m of section and occur within only 5 km of each other[1] (Figs. 1, 2, and 3) (Solounias, 1979). These fossiliferous horizons contain abundant tuffs which allow K-Ar dating analyses. Recent research by Marc Weidmann and myself on the stratigraphy suggests that the Mytilini Formation may represent no more than 0.5 *Ma* of deposition (Fig. 2). According to the available K-Ar dates, the age of these bone beds is approximately 8.5 *Ma*. Thus their age is exclusively Turolian unlike other reports (Van Couvering and Miller, 1971; Berggren and Van Couvering, 1974; Mein, 1975). More detailed research on age determination and stratigraphy is in progress (Curtis, Drake, Solounias, and Weidmann).

Within the Mytilini Formation most of the bone occurs in the Main Bone Bed member except for two minor accumulations (Figs. 1, 2 and 3). The Main Bone Beds include the following lithologies: (a) poorly sorted volcanicalistic marls and mudstones, 50 to 150 cm thick; (b) marls and mudstones differing from (a) in being better sorted, unstratified and without major pebble and gravel horizons; (c) bedded clay nodule horizons which occur within (a) and (b). Most of the nodules are composed of the same material as the surrounding matrix; some encase pebbles or bone. These horizons are one nodule thick, approximately 3 to 10 cm, and are not laterally continuous for more than 6 to 8 m; (d) well defined lenticular gravel and pebble conglomerates, 40

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[1] L, Q5, Q1, Q2, Q3, S2, S3, S4 and Q4 only 1.2 km by .5 area (see Fig. 1).

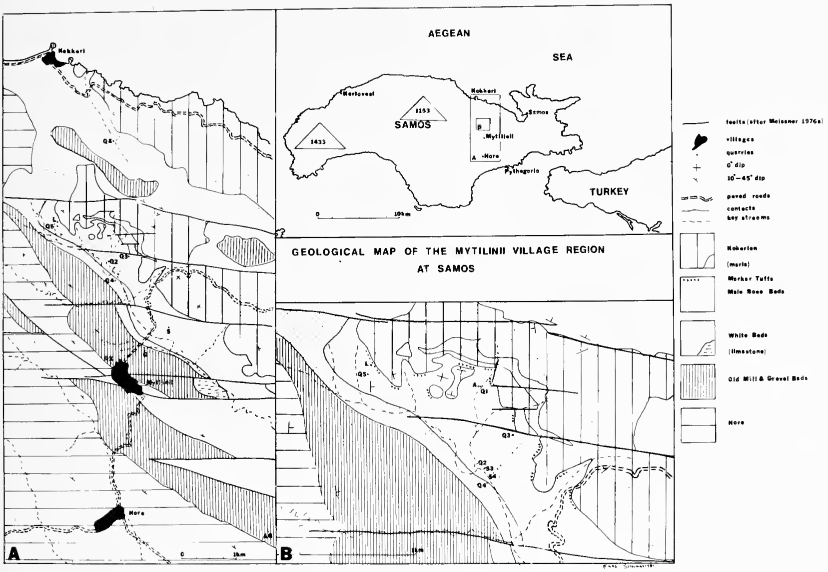

Fig. 1.—Geological map of the Mytilinii Village Region at Samos.

to 350 cm thick. They are often deep and narrow but can also be shallow and broad. The clasts are poorly sorted, angular limestone or marble, and originated from formations older than the Mytilini Formation; (e) water-lain pumice tuffs, 50 to 150 cm thick, which change laterally into other lithologies. Most of the tuffs fine upward. Their lower contact is often transitional but the upper is abrupt.

THE BONE BEDS

I define a bone bed as follows: a region where bones from various animals are densely concentrated and surrounded by regions where bones are absent or not concentrated.

The taphonomy of Samos and Pikermi has not been studied, and taphonomic information is limited because most of the fossils have already been excavated. However, a few observations can be made from unprepared museum blocks from Samos and Pikermi, from field study of old quarries on Samos only, from bone beds still containing fossils on Samos only, and from the tens of thousands of bones from Samos and Pikermi which are now in museums.

At both sites bone forms lenses. Only rarely can isolated fossils be found, but this might be due to the absence of flat exposures where more of the bedding planes can be observed. Some of the bone beds were 30 by 15 m in area and about 25 to 60 cm thick. Others were only 3 by 10 m in

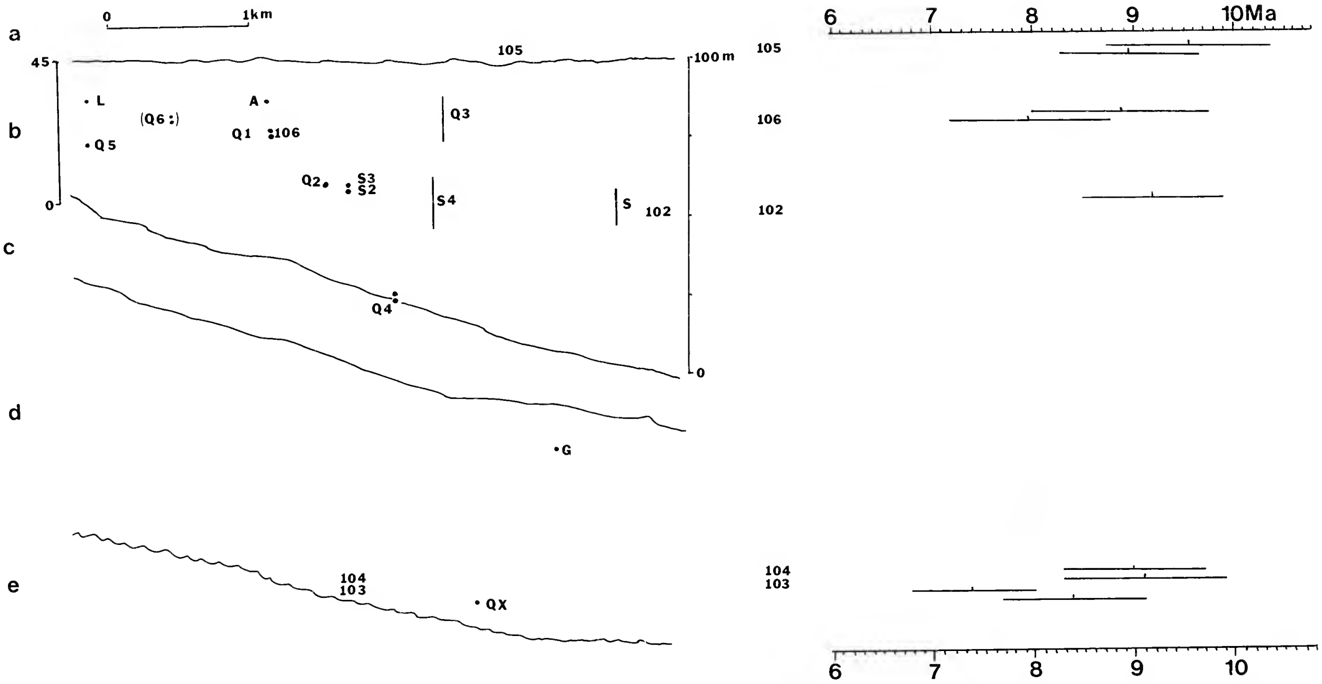

Fig. 2.—Stratigraphic distribution of the K-Ar samples and the bone beds. A dot indicates the exact position of a particular bone bed. Two dots indicate two-layered bone beds. A line indicates that the exact stratigraphic position is known only within the limits of the line. A good estimate for the Samos fauna is 8.5–9 *Ma*. Bone bed abbreviations as in Table 4. 102, 103, 104, 105 and 106 are radiometric sample numbers of Van Couvering and Miller, 1971. a, Marker Tuffs; b, Main Bone Beds; c, White Beds; d, Old Mill Beds and Gravel Beds; e, Hora Formation.

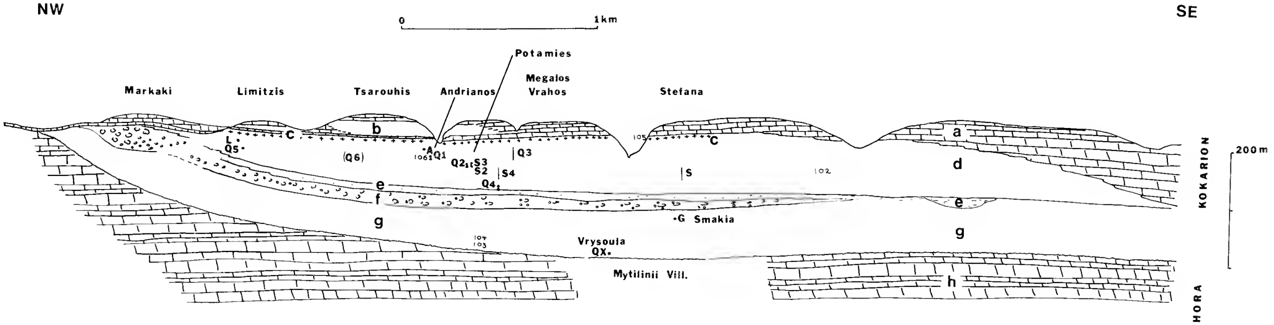

Fig. 3.—Schematic NW-SE cross section of the Mytilinii Valley showing the position of the bone beds. Abbreviations as in Fig. 2 and Table 4. Q6 is projected in the valley. 102, 103, 104, 105, 106 are radiometric sample numbers of Van Couvering and Miller, 1971. a, Kokarion (limestones); b, Kokarion (marls); c, Marker Tuffs; d, Main Bone Beds; e, White Beds; f, Gravel Beds; g, Old Mill Beds; h, Hora. In a different direction the extent of the lithologies is different.

area and 25 cm thick. In quarries, bone was often discontinuous in distribution. In most cases, bone was densely packed with no particular orientation; skulls, jaws, limbs, and horns of all sizes were mixed. Remains of proboscideans, small to large carnivores and antelopes, rodents and bats were found next to each other. At both there is a notable absence of aquatic elements, such as invertebrates, fish, water turtles, and crocodiles. At both, most of the taxa are ungulates. Rodents, small mammals, carnivores, and primates are not as represented as in other synchronous localities.

Few of the bones from Samos and Pikermi are weathered; they show little transport as the complex surfaces of skulls, teeth, and bones are often unbroken and unabraded. Isolated teeth and abraded bone are rare. Many broken surfaces are clearly due to poor excavation techniques while others are due to weathering before fossilization. In artiodactyls, skeletal parts not commonly preserved are premaxillae, anterior dentitions and symphyses, tips of horns, mandibular ascending rami and angles. Complete long bones and their distal and proximal ends are common. Hands and feet are often articulated. Juvenile epiphyses are not commonly preserved.

At Pikermi most of the bones and skulls are flattened and crushed. Many bones were found either as parts of articulated skeletons (especially the extremeties) or as isolated skulls, skull fragments, and limb fragments. Isolated bovid horn cores and frontlets were also common. Jaws are rarely associated with skulls.

In comparison, at Samos much less bone is flattened. There are fewer partially articulated skeletons and also unlike Pikermi, there is a more pronounced absence from Samos of ribs, scapulae, pelves, and axial vertebrae of larger mammals and the absence of axial bones and limbs of smaller mammals.[1] It is this absence of axial elements that makes the abundance of skulls, jaws, and limbs so noticeable. Bovid horn cores and frontlets are common, but again the jaws are usually not associated with the skulls. Unlike those of Pikermi, about one third of the bones of Samos are coated with a crust of marly limestone.

At Samos, bone is not associated with the channel deposits, but occurs mainly within the fine marls and the clay nodule horizons.

INTERPRETATION

The preliminary depositional interpretation for Pikermi is as follows: lithology (a) represents overbank flood plain deposits; (b) paleosols; (c) channel deposits of well developed, mature streams not particularly near the source; (d) freshwater lakes.

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[1] April 4, 1924, Brown's letter to Osborn: ". . . there are many perfect horse skulls and sufficient limb bones for a restoration, but I am still short of vertebrae and ribs . . . ."

The preliminary depositional interpretation for Samos is as follows: lithologies (a) and (b) represent overbank deposits; (c) paleosols or sheet flow deposits; (d) channel deposits of small streams near the source; (e) overbank deposits. The source of the ash is not known. The clastics come from the basement and from formations older than the Mytilini.

Presently Pikermi and Samos can be considered relatively instantaneous samples of late Miocene biotas when compared with longer time sequences such as Maragheh, the Chinji, or the Shan Si deposits (Van Couvering, Raza, and Tedford, personal communication).

Interpreting the origin of bone beds is not simple. There are no data on recent bone beds similar to those of Samos and Pikermi. The Samos bone beds are probably the result of a number of processes that have occurred between the living community and the final deposition of bones including an unknown accumulation time. As for the last step in this long chain of bone deposition events, I propose two plausible explanations knowing that they are merely speculative and certainly not sufficient. One is that some bone beds could be the result of sheet wash. Another is that they could be depression accumulations.

Behrensymeyer (personal communication) has observed that during floods, sheet wash may occur. Sheet wash is flood water flowing with such speed that it does not fill depressions and channels but flows over the higher areas. (1) This flow could accumulate bones from a floodplain surface. (2) While bones in depressions of a floodplain would be protected from such flow, bones at higher topographic regions would be carried away.

Bones are in general well preserved. A plausible explanation for this would be minimal transport, although cadavers can sometimes be transported with no apparent damage to the bones and teeth. Bones are also closely packed together in piles with no consistent orientation. Topographic depressions would favor this type of accumulation.

Additional evidence for a depression hypothesis comes from the bone beds and the local stratigraphy. At least three of the largest bone beds, Brown's Quarries 1, 2, and 4 were two superimposed layers of bone.[1] The same was true for S-3 and S-2 which were separated by 1

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[1] December 4, 1923. Letter to Matthew from Barnum Brown about his Q1. ". . . Specimens so far seen in this quarry are a wash accumulation. Only a few bones such as feet are associated, and many have been rotted or broken before fossilization. There are two bone strata over part of the quarry, separated by one and a half feet of earth, the lowermost carrying the best material was deposited in turgid water with thin fine grained clay seams overlying bones, while the upper strata has pebbles and large stones intermingled with the bones. It seems to be of common occurrence in the Mytilinos area to find two bone layers close together, one underlying the other . . ." American Museum of Natural History Archives. Also personal field observation of bone fragment distribution suggests that Quarries 2 and 4 were two layers.

m of tuffaceous marl. If bones were accumulating in depressions for some time, they would permit other layers of bone to form in superposition (Behrensmeyer, personal communication). At Quarries 1 and 2 and the S-3 and S-2 sites the lower layer of bone was less extensive than the upper. This observation also suggests the presence of depressions. Concave regions would tend to contain less bone in their lower part.

Preliminary work on the sediments suggests the existence of larger local depressions. Several lithologic members of the Mytilini thin out and do not occur except at the bone bed region. Laterally neither these members nor bones were ever found. These are the Gravel Beds, the White Beds, the Marker Tuffs, the unrounded conglomerates of the Main Bone Beds, and finally thick marl beds which occur within the Kokarion Formation only in the vicinity of the bone beds (Fig. 3). Depressed areas probably favored the formation of these local deposits and the better preservation of bone. It is important to note here that the depressions favoring the accumulation of bone would be between 8 to 30 square m. The depressions favoring the deposition of the previously mentioned lithologic members would be between 3 to 6 square km. Hence there may not be a close relationship between the two.

Criteria for distinguishing catastrophic from attritional mortality in fossil samples by means of age-frequency distributions have been proposed by Voorhies (1969: plate 13). Attritional mortality in fossil mammal samples results in the accumulation of primarily the young and old, because they have higher mortality rates than the adults. Catastrophic mortality results in a census of the living population; age distributions for medium-sized mammals tend to be dominated by adults. Hence catastrophic death samples, being relatively instantaneous events, resemble theoretical age distributions (for example Pianka, 1978; fig. 5-3; Ricklefs, 1973: fig. 34-1 through 4).

Although neither the fossil population from Samos nor Pikermi has yet been studied in detail, preliminary work indicates that most individuals are adults, suggesting that some of the bone beds could be caused by catastrophic deaths. Abel (1922) suggested a catastrophic death at Pikermi. He hypothesized that brush fires drove the herds over cliffs. Ungulate tibiae (unreported number) in his collections displayed spiral fractures similar to those that occur in skiers. The tibiae display the V-shaped fracture pointing downward on the longer fractured portion (Abel, 1922, 1927: fig. 138). In his reconstruction ungulates falling over the cliffs would break their legs, but primates and carnivores could climb down (Abel, 1927: fig. 139). Abel's samples were unavailable for study but many collections from Pikermi do not show such fractures.

Other reasons for bone accumulations have been suggested. For example Gaudry (1854; 1867), Lepsius (1893), and Schlosser (1904:115) have proposed that bone beds are the result of flood accumulations. Lepsius (1893) also suggested the possibility of carnivore den accumulations. Judith Van Couvering and I have noticed that the Turolian is characterized by rich bone beds throughout Eurasia while the Vallesian and other older stages have deposits where bone is frequently uniformly abundant (background bone) but not particularly concentrated into bone beds. The marked faunal change during the Turolian might be the result of more seasonal climates implying that during droughts more animals would die. Hence, Vallesian, and especially pre-Vallesian stages, record less seasonal environments, Turolian and post-Turolian stages more seasonal ones with periodic droughts resulting in rich bone beds.

The depression and drought hypotheses for Pikermi and Samos are not necessarily mutually exclusive. Our research team is presently investigating these possibilities (Badgley, Behrensmeyer and Solounias, work in progress).

How much time does a single bone horizon represent? Recent bone accumulations need to be studied in order to answer this question. Some of the Samos bone beds could be either a day or hundreds of years old. Future research with recent bone depositions and the development of a nomenclature for different types of bone beds is needed in order to understand better the Pikermi, Samos, Maragheh, and Shan Si localities.

The absence of aquatic elements is significant and needs to be investigated further. Two tentative speculations are that no permanent water systems were developed in the vicinity of the bone beds and that the bones accumulated primarily on hard surfaces This is contrary to the assumed interfingering of the Kokarion Formation (freshwater lakes) (Fig. 3). Perhaps the Kokarion is significantly younger throughout and filled low areas to the southwest (Fig. 3). The absence of aquatic elements is in agreement with a drought hypothesis and the brief time of deposition.

Carnivore action is a plausible explanation for the absence of vertebrae, ribs, and the smaller limbs at Samos. Hence the Pikermi bones could have been buried relatively faster.

Crusts around the bones from Samos suggest the presence of some organic material during deposition, or of algal growth on the bones, or of a precipitate on the bones because they were in supersaturated standing water (Behrensmeyer, personal communication).

RECONSTRUCTION OF SPECIES LISTS

Most of the vertebrate familes represented at Pikermi and Samos have been systematically studied. A literature review is presented in

Table 5.—*Literature review.*

Most significant publications on the fauna as a whole
Wagner, 1847
Roth and Wagner, 1854
Gaudry, 1862–1867
Weithofer, 1888
Abel, 1922, 1927
Major, 1891*a,* 1894

Molluscs
de Stefani et al., 1891

Turtles
Szalai, 1933

Birds
Gaudry, 1862–1867

Insectivores
Rumke, 1976
Black et al., 1980

Chiroptera
Revilliod, 1922

Primates
Wagner, 1847
Roth and Wagner, 1854
Gaudry, 1862–1867
Delson, 1973

Rodents
Dames, 1883*a*
Schaub, 1926
Abu, 1959
Freudenthal, 1970
de Bruijn, 1976
Black et al., 1980

Lagomorphs
Martinez, 1976

Carnivores
Gaudry, 1861*a*
Gaudry, 1862–1867
Hensel, 1862
Major, 1902*a*
Schwarz, 1912
Dietrich, 1927
Pilgrim, 1931
Helbing, 1932
Pilgrim, 1933
Kurtén, 1954
Abu, 1959
Ficarelli and Torre, 1970
de Beaumont, 1961, 1964, 1967, 1968, 1969

Tubulidentates
Major, 1893
Andrews, 1896
Colbert, 1941

Proboscideans
Schlesinger, 1922
Lehmann, 1950

Hyracoids
Major, 1899*a,* 1899*b*
Schlosser, 1899
Osborn, 1899

Hipparions
Hensel, 1860
Kormos, 1911
Studer, 1911
Abel, 1926
Wehrli, 1941
Forstén, 1968, 1980
Sondaar, 1971
Woodburne and Bernor, 1980

Rhinocerotids
Weber, 1904, 1905
Andree, 1921
Heissig, 1975

Chalicotheres
Dietrich, 1928
Schaub, 1943
Schaffer and Zapfe, 1971
Symeonidis, 1973

Suids
Pilgrim, 1926
Thenius, 1950

Giraffids
Wagner, 1861
Gaudry, 1861*b,* 1861*c*
Major, 1891*b,* 1894, 1901, 1902*b,* 1902*c*
Black, 1915
Schlosser, 1921
Bohlin, 1926, 1935*a*
Colbert, 1938
Churcher, 1970
Hamilton, 1978

Bovids
Gaudry, 1861*c,* 1862–1867
Dames, 1883*b*

Table 5.—*Continued.*

de Beaumont and Mein, 1972	Major, 1894
Hunt, 1974	Schlosser, 1904
Schmidt-Kittler, 1976	Andree, 1926
Galiano and Frailey, 1977	Pilgrim and Hopwood, 1928
Hendey, 1978	Sickenberg, 1929, 1932, 1933
Howell and Petter, 1980	Bohlin, 1935*b*, 1935*c*
Kurtén, 1981	Sickenberg, 1936
	Gentry, 1970, 1971, 1974

Table 5. They all deal with selected specimens, selected species, and/or "wastebasket" species. Selected specimens and assignments to "expected" species have given a simplified picture of the number of taxa represented. A few studies have considered biological variation. Until this study the only comprehensive faunal studies were the originals—Gaudry's 1862–1867 for Pikermi and Major's 1894 for Samos. Consequently, the fauna had never been revised using modern systematics and all available specimens.

More than 30 natural history museums house the specimens. The examination of most specimens from a given locality is of utmost importance in reconstructing species lists because this method provides the only reference for overlooked and unreported species. It is not unusual for new genera, families, and even orders to be added to the fauna. Table 6 lists the new species whose paleogeographic range has been extended now to Pikermi and Samos. It is interesting to note that all these new taxa are rare and are represented by no more than one to five specimens, indicating that all the collected specimens should be examined in order to obtain the most comprehensive species lists. Constructing comprehensive species lists should be brought to the attention of researchers (1) comparing localities of heterogeneous geographic and stratigraphic magnitudes and of varying collecting time; (2) scientists who are recently excavating localities and are reporting species lists after few seasons of collecting; (3) scientists using poorly known localities for biochronology and biostratigraphy. The recognition of unreported taxa is strengthened when specimens are not assigned to "expected species" without examination.

SYSTEMATIC REVISION

Systematic revisions are often elaborate because they involve the comparison of species from a number of localities. Since many of the Pikermi and Samos taxa were originally described from these localities, revisions have been possible. The present revision (Table 7) was

Table 6.—*New occurrences of fossil animals at Pikermi and Samos.*

Specimen	Number (where known)	Pikermi	Samos
Rumina decolata			x
Parmacella sp.			x
Hellicella sp.			x
?Hymenoptera gen. and sp. indet.			x
Testudo cf. *marmorum*			x
Testudo schafferi	1–5	x	
Testudo sp. (very large)	1		x
Varanus marathonensis	1		x
Struthio caratheodoris	1	x	
Grus pentelici	1–5		x
Galerix atticus	3		x
Spermophilinus cf. *bredai*	1		x
Occitanomys? provocator	2		x
Pliospalax cf. *sotirisi*	3		x
Pseudomeriones pythagorasi	7		x
Ursavus cf. *depereti*	2		x
Parataxidea maraghana	1		x
Ictitherium viverrinum	2–5		x
Hyaena sp.	1		x
Thalassictis hyaenoides	3	x	
Thalassictis (*Lycyaena*) sp. nov.	1		x
Hyaeninae gen. and sp. indet.	2		x
Felis sp.	1	x	
Metailurus parvulus	1		x
Metailurus major	1		x
Mammut borsoni	1		x
Hipparion sp. small		x	x
Hipparion sp. large			x
Hipparion matthewi	1	x	
Sus sp.	1	x	
Dorcatherium naui	1		x
Muntiacus sp.	3–5		x
Cervidae gen. and sp. indet. (large)	1	x	
Pliocervus pentelici	1		x
?*Helladotherium* sp.	1		x
Samotherium sp.			x
Palaeotragus sp.			x
Miotragocerus valenciennesi	1		x
Samokeros minotaurus	1–5		x
Prosinotragus sp. nov.	1		x
Selenoportax sp. nov. indet.	1	x	
Rupicaprini gen. and sp.	3		x

accomplished over a 6-year period with the kind help of several specialists although the degree to which I have allowed myself to be influenced by their advice is my responsibility. I have also used my own knowledge of the hyaenids, equids, rhinocerotids, giraffids, and bo-

Table 7.—*Taxonomical revision of traditional nomenclature for the Pikermi and Samos species.*

Original taxa	Revised taxa
Carnivora	
Melodon maraghanus	*Parataxidea maraghana*
Promephitis majori	*Promephitis lartetii*
Ictitherium robustum	*Ictitherium viverrinum*
Palhyaena hipparionum	*Thalassictis wongii*
Palhyaena hipparionum (in part)	*Thalassictis hyaenoides*
Hyaena sp.	*Hyaeninae* gen. and sp. indet.
Lycyaena chaeretis (in part)	*Thalassictis* (*Lycyaena*) *chaeretis*
Lycyaena chaeretis (in part)	*Thalassictis* (*Lycyaena*) sp. nov.
Proboscidea	
Tetralophodon longirostris	*Stegotetrabelodon grandincisivus*
Zygolophodon turicensis or (?*Mastodon*) *tapiroides*	*Mammut borsoni*
Perissodactyla	
Hipparion mediterraneum	*Hipparion* sp. large
Hipparion cf. *proboscideum*	*Hipparion* sp. large
Hipparion matthewi (in part)	*Hipparion* sp. small
Stephanorhinus pachygnathus	*Dicerorhinus schleiermacheri*
Diceros neumayeri	*Diceros pachygnathus*
Artiodactyla	
Microstonyx erymanthius	*Sus major*
Palaeotragus quadricornis	*Palaeotragus coelophrys*
Palaeotragus rouenii (in part)	*Palaeotragus* sp.
Samotherium boissieri (in part)	*Samotherium* sp.
Bohlinia or *Giraffa speciosa*	*Honanotherium speciosum*
Bohlinia or *Giraffa attica*	*Honanotherium atticum*
Miotragocerus amalthea (in part)	*Miotragocerus monacensis*
Miotragocerus amalthea (in part)	*Tragoportax amalthea*
Miotragocerus rugosifrons (in part)	*Tragoportax curvicornis*
Miotragocerus rugosifrons (in part)	*Tragoportax rugosifrons*
Gazella pilgrimi (in part)	*Gazella capricornis*
Gazella pilgrimi (in part)	*Gazella dorcadoides*
Gazella deperdita (in part)	Rupicaprini gen. and sp. indet.
Ovis kuhlmanni	*Prosinotragus kuhlmanni*
Pachytragus crassicornis	*Protoryx crassicornis*
Pachytragus laticeps	*Protoryx laticeps*
Antilope of unknown genus	*Selenoportax* sp.
Samotragus crassicornis	*Sinotragus crassicornis*

vids. The revised species lists from Pikermi, Samos, and Maragheh, Iran, are shown in Table 8. There are 80 species at Pikermi and 100 at Samos. Maragheh is less species rich. The number of mammals is 68 at Pikermi and 86 at Samos. Pikermi and Samos share 45 common mammalian taxa. The number of species present at Pikermi and absent

Table 8.—*A cumulative species list for the localities at Pikermi and Samos, Greece, and Maragheh, Iran.*

Taxa	Pikermi	Samos	Maragheh
Mollusca			
Gastropoda			
Prosobranchia or Archaeogastropoda			
Rissoacea			
Hydropodidae			
Hydrobia cf. *ventricosa*	x	–	
Pulmonata or Stylommatophora			
Vertiginacea			
Enidae			
Buliminus samius	–	x	
Achatinacea			
Subulinidae			
Rumina decollata	–	x	
Zonitacea			
Limacidae			
Parmacella sp.	–	x	
Helicacae			
Pleurodontidae			
Hellicella sp.	–	x	
Helicidae			
Otala vermiculata	x	–	
Helix barbeyana var. *nasseana*	–	x	
Helix sprattiana	–	x	
Helix palaeocastrensis	–	x	
Arthropoda			
Insecta			
?Hymenoptera			
Gen. and sp. indet.	x	x	
Chordata			
Reptilia			
Chelonia			
Testudinidae			
Testudo cf. *marmorum* (small)	x	x	
Testudo schafferi (medium)	x	x	
Testudo sp. (very large)	–	x	
Squamata			
Varanidae			
Varanus marathonensis	x	x	
Aves			
Struthioformes			
Struthionidae			
Struthio caratheodoris	x	x	x
Ciconiiformes			
Ciconidae			
Ciconia sp.	x	–	
Galliformes			
Phasianidae			
Gallus aesculapii	x	–	
?*Phasianus archaiaci*	x	–	

Table 8.—*Continued.*

Taxa	Pikermi	Samos	Maragheh
Ralliformes			
Gruidae			
Grus pentelici	x	x	
Ralliformes gen. and sp. indet.	x	–	
Urmiornis maraghanus	–	–	x
Eutheria			
Insectivora			
Talpidae			
Uropsilinae			
Desmanella dubia	x	–	
Erinaceidae			
Gymnurinae			
Galerix atticus	x	x	
Galerix moedlingensis	x	–	
Chiroptera			
Vespertilionidae			
Vespertilioninae			
Samonycteris majori	–	x	
Primates			
Cercopithecidae			
Colobinae			
Mesopithecus pentelici	x	–	x
Lagomorpha			
Ochotonidae			
Prolagus cf. *crusafonti*	x	–	
Leporidae			
Alilepus sp.	x	–	
Rodentia			
Sciuridae			
Spermophilinus cf. *bredai*	–	x	
Cricetidae			
Cricetinae			
Kowalskia cf. *lavocati*	x	–	
Cricetodontinae-Tribe Cricetodontini			
Byzantinia hellenicus	–	x	
Byzantinia pikermiensis	x	–	
Gerbillinae			
Pseudomeriones pythagorasi	–	x	
Muridae			
Murinae			
Parapodemus gaudryi	x	–	
Occitanomys ? *neutrum*	x	–	
Occitanomys ? *provocator*	x	x	
?*Gerboa* sp.	–	–	x
Spalacinae			
Pliospalax cf. *sotirisi*	–	x	
Gliridae			
Glirinae			
Muscardinus sp.	x	–	
Myomimus cf. *dehmi*	x	–	

Table 8.—*Continued.*

Taxa	Pikermi	Samos	Maragheh
Hystricidae			
Hystricinae			
Hystrix primigenia	x	x	–
Carnivora			
Family indet.			
Simocyon primigenius	x	–	–
Ursidae			
Ursavus cf. *depereti*	–	x	–
Indarctos atticus	x	x	x
Mustelidae			
Mustelinae			
Sinictis pentelici	x	–	–
Martes sp.	–	–	x
Martes woodwardi	x	–	–
?*Plesiogulo* sp.	x	–	–
Melinae			
Promeles palaeattica	x	x	x
Parataxidea maraghana	–	x	x
Parataxidea polaki	–	–	x
Mephitinae			
Promephitis lartetii	x	x	–
Lutrinae			
?*Enhydriodon laticeps*	x	–	–
Hyaenidae			
Subfamily A			
Plioviverrops orbignyi	x	x	–
Subfamily B			
Thalassictis wongii	–	x	x
Thalassictis hyaenoides	x	–	–
Thalassictis (*Lycyaena*) *chaeretis*	x	x	–
Thalassictis (*Lycyaena*) sp. nov.	–	x	–
Subfamily C			
Ictitherium viverrinum	x	x	–
Hyaeninae			
Hyaena sp.	–	x	–
Gen. and sp. indet.	–	x	–
Subfamily D			
Hyaenictis graeca	x	–	–
Percrocuta eximia	x	x	x
Felidae			
Felinae			
Felis sp.	x	–	–
Felis attica	x	x	x
Subfamily indet.			
Metailurus parvulus	x	x	x
Metailurus major	x	x	–
Machairodontinae			
Machairodus giganteus	x	x	x
Paramachairodus orientalis	x	–	x
Tubulidentata			

Table 8.—*Continued.*

Taxa	Pikermi	Samos	Maragheh
Orycteropodidae			
Orycteropus gaudryi	–	x	x
Proboscidea			
Palaeomastodontidae			
Mammut borsoni	x	x	–
Gomphotheriidae			
Gomphotheriinae			
Stegotetrabelodon grandincisivus	x	x	–
Choerolophodon pentelici	x	x	x
Dinotheriidae			
Deinotherium cf. *giganteum*	x	x	–
Hyracoidea			
Procaviidae			
Pliohyrax graecus	x	x	–
Pliohyrax kruppii	–	x	–
Perissodactyla			
Equidae			
Hipparion sp. (large, one preorbital fossa)	x	x	x
Hipparion sp. (small, one preorbital fossa)	?x	x	x
Hipparion proboscideum (large, two preorbital fossae)	–	x	–
Hipparion dietrichi (medium, no preorbital fossa)	–	x	x
Hipparion mattewi (small, no preorbital fossa)	x	x	–
Chalicotheriidae			
Chalicotherium goldfussi	x	–	–
Ancylotherium pentelicum	–	x	x
Rhinocerotidae			
Aceratheriinae-Tribe Aceratherini			
Aceratherium cf. *incisivum*	x	–	–
Chilotherium samium	–	x	–
Chilotherium schlosseri	–	x	–
Chilotherium kowalewski	–	x	–
Chilotherium persiae	–	–	x
Rhinocerotinae-Tribe Rhinocerotini			
Dicerorhinus schleiermacheri	x	x	–
Diceros pachygnathus	x	x	x
Rhinocerotinae-Tribe Elasmotherini			
Iranotherium morgani	–	–	x
Artiodactyla			
Suidae			
Sus sp.	x	–	–
Sus major	x	x	x
Potamochoerus hytheriordes	–	x	–
Tragulidae			
Dorcatherium naui	–	x	–
Cervidae			

Table 8.—*Continued.*

Taxa	Pikermi	Samos	Maragheh
Muntiacinae			
Muntiacus sp.	–	x	–
Cervinae			
Cervinae gen. and sp. indet. large	x	–	–
Pliocervus pentelici	x	x	x
Giraffidae			
Palaeotraginae			
Palaeotragus rouenii	x	x	–
Palaeotragus sp.	–	x	–
Palaeotragus coelophrys	–	x	x
Samotherium boissieri	–	x	x
Samotherium sp.	–	x	–
Sivatheriinae			
Helladotherium duvernoyi	x	x	x
?*Helladotherium* sp.	–	x	–
?Giraffinae			
Honanotherium speciosum	x	x	–
Honanotherium atticum	x	–	x
Bovidae			
Miotragocerus-Tragoportax Complex			
Miotragocerus monacensis var. A	x	x	–
Miotragocerus monacensis var. B	x	x	x
Miotragocerus valenciennesi	x	x	–
Tragoportax amalthea	x	x	–
Tragoportax curvicornis	–	x	–
Tragoportax rugosifrons	?x	x	–
**Samokeros minotaurus* var. A	–	x	x
**Samokeros minotaurus* var. B	–	x	–
Tribe Antilopini			
Prostrepsiceros rotundicornis var. A	x	–	–
Prostrepsiceros rotundicornis var. B	–	x	x
Prostrepsiceros houtumschindleri var. A	–	x	–
Prostrepsicerus houtumschindleri var. B	–	–	x
Protragelaphus skouzesi	x	x	x
Gazella capricornis	x	x	–
Gazella mytilinii	–	x	–
Gazella dorcadoides	–	x	–
Gazella deperdita	–	–	x
Oioceros rothi	x	–	x
Oioceros atropatenes	–	–	x
Oioceros wegneri	–	x	–
?*Oioceros rodleri*	–	–	x
Sinotragus crassicornis	–	x	–
Sinotragus sp. nov.	–	–	x
Prosinotragus kuhlmanni	–	x	–
Prosinotragus sp. nov.	–	x	–
Tribe Ovibovini			
Palaeoreas lindermayeri	x	x	–
Criotherium argalioides	–	x	–

Table 8.—*Continued.*

Taxa	Pikermi	Samos	Maragheh
Parurmiatherium rugosifrons	–	x	–
Urmiatherium polaki	–	–	x
Protoryx Complex			
Palaeoryx pallasi	x	x	–
Palaeoryx sp.	–	x	–
Tragoreas oryxoides	–	x	–
Sporadotragus parvidens	x	x	–
Protoryx carolinae	x	–	–
Protoryx crassicornis (short-brained)	–	x	x
Protoryx laticeps (long-brained)	–	x	x
Protoryx laticeps (short-brained)	–	x	?x
Pseudotragus capricornis	–	x	–
Tribe Tragelaphini			
Selenoportax sp. nov.	x	–	–
Tribe Rupicaprini			
Gen. and sp. indet.	–	x	–

x Present. – Not present. An empty space means unverified absence due to lack of excavating for small animals.

* This is a new genus and species officially described in Solounias, 1981; see also Solounias, 1979.

from Samos is 35. Similarly there are 45 species at Samos which are absent from Pikermi.

SAMOS: STRATIGRAPHIC AND BIOSTRATIGRAPHIC COMPARISONS

Comparisons within bone horizons.—Most species occur together within a bone bed (Table 9). Specifically, Major's Andriano, quarry A, and Brown's Q1–6 and X show similarities in contained elements, species, and relative abundance (unpublished data).

Comparisons between bone horizons.—The stratigraphic location of some species may never be known because most Samos collectors did not keep field data (Table 3). Table 9 lists localities for species where known. These localities can be subdivided into stratigraphic levels (Table 9; Figs. 2 and 3) but again the species differences are minor and could be attributed to sampling bias. The major bone horizons at Samos are relatively the same age, 8.9–9.0 *Ma* (Figs. 2 and 3).

Many European collections with no stratigraphic data were almost certainly collected in the same locations where Brown's quarries were located (Figs. 1, 2, and 3). Brown, in a letter to Matthew, says that he had the same guide who had reputedly worked for the German parties. Brown reports that he reopened most of the German quarries because these were the only locations with bone at Samos. I also found bone

Table 9.—*Individual locality species lists for Samos. Non-included taxa have no stratigraphic information.*

	Bone beds of known stratigraphic position											Bone beds of unknown stratigraphic position				
	L1	L2	Level 3									Schlosser, 1904				Munster
Taxa	Qx	Q4	S	Q2	S2	S3	S4	Q5	A	Q1	Q6	1	2	3	4	PIM
Buliminus samius									X							
Rumina decollata						X										
Parmacella sp.						X										
Hellicella sp.						X										
Helix barbeyana var. *nasseana*				X	X				X							
Helix palaeocastrensis					X											
?Hymenopera gen. and sp. indet.										X						
Testudo cf. *marmorum*									X							
Testudo schafferi						X										
Testudo sp. (very large)										X						
Varanus marathonensis						X				X						
Struthio caratheodoris									X							
Grus pentelici										X						
Galerix atticus						X										
Samonycteris majori									X							
Spermophilinus cf. *bredai*						X										
Pliospalax cf. *sotirisi*						X										
Byzantinia hellenicus						X			X							
Occitanomys? *provocator*						X										
Pseudomeriones pythagorasi						X			X							
Hystrix primigenia								X								X
Ursavus cf. *depereti*									X							
Promeles palaeattica									X	X						
Parataxidea maraghana									X	X						

Table 9.—*Continued.*

	Bone beds of known stratigraphic position											Bone beds of unknown stratigraphic position				
	L1	L2	Level 3									Schlosser, 1904				Mun-ster
Taxa	Qx	Q4	S	Q2	S2	S3	S4	Q5	A	Q1	Q6	1	2	3	4	PIM
Thalassictis wongii		x				x		x	x	x					x	x
Thalassictis sp. nov.									x							
Promephitis larteti				x					x	x	x					
Plioviverrops orbignyi									x	x						
Ictitherium viverrinum									x	x						
Percrocuta eximia		x				x		x	x	x			x		x	x
Felis attica									x							
Metailurus parvulus								x	x							
Machairodus giganteus									x							
Orycteropus gaudryi									x						x	
Choerolophodon pentelici									x	x		x	x			
Mammut borsoni										x						
Deinotherium cf. *giganteum*									x							
Pliohyrax graecus												x				
Hipparion sp. large		x														
Hipparion sp. small							x		x							x
Hipparion matthewi								x	x					x		x
Hipparion proboscideum	x		x			x	x		x	x						x
Hipparion dietrichi						x	x		x	x						x
Ancylotherium pentelicum			x						x	x		x				x
Chilotherium samium		x	x	x			x		x	x		x				x
Chilotherium schlosseri														x	x	x
Chilotherium kowalewski																x
Dicerorhinus schleiermacheri			x					x	x	x		x		x		
Diceros pachygnathus		x	x					x	x	x		x	x		x	x
Sus major									x	x		x				x

Table 9.—*Continued.*

	Bone beds of known stratigraphic position											Bone beds of unknown stratigraphic position				
	L1	L2	Level 3									Schlosser, 1904				Munster
Taxa	Qx	Q4	S	Q2	S2	S3	S4	Q5	A	Q1	Q6	1	2	3	4	PIM
Muntiacus sp.									X		X					X
Pliocervus pentelici									X							X
Palaeotragus rouenii			X						X	X			X			X
Palaeotragus sp.													X			
Palaeotragus coelophrys	X		X		X				X	X						X
Samotherium boissieri		X		X	X	X		X	X	X	X		X			X
Samotherium sp.										X						
Helladotherium duvernoyi									X	X						X
Honanotherium speciosum												X	X		X	
Miotragocerus monacensis				X						X						X
Miotragocerus valenciennesi								X								
Tragoportax amalthea			X	X					X	X	X			X		
Tragoportax curvicornis								X		X						X
Tragoportax rugosifrons		X						X	X	X				X		X
Samokeros minotaurus													X	X		X
Gazella capricornis	X					X		X	X	X	X		X		X	X
Gazella mytilinii								X	X						X	X
Gazella dorcadoides								X	X	X						X
Prostrepsiceros rotundicornis									X							
Prostrepsiceros houtumschindleri								X	X							
Protragelaphus skouzesi									X				X	X	X	
Oioceros wegneri									X							X
Prosinotragus kuhlmanni																X
Palaeoreas lindermayeri			X								X					
Criotherium argalioides				X					X	X	X		X			X

Table 9.—*Continued.*

	Bone beds of known stratigraphic position											Bone beds of unknown stratigraphic position				
	L1	L2	Level 3									Schlosser, 1904				Munster
Taxa	Qx	Q4	S	Q2	S2	S3	S4	Q5	A	Q1	Q6	1	2	3	4	PIM
Palaeoryx pallasi		X						X	X		X				X	X
Palaeoryx sp.									X							
Tragoreas oryxoides									X				X	X		X
Sporadotragus parvidens	X	X			X			X	X	X			X	X		X
Protoryx crassicornis					X			X						X		X
Protoryx laticeps		X	X		X		X		X	X				X		X
Pseudotragus capricornis					X				X		X	X				
Rupicaprini								X		X						

Within each level the bone beds are not listed in a stratigraphic order.

fragments only where quarries are reported to have been, confirming the existence of no more than 15 localities (Table 4).

Q1, A, Q2, S3, S2, S4, Q5, A6, S, and probably the PIM collection are stratigraphically close to one another; they could be as close as 30 m and no more than 60 m within the Main Bone Bed Member of the Mytilini Formation (Figs. 2 and 3) (Solounias, 1979; 1981). The degree of resolution is hindered by hundreds of small faults, plant cover, and absence of stratigraphic markers. The Marker Tuffs are above all bone beds and the White Beds below the Main Bone Bed Member (Figs. 2 and 3).

Mytilinii Village, Vrysoula district.—The oldest bone bed at Samos is QX. It is located 10 m above the Hora limestones and is within the Old Mill Beds Member of the Mytilini Formation (Figs. 2 and 3). The few specimens collected there by Brown show no differences from similar specimens of the Main Bone Bed Member. The BM(NH) 1889 Major collection could have come from QX. Again this collection shows no major faunal differences.

Smakia district.—At Smakia, G indicates the location of either all Munich collections or one of them. Schlosser (1904:112–115) reports fossils found in four distinct horizons. It is not certain whether they were all located together in superposition at Smakia or whether one of them was there and the others were perhaps at Potamies and/or Andrianos. The horizons at Smakia are presently covered with farms. The type of preservation of the Munich collection indicates that the fossils had been collected at Smakia only.

Stefana district.—Major's 1887 collection occurs at Stefana Hill and is at the same level as the Main Bone Beds.

Tholorema district.—Q6 is the most distant quarry. It contained two layers of bone like Q1, Q2, Q4, and S3–S2. The Q6 bones are few, they are fragmented and show indications of flood transport.

Andrianos district.—Major's quarry A is 9 m above Brown's Q1. There is a possibility that a fault may exist between the two that could make them the same level. Presently Brown's Q1 dump covers the area between Q1 and A. The Andrianos area is bound by faults.

Potamies district.—There is a syncline between Q1 and Andrianos and Q2 at Potamies which brings Q2 and Q1 stratigraphically close. The fault that separates Q1 from Q2 (Solounias, 1981: map 1) is in the middle of the syncline. The same fault disrupts the Kokarion limestones showing minor displacement. My micromammal locality S3 is horizontally 35 m from Q2. The type of preservation of Werner's 1909 collection at PIM is most similar to that of Q2 at the AMNH. It is possible that the PIM collection came from the Q2 or S3 region (Tables 3 and 4).

Limitzis district.—L is Acker's quarry and hence some of the Vienna, Ludwigsburg, and Frankfurt specimens could have come from there (Table 4). Q5 has been presented as a younger quarry (Sondaar, 1971; Gentry, 1971; Van Couvering and Miller, 1971; Mein, 1975). The reason was the presence of *Hipparion matthewi* and *Protoryx* (*Pachytragus*) *crassicornis* and the absence of *Hipparion proboscideum* and *Protoryx* (*Pachytragus*) *laticeps* at Q5. There are a few exposures between Q5 and Q1 but the Marker Tuffs are above Q5 and the White Beds below it as for all other quarries of the Main Bone Bed Member (Figs. 2 and 3). Thus Q5 is also part of the sequence. Q5 may even be slightly older than Q1, if actual sedimentary thicknesses are taken into consideration. *Protoryx* (*Pachytragus*) *crassicornis* is also found at S2 which is at the same level as Q2 and Q1. The type of *Protoryx* (*Pachytragus*) *crassicornis* comes from G which is older than Q1 (Figs. 2 and 3). In addition, specimens from A and PIM could be assigned to *Hipparion matthewi.*

PIKERMI VERSUS SAMOS: SPECIES COMPARISONS AND INTERPRETATION

In the future Pikermi and Samos will be compared to other fossil sites and with recent communities. The Aegean separates the two sites but is a relatively recent epicontinental sea and would not have been a barrier for late Miocene animals. The distance between Pikermi and Samos is 280 km. This distance is comparable with Siwalik localities (200 km), Shan Si localities (350 km) and no more than the Serengeti-Mara ecosystem (240 km).

There have been a number of attempts to compare Pikermi with Samos (Major, 1888, 1891*a,* 1891*c,* 1894; Abel, 1927; Pilgrim and Hopwood, 1928; Pilgrim 1931; Gentry, 1971; Van Couvering and Miller, 1971; Solounias, 1979, 1981, to name just a few). Most authors have correctly postulated that the differences are primarily the result of sampling, time, and ecology. The question, however, still remains unanswered: what is the relative importance of each? I treat each factor separately ignoring the others in order to simplify this discussion.

Differences attributable to sampling.—A similar number of specimens has been found at Pikermi and Samos.[1] Hence species comparisons ignoring relative numbers of specimens is possible.

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[1] Unpublished data; approximately 50,000 specimens in each. This number may seem low when compared to other localities (Pilbeam et al., 1977). Absolute number of specimens can be misleading. For example, the Siwalik material is more fragmented than the Pikermi and Samos material. Also the size of the area prospected and the stratigraphic thickness sampled should be taken into consideration.

Table 10.—*Abundant and rare species at Pikermi and Samos.*

Shared abundant species (more than 30 specimens)

Percrocuta eximia
Choerolophodon pentelici
Diceros pachygnathus
Palaeotragus rouenii
Gazella capricornis
Palaeoryx pallasi

Shared rare species (less than 30 specimens)

?*Hymenoptera* gen. and sp. indet.
Testudo cf. *marmorum* (small)
Testudo schafferi (medium)
Varanus marathonensis
Struthio caratheodoris
Grus pentelici
Galerix atticus
Occitanomys ?provocator
Hystrix primigenia
Indarctos atticus
Promeles palaeattica
Promephitis lartetii
Plioviverrops orbignyi
Thalassictis (*Lycyaena*) *chaeretis*
Ictitherium viverrinum
Felis attica
Metailurus parvulus
Metailurus major
Machairodus giganteus
Mammut borsoni
Stegotetrabelodon grandincisivus
Deinotherium cf. *giganteum*
Pliohyrax graecus
Hipparion sp. (small, one preorbital fossa)
Dicerorhinus schleiermacheri
Pliocervus pentelici
Honanotherium speciosum
Honanotherium atticum
Miotragocerus valenciennesi
Protragelaphus skouzesi

In theory, sampling bias can never be excluded as the cause of the absence of a particular species, although for some species it is more unlikely than others.

In theory, the differences between Tables 8 and 10 as well as the abundance differences shown in Table 11 could be attributed to sampling bias. In this case Pikermi would be less different from Samos than Table 8 shows.

Time differences.—The similarity between the faunas (Tables 8, 10, and 11) suggest that the time differences are small. Pikermi cannot be dated radiometrically.

If Pikermi is older than Samos, perhaps late Vallesian or early Turolian (10.5–9.0 *Ma*), then the less diverse ungulates sampled at Pikermi would predate the radiation recorded at Samos (8.5 *Ma*). If Pikermi is younger than Samos, perhaps late Turolian or early Ruscinian (7.0–5.5 *Ma*), the less diverse ungulates would postdate the radiation recorded at Samos and precede the more pronounced decrease in carnivores and ungulates that occurred during the Pliocene. The absence of certain cosmopolitan species from Pikermi that occur at Samos and several other Eurasian and African localities could suggest a time difference. Similarly, certain Pikermi taxa that occur in several Eurasian

Table 11.—*Significant faunal differences between Pikermi and Samos—species which are abundant at one site and rare at the other.*

Species	Pikermi	Samos
Hipparion proboscideum	R	A
Hipparion dietrichi	R	A
Hipparion sp. (large, one preorbital fossa)	A	R
Hipparion matthewi	R	A
Sus major	A	R
Pliocervus pentelici	A	R
Helladotherium duvernoyi	A	R
Miotragocerus monacensis	A	R
Tragoportax spp.	R	A
Palaeoreas lindermayeri	A	R
Sporadotragus parvidens	R	A

A = Abundant (more than 30 specimens).
R = Rare (less than 30 specimens).

and African localities but not at Samos, again could be attributed to time.

In general there are no ancestral species at Pikermi with descendents at Samos. For most subfamilies Pikermi has fewer species than Samos except for Murinae, Mustelinae, Lutrinae, Hyaenidae subfamily D, Machairodontinae, and ?Giraffinae (Table 8). In the cases where the

Table 12.—*Significant faunal differences between Pikermi and Samos—presence and absence only of the abundant species.*

	Pikermi	Samos
1.	More birds	Less birds
2.	*Mesopithecus pentelici*	—
3.	—	*Thalassictis wongii*
4.	—	*Orycteropus gaudryi*
5.	*Chalicotherium goldfussi*	—
6.	—	*Ancylotherium pentelicum*
7.	—	*Chilotherium* four species
8.	—	*Samotherium boissieri*
9.	—	*Tragoportax rugosifrons*
10.	—	*Prostrepsiceros houtumschindleri*
11.	*Oioceros rothi*	—
12.	—	*Criotherium argalioides*
13.	—	*Protoryx laticeps*
14.	—	*Protoryx crassicornis*

possibility of an ancestral species may exist, that species occurs at Samos also. Thus if time differences exist they probably are approximately plus or minus one million years.

Ecologic differences.—Table 11 shows species that are abundant at one locality but rare at the other. Table 12 shows the presence and absence of the abundant species. The differences indicated by these tables could be attributed to ecology. Presently, neither the general nor the degree of ecological differences between Pikermi and Samos are known. We have speculated elsewhere (Bernor et al., 1979) that the Mediterranean and northern China comprised a province characterized by the climaxing late Miocene sclerophyllous evergreen woodland. At the same time central Europe, the Siwaliks of India (Nagri and Dhok Pathan), and southern China were laurophyllous woodlands. In general there are more ungulates at Samos than at Pikermi. This may suggest minor ecological or seasonal differences. Presently it may be best to regard Pikermi and Samos as representing one or two relatively similar faunas (I am presently reconstructing the paleoecology).

SIGNIFICANCE

Pikermi and Samos are exceptional localities. They contain species-rich faunas, which are concentrated in space and time. They are presently the best single time species-rich accumulations known and can be used as reference localities for biostratigraphy. The species-richness, the numbers of individuals, and the concentration of bone in space and stratigraphic thickness is of utmost importance for exploring further the rising possibility that the Samos species may represent communities close in space or perhaps one community. The quality of preservation is also exceptional and useful for systematics and paleobiology.

SUMMARY AND CONCLUSIONS

1. The Pikermi and Samos localities have been excavated for over 100 years. The brief history of the known expeditions is presented. The Samos quarries have been relocated.

2. Preliminary stratigraphic research indicates that most specimens were recovered in bone beds within overbank and paleosol sediments. At both Pikermi and Samos the bone beds are concentrated in space and time. At Samos all bone beds occur within the Mytilini Formation which could be considered to represent no more than 0.5 *Ma* of deposition. The age of the Samos fauna is 8.5–9 *Ma* only.

3. As a general rule, bone is well preserved indicating relatively minimal transport and relatively rapid burial. In addition, both localities represent species-rich faunas with many specimens. The origin of bone beds is not presently well understood. A tentative hypothesis proposes differential deposition of bones resulting in bone bed for-

mation; preferred accumulation and preservation in local depressions with bone destruction and removal from adjacent non depressed areas of the flood plains. Although other causes, such as droughts, are plausible causes for bone bed formation, it may not be necessary to hypothesize such catastrophies.

4. Reconstruction of species lists was accomplished with the help of many scientists and by identifying most specimens. Despite the number of previous studies, many unreported taxa almost doubled previous species lists. Revision of taxa shows the presence of many interesting species. Their systematic and paleobiologic study has just begun.

5. There are no major differences in stratigraphic level and in faunal content between the Samos bone beds. In general the faunal differences between Pikermi and Samos are small and attributable in part to sampling bias, time and ecology. The relative weight of each factor is not yet known. Presently, Pikermi and Samos are believed to represent one fauna or two relatively similar faunas. Samos has more ungulates and perhaps represents slightly more open habitat conditions than Pikermi or seasonal differences.

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SYSTEMATIC STATUS OF DORMICE (RODENTIA: GLIRIDAE) FROM SOUTHERN CAMEROON, AFRICA

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Abstract

The systematic status of dormice, genus *Graphiurus*, in southern Cameroon, Africa, is reviewed. From an analysis of measurements, morphological differences and geographic distributional data, five species are recognized in southern Cameroon—*Graphiurus crassicaudatus, G. hueti, G. christyi, G. lorraineus,* and *G. surdus.*

Introduction

The genus *Graphiurus* is widely distributed in sub-Saharan Africa. Because there are usually insufficient numbers of specimens from any one locality to adequately assess individual variation or the variability among populations, many names have been proposed within this genus. At present, many of these taxa are considered synonyms of *G. murinus* (Ellerman et al., 1953 and Genest-Villard, 1979). Recently, Genest-Villard (1979) published a systematic revision of *Graphiurus*. She recognized six species in the genus, with *G. murinus, G. crassi-*

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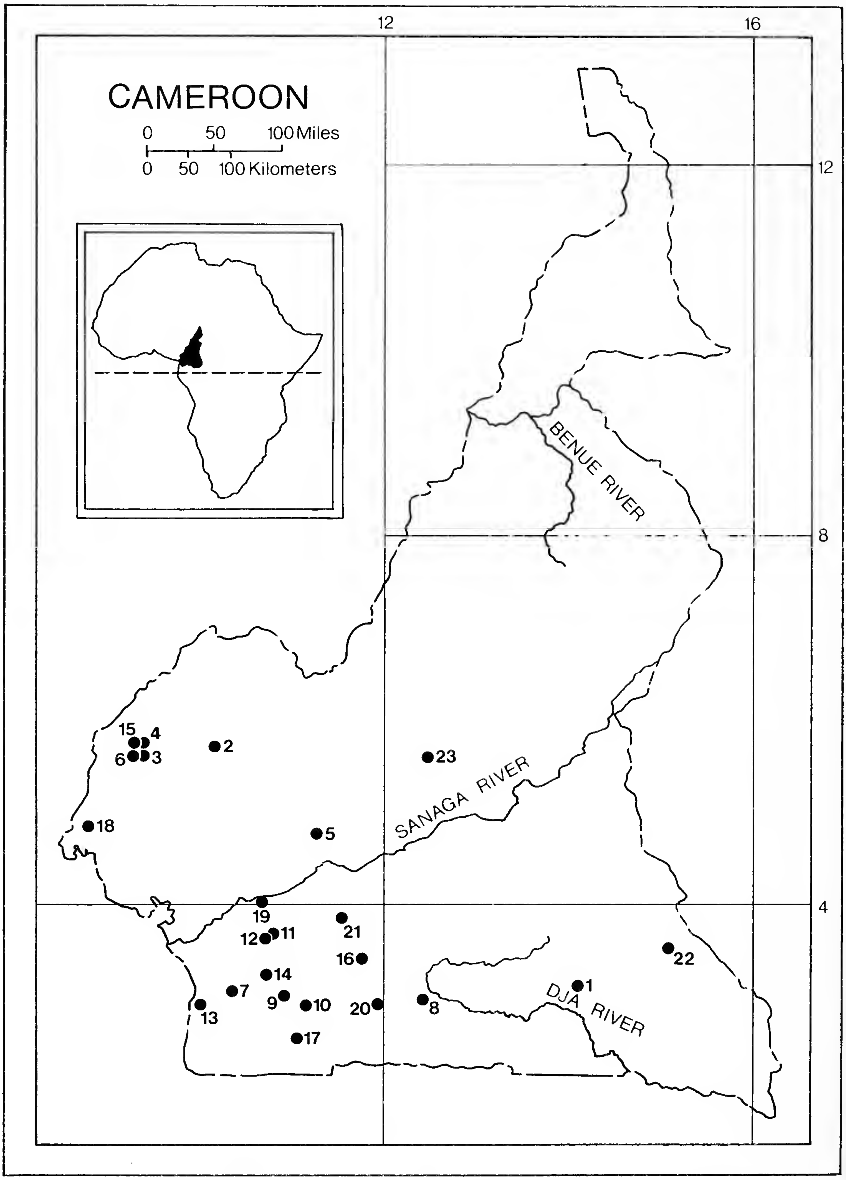


Fig. 1.—Map showing Cameroon localities from which specimens have been examined, arranged in alphabetical order as follows: 1) Assobam, 2) Babadjou, 3) Bachuntai, 4) Bashauo, 5) Bafia, 6) Besongabang, 7) Bipindi, 8) Bitye, 9) Efulen, 10) Ebolowa, 11) Eseka, 12) 8 km SW Eseka, 13) Kribi, 14) Lolodorf, 15) Mamfe, 16) Metet, 17) Meyo, 18) Ndian Estate, 19) Sakbayeme, 20) Sangmelima, 21) Yaounde, 22) Yokadouma, and 23) Yoko.

caudatus and *G. hueti* from the area represented by our study. Our objective is to evaluate the taxonomic status of the *Graphiurus* from the tropical forests of southern Cameroon.

We have examined a large number of specimens from a small geographic area in southern Cameroon (Fig. 1) and conclude five species are represented: *G. crassicaudatus* and *G. hueti,* currently recognized by most mammalogists as distinct species, and *G. christyi, G. lorraineus,* and *G. surdus.* The latter three taxa were formerly synonymized with *G. murinus,* but our studies indicate the presence of morphological differences warranting specific recognition.

METHODS AND MATERIALS

This study was based primarily on the examination of specimens in two collections from Cameroon, one made by A. I. Good between 1913 and 1948 and the other by L. W. Robbins in 1973 and 1974.

The specimens we examined are housed in the mammal collections of the American Museum of Natural History, New York (AMNH); British Museum (Natural History), London (BMNH); Carnegie Museum of Natural History, Pittsburgh (CM); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); and the National Museum of Natural History, Washington, DC (USNM).

Cranial measurements were taken to the nearest 0.1 mm with dial calipers. The 18 mensural characters used are listed in Table 1. Length of hind foot includes claws; height of rostrum was taken behind incisors. Univariate analysis of variance was computed by the UNIVAR program (Power, 1970).

All specimens used in the statistical comparisons are from areas in or near Cameroon. All examples of *Graphiurus lorraineus* are from southern Cameroon. Specimens of *G. christyi* from Zaire were included with the small sample from Cameroon after analysis indicated that they were not significantly different in most measurements. Most specimens of *G. surdus* are from southern Cameroon; however, two, including the holotype, are from Rio Muni. Specimens of *G. crassicaudatus* are from Cameroon except for the holotype of *G. c. dorotheae,* which is from Nigeria. The *G. hueti* are from Cameroon and include the holotype of *G. h. argenteus.* For comparative purposes, some additional samples were examined from other African countries. With the exception of a specimen of *G. murinus* from the Republic of South Africa (19 km S Aliwal North, USNM), these are listed under specimens examined in appropriate accounts.

Localities in Cameroon from which specimens were examined are shown in Fig. 1. Exact coordinates for these localities are listed, where known, in a gazetteer.

RESULTS

Graphiurus hueti, a West African species, is significantly larger in all characters examined than the other species studied. Crown breadth of molars was not measured in this species. *Graphiurus lorraineus* is separable from the other four species on the following cranial measurements: greatest length of skull; condylobasal length; greatest zygomatic breadth; interorbital breadth; breadth of braincase; length of palate. *Graphiurus surdus* is separable from all other species by condylobasal length. *Graphiurus crassicaudatus* is distinguishable on the basis of greatest zygomatic breadth and length of maxillary toothrow. *Graphiurus christyi* does not differ significantly in any one character

Table 1.—*Variation in external and cranial measurements in five species of Cameroon* Graphiurus.

Species	N	Mean ± 2 SE	Range	CV	SS-STP
Total length					
Graphiurus hueti	15	261.0 ± 11.90	(205.0–287.0)	8.8	I
Graphiurus christyi	10	172.6 ± 6.85	(150.0–185.0)	6.3	I
Graphiurus surdus	4	172.3 ± 9.46	(160.0–183.0)	5.5	II
Graphiurus crassicaudatus	10	148.8 ± 4.22	(136.0–156.0)	4.5	II
Graphiurus lorraineus	33	146.2 ± 2.50	(129.0–158.0)	4.9	I
Tail length					
Graphiurus hueti	15	118.1 ± 9.49	(84.0–142.0)	15.6	I
Graphiurus christyi	10	77.8 ± 8.19	(45.0–90.0)	16.6	I
Graphiurus surdus	5	70.0 ± 9.00	(56.0–82.0)	14.3	II
Graphiurus lorraineus	33	67.3 ± 2.23	(50.0–77.0)	9.5	II
Graphiurus crassicaudatus	10	56.5 ± 4.10	(45.0–70.0)	11.5	I
Length of hind foot					
Graphiurus hueti	15	31.8 ± 0.31	(28.0–33.0)	3.7	I
Graphiurus surdus	7	20.9 ± 1.10	(18.0–22.0)	7.0	I
Graphiurus christyi	10	17.9 ± 0.63	(16.0–19.0)	5.6	I
Graphiurus lorraineus	27	17.6 ± 0.25	(16.0–19.0)	3.6	I
Graphiurus crassicaudatus	10	17.3 ± 0.95	(15.0–19.0)	8.6	I
Length of ear					
Graphiurus hueti	7	21.4 ± 0.86	(20.0–23.0)	5.3	I
Graphiurus surdus	7	14.0 ± 1.07	(13.0–17.0)	10.1	I
Graphiurus christyi	7	13.9 ± 1.02	(12.0–15.0)	9.7	II
Graphiurus crassicaudatus	9	13.0 ± 0.67	(11.0–14.0)	7.7	II
Graphiurus lorraineus	12	12.3 ± 0.56	(11.0–14.0)	7.9	I
Greatest length of skull					
Graphiurus hueti	14	38.2 ± 0.58	(36.5–39.7)	2.8	I
Graphiurus surdus	7	28.0 ± 0.86	(26.5–29.7)	4.1	I
Graphiurus christyi	12	27.4 ± 0.36	(26.8–28.9)	2.3	II
Graphiurus crassicaudatus	8	26.3 ± 0.59	(25.3–27.9)	3.1	I
Graphiurus lorraineus	30	24.3 ± 0.29	(22.4–25.6)	3.2	I
Condylobasal length					
Graphiurus hueti	13	35.4 ± 0.49	(33.6–36.7)	2.5	I
Graphiurus surdus	7	25.8 ± 0.83	(24.1–27.2)	4.3	I
Graphiurus christyi	12	24.2 ± 0.61	(22.8–25.7)	3.1	I
Graphiurus crassicaudatus	8	24.1 ± 0.25	(19.5–22.9)	3.4	I
Graphiurus lorraineus	36	21.6 ± 0.25	(19.5–22.9)	3.4	I
Zygomatic breadth					
Graphiurus hueti	15	21.8 ± 0.37	(20.6–22.8)	3.2	I
Graphiurus crassicaudatus	5	15.9 ± 0.43	(15.4–16.4)	3.0	I
Graphiurus surdus	8	14.7 ± 0.36	(14.1–15.7)	3.5	I
Graphiurus christyi	8	14.6 ± 0.39	(14.0–15.6)	3.8	I
Graphiurus lorraineus	19	13.7 ± 0.30	(12.7–14.9)	4.7	I

Table 1.—*Continued.*

Species	N	Mean ± 2 SE	Range	CV	SS-STP
Interorbital breadth					
Graphiurus hueti	17	6.1 ± 0.13	(5.7–6.6)	4.5	I
Graphiurus crassicaudatus	10	5.0 ± 0.13	(4.7–5.3)	4.2	I
Graphiurus christyi	13	4.8 ± 0.09	(4.5–5.1)	3.5	II
Graphiurus surdus	10	4.7 ± 0.12	(4.3–5.0)	4.1	I
Graphiurus lorraineus	49	4.3 ± 0.04	(4.0–4.7)	3.3	I
Breadth of braincase					
Graphiurus hueti	16	16.1 ± 0.20	(15.6–16.8)	2.5	I
Graphiurus crassicaudatus	7	12.9 ± 0.21	(12.4–13.3)	2.1	I
Graphiurus surdus	7	12.4 ± 0.27	(11.9–12.8)	2.9	II
Graphiurus christyi	12	12.2 ± 0.09	(12.0–12.5)	1.3	I
Graphiurus lorraineus	34	11.5 ± 0.10	(10.8–12.1)	2.6	I
Greatest length of nasals					
Graphiurus hueti	17	14.6 ± 0.26	(13.6–15.3)	3.7	I
Graphiurus surdus	9	10.7 ± 0.30	(9.9–11.3)	4.1	I
Graphiurus christyi	13	10.3 ± 0.22	(9.8–11.2)	3.8	I
Graphiurus lorraineus	44	9.1 ± 0.10	(8.3–9.9)	3.7	I
Graphiurus crassicaudatus	10	8.7 ± 0.34	(8.2–9.8)	6.1	I
Length of anterior palatine foramen					
Graphiurus hueti	17	3.0 ± 0.14	(2.5–3.4)	9.6	I
Graphiurus crassicaudatus	8	2.5 ± 0.18	(2.3–3.0)	9.9	I
Graphiurus surdus	8	2.5 ± 0.11	(2.3–2.8)	6.5	I
Graphiurus christyi	13	2.5 ± 0.14	(2.0–2.9)	10.2	I
Graphiurus lorraineus	48	2.4 ± 0.07	(2.5–3.4)	9.7	I
Length of maxillary toothrow					
Graphiurus hueti	17	5.1 ± 0.05	(4.9–5.3)	2.2	I
Graphiurus crassicaudatus	9	3.7 ± 0.07	(3.6–3.9)	2.9	I
Graphiurus surdus	8	3.1 ± 0.19	(2.8–3.9)	9.8	I
Graphiurus christyi	9	3.1 ± 0.07	(3.0–3.3)	3.7	II
Graphiurus lorraineus	40	3.0 ± 0.04	(2.7–3.4)	4.3	I
Crown breadth of molars (M^2-M^2)					
Graphiurus crassicaudatus	9	5.8 ± 0.12	(5.6–6.1)	3.2	I
Graphiurus christyi	9	5.6 ± 0.08	(5.4–5.8)	2.1	II
Graphiurus surdus	8	5.4 ± 0.10	(5.4–5.7)	2.6	II
Graphiurus lorraineus	40	5.2 ± 0.05	(4.9–5.5)	3.3	I
Length of bulla					
Graphiurus hueti	17	8.1 ± 0.17	(7.6–8.9)	4.4	I
Graphiurus surdus	7	7.4 ± 0.16	(7.1–7.7)	2.9	I
Graphiurus christyi	13	7.0 ± 0.31	(5.9–7.9)	7.9	II
Graphiurus lorraineus	41	6.7 ± 0.07	(6.2–7.3)	3.3	II
Graphiurus crassicaudatus	8	6.4 ± 0.15	(6.2–6.8)	3.4	I

Table 1.—*Continued.*

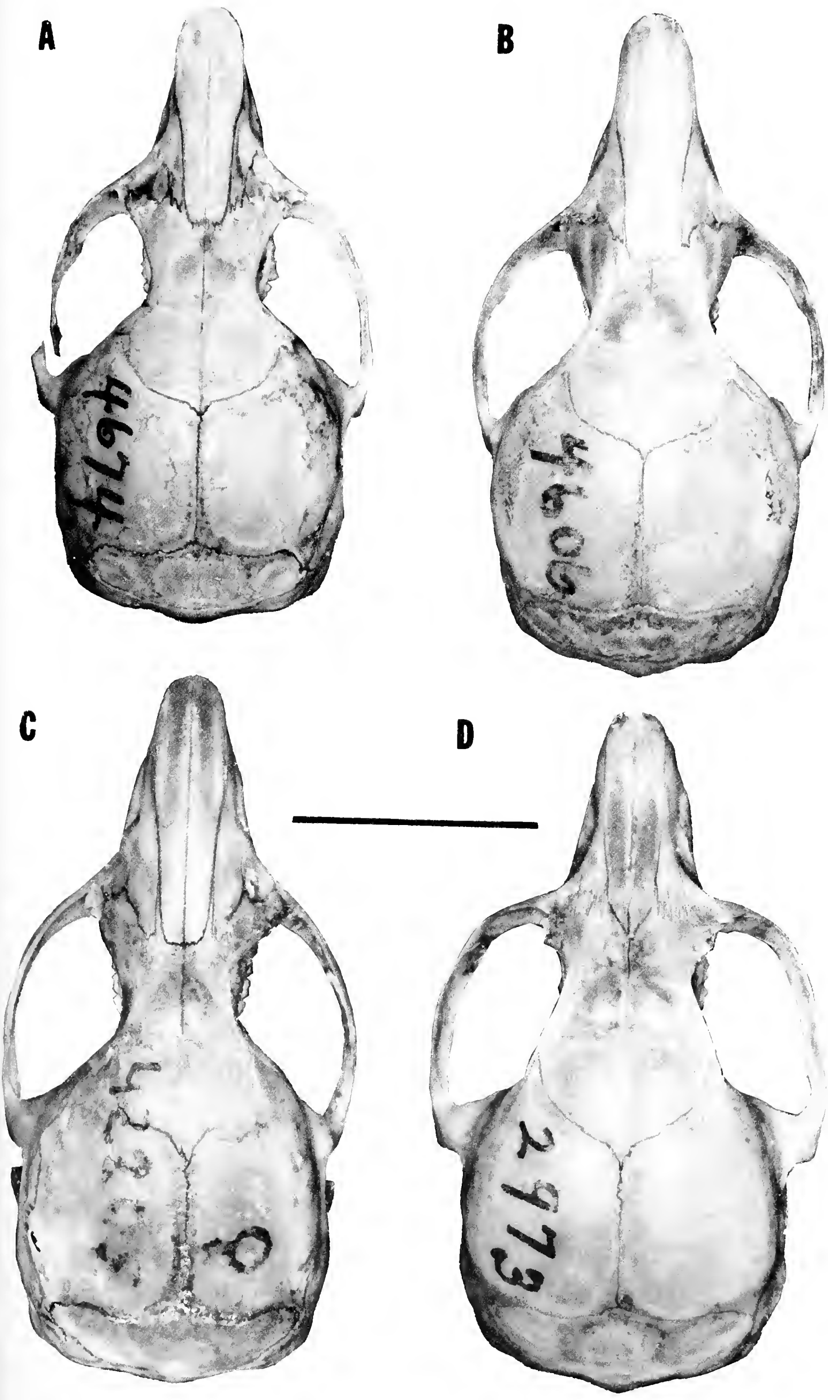
Species	N	Mean ± 2 SE	Range	CV	SS-STP
		Breadth of bulla			
Graphiurus hueti	17	7.0 ± 0.15	(6.6–7.5)	4.3	I
Graphiurus crassicaudatus	8	5.7 ± 0.15	(5.6–6.0)	3.6	I
Graphiurus surdus	7	5.6 ± 0.10	(5.4–5.8)	2.4	II
Graphiurus christyi	13	5.4 ± 0.18	(5.0–6.1)	6.1	II
Graphiurus lorraineus	42	5.2 ± 0.06	(4.8–5.6)	3.4	I
		Length of palate			
Graphiurus hueti	13	16.1 ± 0.32	(14.9–17.0)	3.6	I
Graphiurus surdus	7	11.4 ± 0.35	(10.5–11.9)	4.1	I
Graphiurus crassicaudatus	6	10.9 ± 0.21	(10.5–11.2)	2.4	II
Graphiurus christyi	11	10.3 ± 0.39	(8.9–11.3)	6.2	I
Graphiurus lorraineus	37	9.6 ± 0.17	(8.7–11.0)	5.3	I
		Height of skull			
Graphiurus hueti	16	14.5 ± 0.35	(13.5–15.3)	4.8	I
Graphiurus surdus	7	10.8 ± 0.24	(10.3–11.3)	3.0	I
Graphiurus christyi	12	10.7 ± 0.20	(10.0–11.2)	3.2	I
Graphiurus crassicaudatus	8	10.4 ± 0.20	(10.2–11.0)	2.7	II
Graphiurus lorraineus	34	10.0 ± 0.09	(9.2–10.6)	2.6	I
		Height of rostrum			
Graphiurus hueti	17	7.1 ± 0.17	(6.5–7.6)	5.0	I
Graphiurus christyi	13	5.4 ± 0.16	(5.0–6.0)	5.5	I
Graphiurus crassicaudatus	10	5.3 ± 0.27	(4.8–6.0)	8.0	I
Graphiurus surdus	9	4.8 ± 0.12	(4.3–5.1)	5.6	I
Graphiurus lorraineus	44	4.5 ± 0.06	(4.1–5.0)	4.8	I

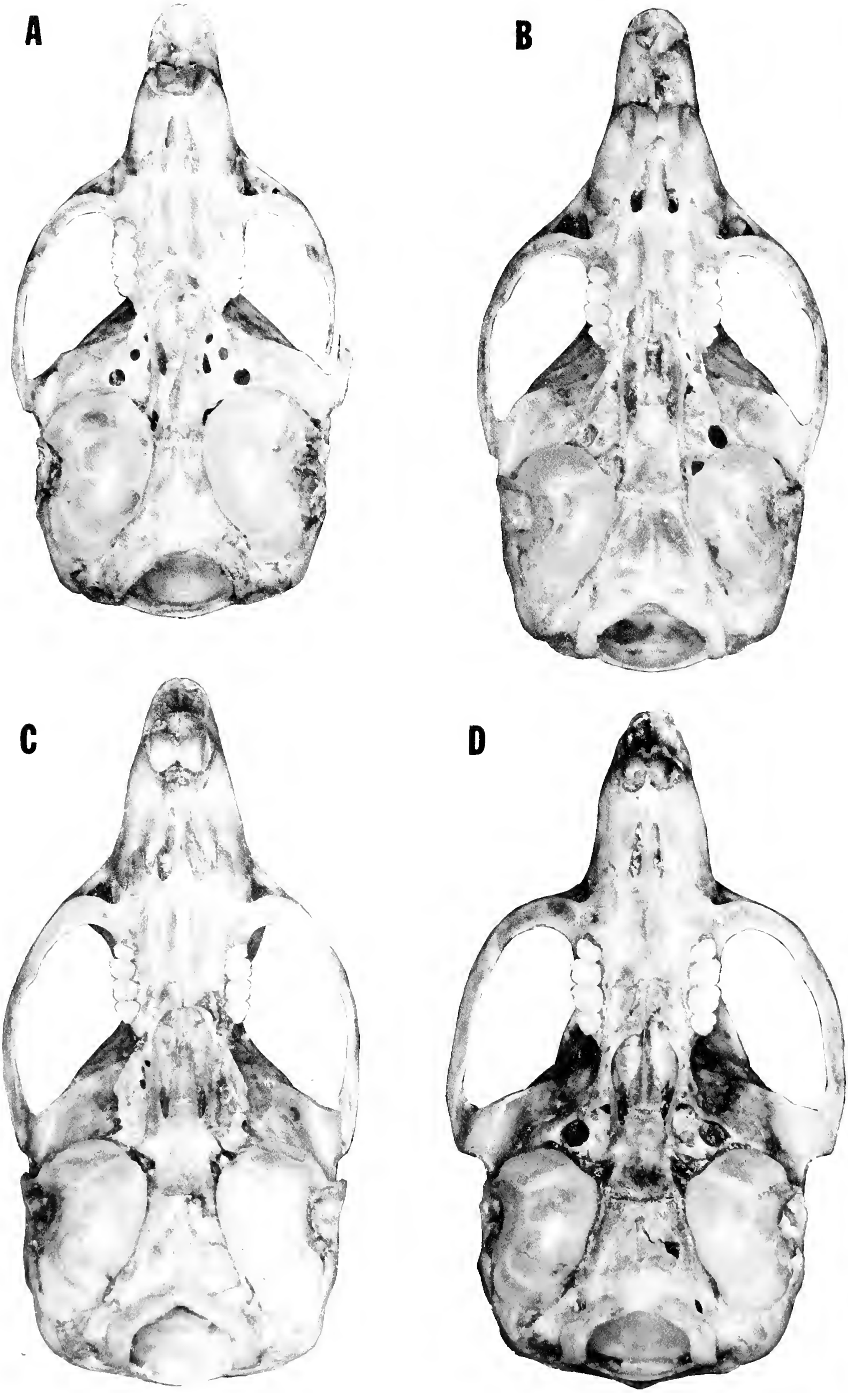
from the other species; specimens of it, however, can be separated from those of *G. surdus* by condylobasal length, length of palate, and height of rostrum; from *G. crassicaudatus* by greatest zygomatic breadth, breadth of braincase, length of nasals, length of maxillary toothrow, length of auditory bulla, and breadth of auditory bulla; and from examples of *G. lorraineus* by greatest length of skull, condylobasal length, breadth of braincase, greatest length of nasals, crown breadth of molars, and height of skull.

External measurements were not used in these comparisons because of inconsistencies among preparators. However, they are included in Table 1 to indicate relative external dimensions of each species.

→

Fig. 2.—Dorsal view of skulls of four species of *Graphiurus* from Cameroon. A. *G. lorraineus*, CM 4674; B. *G. christyi*, CM 4606; C. *G. surdus*, CM 42205; D. *G. crassicaudatus*, CM 2973. Scale: black line equals 10 mm.


A
4674
B
4606
C
4213
♀
D
2973


A
B
C
D

Non-mensural differences can be seen by comparing the cranial photographs (Figs. 2–4). *Graphiurus christyi* is characterized by the anterior development and projection of the premaxillaries and nasals beyond the anterior surface of the incisors (Figs. 3B and 4B). *Graphiurus crassicaudatus* can be distinguished cranially from other similar-sized *Graphiurus* by the increased development of the supraorbital ridges and the straight, rather than rounded, edge of the posterior portion of the interorbital region, the straight ventral edge of the distal portion of the nasals (Fig. 4D), and by the position of the P^4 near the anterior root of the zygomatic arch (Fig. 3D). The skull of *G. lorraineus* is short, with a relatively shortened rostrum and small cheekteeth (Figs. 2A, 3A and 4A). The skull of *G. surdus* is long and narrow, with an elongated rostrum and lengthened braincase (Figs. 2C, 3C, and 4C).

The following key to the forest dwelling species of *Graphiurus* found in Cameroon incorporates characters that were found to be helpful in separating these taxa. It should be used cautiously when identifying specimens from other parts of Africa.

KEY TO THE CAMEROON FOREST SPECIES OF *GRAPHIURUS*

External

1.	Head and body length:	120 mm or greater	*G. hueti*
		less than 120 mm	2
2.	Distinct and complete eye ring		3
	Not as above		4
3.	Hair on belly with pale gray or white tips		*G. lorraineus*
	Not as above		*G. christyi*
4.	Hind foot (with claws) 21–22, tail hairs white tipped		*G. surdus*
	Hind foot (with claws) 17–19 or under, tail not as above and usually shorter (under 65) and broader		*G. crassicaudatus*

Cranial

1.	Greatest skull length:	more than 35.0 mm	*G. hueti*
		less than 35 mm	2

←
Fig. 3.—Ventral view of skulls of four species of *Graphiurus* from Cameroon. A. *G. lorraineus*, CM 4674; B. *G. christyi*, CM 4606; C. *G. surdus*, CM 42205; D. *G. crassicaudatus*, CM 2973. Scale is same as in Fig. 2.

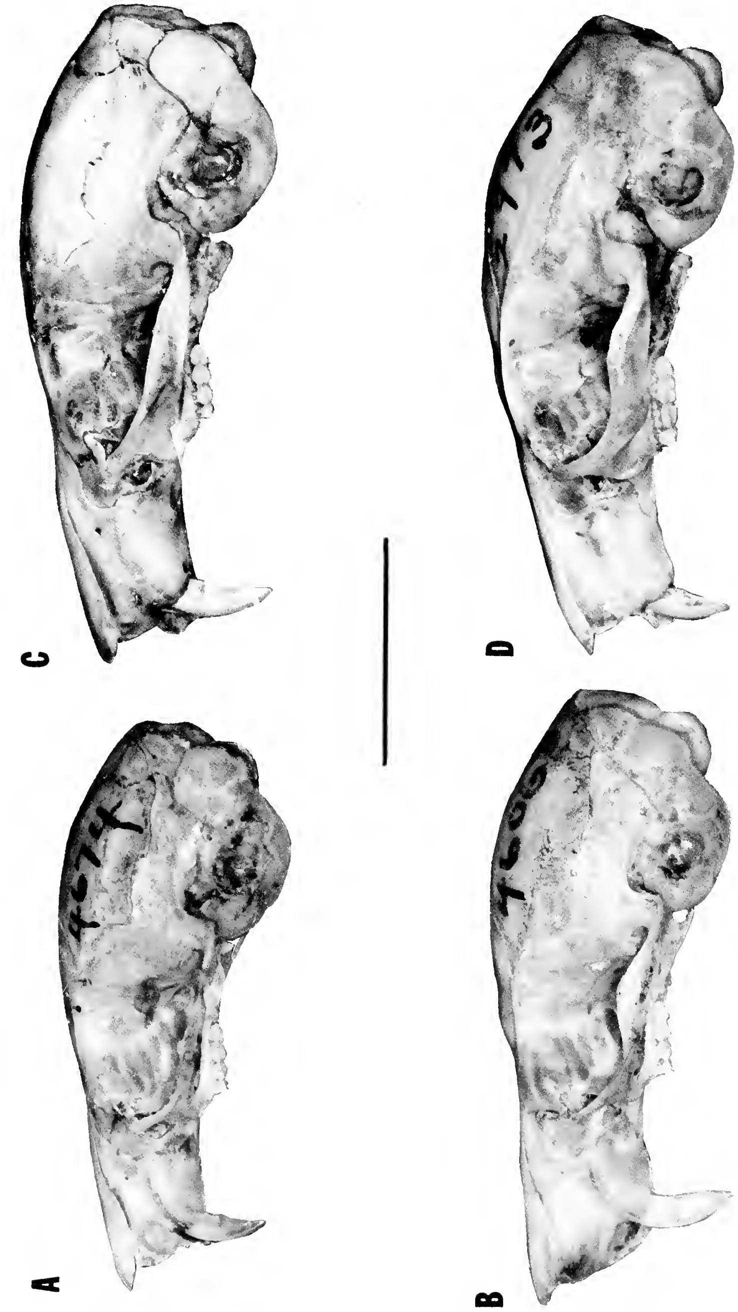


Fig. 4.—Lateral view of skulls of four species of *Graphiurus* from Cameroon. A. *G. lorraineus*, CM 4674; B. *G. christyi*, CM 4606; C. *G. surdus*, CM 42205; D. *G. crassicaudatus*, CM 2973. Scale: black line equals 10 mm.

2. Maxillary toothrow: 3.7–3.9 *G. crassicaudatus*
2.8–3.2 3

3. Height of rostrum: 5.7–6.0 *G. christyi*
4.1–5.1 4

4. Condylobasal length: 24.7–25.5 *G. surdus*
20.0–23.0
(Some individuals from northern savanna may measure up to 25.0, but qualitative characters are distinctive). *G. lorraineus*

DISCUSSION

Our interpretation of the systematic relationships of western African *Graphiurus* differs appreciably from the revision of *Graphiurus* by Genest-Villard (1979). *Graphiurus crassicaudatus* is clearly a distinct species and, although widespread in the forest block of West Africa, seems to be locally uncommon. The largest species, *Graphiurus hueti,* is restricted to the forest block, and is common, especially in hollow trees within the forest block.

In the course of this study, we have examined numerous specimens from throughout the range of *Graphiurus*. Our examination of *G. hueti* revealed little variation in the species throughout West Africa. From this we doubt that *Graphiurus monardi* (St. Leger, 1936) from Angola and Zambia is a subspecies of *G. hueti,* as suggested by Genest-Villard (1979), when morphological and ecological differences between the two taxa are considered. Ansell (1978) considered *G. monardi* as a distinct species in Zambia.

Within the widespread *Graphiurus murinus* species complex, Genest-Villard (1979) recognized two species—*G. parvus* (True, 1893) and *G. murinus* (Desmarest, 1822). She listed the former with two subspecies; the nominate one ranges from Ethiopia southward in East Africa to Zimbabwe and Malawi. A second, *G. p. brockmani* (Dollman 1910), occurs in Somalia and then in a zone from Niger, Nigeria, Mali, Ghana, Ivory Coast to Sierra Leone. We concur that there seems to be a small-sized taxon in the savanna zones of West Africa that is closely related to the forest inhabiting small dormice. The name *G. parvus* is one of the oldest names available for the dormice of the savanna zone. However, the taxonomic relationships of *G. foxi,* described from Kabwir, Nigeria, and *G. olga,* described from Asben, Niger, to the other small dormice in West Africa is still unclear.

Genest-Villard (1979) further distinguished *G. murinus* as a polytypic species including as synonyms all of the taxa described from the West African forest block. We are able to distinguish three species within this group in southern Cameroon. Genest-Villard (1979:409) listed *G. christyi* Dollman, 1914, and *G. surdus* Dollman, 1912, as synonyms of *G. m. lorraineus* (Dollman, 1910). Our results show these two taxa to be distinct species. *Graphiurus spurrelli* (Dollman, 1912) considered by Genest-Villard (1979) to be a distinct subspecies of *G. murinus,* is indistinguishable from *G. lorraineus* and does not warrent subspecific status.

Few karyotypic data are available for any *Graphiurus.* For West Africa, Tranier and Dosso (1979) list a diploid number of 40 for a female *G. hueti* from a non-specified locality in Ivory Coast. This specimen had 14 acrocentrics and 26 metacentrics and submetacentrics. A diploid number of 70 was given by these same authors for *G. murinus* but no other information or a locality was listed.

CONCLUSIONS

We recognize five species of dormice from Cameroon. Two, *G. hueti* and *G. crassicaudatus,* are generally confined to western Equatorial Africa. Three species, previously considered synonyms of *G. murinus,* are distinguished: *G. surdus,* a large species originally reported from Rio Muni; *G. christyi,* originally described from Zaire; *G. lorraineus,* the Cameroon representative of a geographically widespread species that ranges from West Africa as far south as Zambia. This latter species may be a commensal in villages in Cameroon.

Although the distinctness of the five species in southern Cameroon is apparent, a revision of the entire genus may show that one or more of the names we have used for these species are synonyms of earlier described taxa from other parts of Africa.

ACCOUNTS OF SPECIES

Graphiurus christyi Dollman, 1914

Graphiurus christyi Dollman, Revue Zool. Africain, 4:80; 25 July 1914.

Type locality.—Mambaka and Mambo (see Moreau et al., 1946), Belgian Congo (now Zaire).

Distribution.—Previously known only from eastern Zaire; now also from southern Cameroon.

Specimens examined (34).—CAMEROON; Lolodorf (4 CM). ZAIRE; Avakubi (1 AMNH); Mambaka and Mambo (2 BMNH, the holotype and one paratype); Medje (1 USNM, 23 AMNH, 1 BMNH); Gambi, SE of Angu, Mobatti (1 BMNH); Niangara (1 AMNH).

Remarks.—We have referred our specimens from Cameroon to *G. christyi* on the basis of external and cranial measurements, shape of skull, and color of pelage. However, they differ from *G. christyi* from Zaire in the shape of the premaxilla, condylobasal length (those from Zaire being larger), and the height of the rostrum (those from Cameroon being larger). The specimens from Cameroon also have longer and denser fur than do any of the small *Graphiurus* examined. The distance (1,900 km) between known localities of this species probably reflects the lack of collecting. If not, the specimens from Cameroon should be re-examined.

Descriptive, distributional, and ecological information for *G. christyi* from Zaire were summarized by Hatt (1940).

Graphiurus crassicaudatus (Jentink, 1888)

Claviglis crassicaudatus Jentink, Notes Leyden Mus., 10:41; April 1888.
Type locality.—Du Queah River, Liberia.
Graphiurus crassicaudatus dorotheae Dollman, Ann. Mag. Nat. Hist., ser. 8, 9:312; March 1912.
Type locality.—Oban District, Southern Nigeria (actually southeastern Nigeria).

Distribution.—Liberia, Ivory Coast, Ghana, Nigeria, Cameroon, and possibly Fernando Poo.

Specimens examined (24).—CAMEROON: Bashauo (1 BMNH); Bipindi (2 AMNH); Bitye (1 BMNH); Ebolowa (1 CM); Eseka (4 CM, 1 AMNH); 8 km SW Eseka (1 CM); Lolodorf (1 CM); Ndian Estate (3 BMNH). NIGERIA: Oban District (2 BMNH, including holotype of *G. c. dorotheae*); Ekuri Beach (1 BMNH); Umuahia, 400 ft (2 BMNH); Owerri (1 BMNH); Ilobi (2 BMNH). FERNANDO POO: no specific locality (1 BMNH).

Additional records.—Rumfi Hills (Eisentraut, 1973:80). Two specimens in the British Museum reported by Sanderson (1940) from Cameroon as *G. haedulus* from Bashauo (=Bachuo) and one as *G. spurrelli* (from Ekuri Beach) were reidentified by Rosevear (1969) as *G. crassicaudatus*. We concur with Rosevear; however, examination of the map of the Percy Sladen expedition (Sanderson, 1940) reveals that Ekuri Beach is now in Nigeria rather than in Cameroon. One specimen from Fernando Poo in the British Museum might have been collected on Cameroon Mountain according to Rosevear, 1969. Cabrera (1929) stated that *G. crassicaudatus* did not exist on the island of Fernando Poo.

Remarks.—This appears to be the only small dormouse from western and central Africa that has been recognized as a distinct species by all who have examined it. Jentink (1888) described the genus *Claviglis* (type species, *G. crassicaudatus*) based on the shape of the tail (club-shaped and not distichous). Dollman (1912), however, stated that Jentink's type had a regenerated club-shaped tail. This club-shaped or fanned-tip-of-tail condition is common in dormice that appear to have injured tails. Dollman's (1912) description of *G. crassicaudatus* is good, but his color and size criteria for distinguishing *G. c. dorotheae* from the nominate subspecies are unsatisfactory when additional specimens are compared. Dollman (1912) and Rosevear (1969) stated that comparison of cranial and external characters of *G. crassicaudatus* support a closer relationship to *G. hueti* than to the *G. murinus* group.

One specimen trapped in Eseka on 24 October 1973 (mammae: 0 pectoral, 2 pairs inguinal—4) contained two embryos. Other information on *G. crassicaudatus* was summarized by Rosevear (1969). Specimens from the vicinity of Eseka were trapped in Sherman nonfolding aluminum live-traps set on vines and horizontal branches in secondary high forest. No hollow trees were seen in the immediate area. All traps were baited with the nut of the oil palm (*Elaeis*). Traps were in position for two or more weeks before dormice entered.

Graphiurus hueti (Rochebrune, 1883)

Aethoglis hueti Rochebrune, Actes Soc. Linn. de Bordeaux (4) 7:110; 1883.
Type locality.—Environs of St. Louis, Sorres, Senegal.
Aethoglis hueti argenteus G. M. Allen, J. Mamm., 17:293; 1936.
Type locality.—Lolodorf, Cameroon.

Distribution.—Senegal, Sierra Leone, Liberia, Ivory Coast, Ghana, Nigeria, Cameroon, Central African Republic, and Gabon.

Specimens examined (35).—CAMEROON: Bachuntai (1 BMNH); Bashauo (4 BMNH); Besongabang (3 BMNH); Bipindi (2 BMNH); Efulen (2 BMNH); 8 km SW Eseka (5 CM); Lolodorf (7 CM, 1 MCZ, the holotype of *G. h. argenteus*); Mamfe (1 BMNH); Metet (1 MCZ); Sangmelima (8 CM).

Additional records.—Malende (Eisentraut, 1963); Eshobi (Sanderson, 1940); Ngam (Perret and Aellen, 1956).

Remarks.—There are questions regarding the validity of the subspecies. *Graphiurus hueti argenteus* is the subspecies of Cameroon and the Central Africa Republic; Allen (1936) described this subspecies as being drabber in color of pelage than the nominate taxon and as having whitish-tipped rather than gray hairs on the venter. We agree with Rosevear (1969) that color varies too much within populations to be used as the sole criterion for taxonomic separation. There is, however, a consistent size difference; specimens from Cameroon are larger in most measurements than those from western portions of the range.

One specimen obtained 8 km SW Eseka on 21 February 1974 contained two embryos and another obtained at the same locality on 7 April 1974 was lactating. Other information on the natural history of this species was summarized by Rosevear (1969). The specimens from 8 km SW Eseka were trapped in Sherman non-folding aluminum live-traps set on vines in secondary high forest, and were taken near hollow trees. Traps were baited with the nut of the oil palm (*Elaeis*) and were in place for more than one week before any dormice entered.

Graphiurus lorraineus Dollman, 1910

Graphiurus lorraineus Dollman, Ann. Mag. Nat. Hist., ser. 8, 5:284; March 1910.
Type locality.—Molegbe, south of Setema Rapids, Welle River, Belgian Congo (now Zaire).
Graphiurus spurrelli Dollman, Ann. Mag. Nat. Hist., ser. 8, 8:315; March 1912.
Type locality.—Bibianaha, 60 mi W Kumasi, Gold Coast (now Ghana).

Graphiurus haedulus Dollman, Ann. Mag. Nat. Hist., ser. 8, 9:316; March 1912.
Type locality.—Assobam, Bumba River, Cameroon.
Graphiurus schwabi G. M. Allen, Bull. Mus. Comp. Zool., 54:441; April 1912.
Type locality.—Kribi, Cameroon.

Distribution.—Sierra Leone, Liberia, Ivory Coast, Ghana, Nigeria, Cameroon, Rio Muni, Gabon, and Zaire; probably also southern Central African Republic, Republic of the Congo, northern Angola, and northern Zambia. Distribution may be limited to tropical forests.

Specimens examined (120).—CAMEROON: Assobam, Bumba River, 200 ft (1 BMNH, the holotype of *G. haedulus*); Babadjou (5 CM); Bafia (2 CM); Bitye (3 BMNH) Ebolowa (2 CM); Kribi (1 AMNH, 5 MCZ, including the holotype of *G. schwabi*); Lolodorf (31 CM, 4 MCZ); Metet (4 CM, 3 MCZ); Osundan (1 MCZ); Sakbayeme (1 MCZ); Sangmelima (5 CM); Yaounde (1 CM); Yokadouma (1 CM); Yoko (2 CM). GABON: Mityic (1 BMNH). GHANA: Bibianaha, 60 mi Kumasi (1 BMNH, the holotype of *G. spurrelli*); Kade (1 USNM); Bulima (1 USNM). IVORY COAST: Kahin (3 USNM). NIGERIA: Jos Plateau, Panyam Fish Farm (9 USNM). ZAIRE: Bafwabaka (2 AMNH); Faradji (2 AMNH); Lukolela (4 AMNH); Luluabourg (13 AMNH); Medje (2 AMNH); Molegbwe, Welle River (1 BMNH, the holotype of *G. lorraineus*); Niangara (4 AMNH); Vankerckhovenville (1 AMNH). ZAMBIA: Balovale (3 AMNH).

Remarks.—Hatt (1940) stated that *G. haedulus* and *G. spurrelli* were most likely subspecies of *G. lorraineus*. Ellerman et al. (1953), Rosevear (1969), Eisentraut (1973), and Genest-Villard (1979) regarded *G. lorraineus* as a subspecies of *G. murinus* (Desmarest, 1822). Examination of specimens of these taxa, as well as of *G. murinus* from South Africa, leads us to agree with Hatt. Specimens from the mountains (Eisentraut, 1963, 1973) and the savannas of Cameroon (Bafia, Babadjou, and Yoko) are larger and more variable in color than the forest species. The measurements of some of these specimens more nearly approach those of *G. murinus* from South Africa than those of *G. lorraineus*.

Graphius lorraineus frequently is found in thatch-roofed houses in the forested region of southern Cameroon (Good, 1947). Hatt (1940) and Rosevear (1969) provided ecological information on this species.

Graphiurus surdus Dollman, 1912

Graphiurus surdus Dollman, Ann. Mag. Nat. Hist., ser. 8, 9:314; March 1912.
Type locality.—Benito River, French Congo (now in Rio Muni).

Distribution.—Rio Muni and southern Cameroon.

Specimens examined (12).—CAMEROON: Bitye (1 BMNH); Efulen-Kribi (1 AMNH); Eseka (6 CM, 1 AMNH). RIO MUNI: Benito River (3 BMNH, including holotype).

Remarks.—Allen (1939) placed *G. schwabi* in synonomy with *G. haedulus,* but Perret and Aellen (1956) stated that *G. schwabi* was probably a synonym of *G. surdus* rather than of *G. haedulus*. Both

CAMEROON GAZETTEER

Locality	Coordinates	Species recorded
Assobam	3°15N, 14°02E	*G. lorraineus*
Babadjou	5°45N, 10°12E	*G. lorraineus*
Bachuntai	5°40N, 9°26E	*G. hueti*
Bashauo (=Bachuo)	5°45N, 9°26E	*G. crassicaudatus, G. hueti*
Bafia	4°40N, 11°05E	*G. lorraineus*
Besongabang	5°44N, 9°17E	*G. hueti*
Bipindi	3°06N, 10°30E	*G. crassicaudatus, G. hueti*
Bitye	3°10N, 12°20E	*G. crassicaudatus, G. lorraineus, G. surdus*
Efulen	2°46N, 10°42E	*G. hueti, G. surdus*
Ebolowa	2°56N, 11°11E	*G. crassicaudatus, G. lorraineus*
Eseka	3°38N, 10°47E	*G. crassicaudatus, G. surdus*
Eseka, 8 km SW	3°35N, 10°44E	*G. crassicaudatus, G. hueti*
Kribi	2°55N, 9°54E	*G. lorraineus, G. surdus*
Lolodorf	3°14N, 10°48E	*G. crassicaudatus, G. hueti, G. christyi, G. lorraineus*
Mamfe	5°46N, 9°17E	*G. hueti*
Metet	3°23N, 11°43E	*G. hueti, G. lorraineus*
Meyo	2°25N, 11°14E	*G. surdus*
Ndian Estate	4°54N, 8°54E	*G. crassicaudatus*
Osundan	not found	*G. lorraineus*
Sakbayeme	4°02N, 10°34E	*G. lorraineus*
Sangmelima	2°56N, 11°58E	*G. hueti, G. lorraineus*
Yaounde	3°51N, 11°31E	*G. lorraineus*
Yokadouma	3°25N, 15°08E	*G. lorraineus*
Yoko	5°29N, 12°19E	*G. lorraineus*

G. surdus and *G. schwabi* were originally described as having small ears (9 and 7 mm, respectively). However, external measurements of *G. surdus* were taken from fluid preserved specimens, whereas those of *G. schwabi* were from a dried skin originally preserved in formalin. The ears of our specimens measured 12 to 14 mm. A specimen (not seen by us) from Meyo reported as *G. surdus* by Perret and Aellen (1956) had short ears (9 mm), but does not correspond to *G. surdus* in cranial measurements.

Graphiurus surdus has a long and narrow skull with a short maxillary toothrow and short depth of rostrum. Examination of specimens from Rio Muni and southern Cameroon indicates that *G. surdus* is a species distinct from *G. haedulus* and *G. schwabi*; the latter two taxa are synonyms of *G. lorraineus*.

One female from Eseka contained two embryos on 14 January 1974 (mammae: 1 pair pectoral, 2 pairs inguinal = 6). The specimens from Eseka were taken in the same trapline as *G. crassicaudatus*.

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NEW OLIGOCENE RODENTS FROM WESTERN NORTH AMERICA

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Abstract

A new scuirid, *?Protosciurus douglassi,* from the Orellan of Nebraska is described. *?P. douglassi* is viewed as a member of an early lineage of sciurids, represented by *?P. jeffersoni* (Douglass) from the Chadronian of Montana. This lineage is viewed as distinct from that represented by *Protosciurus mengi* Black also from the Orellan of Nebraska.

An anomalous dentition of the Whitneyan cricetid *Eumys brachyodus* Wood is described and possible homologies are suggested.

Three new species of the cricetid *Scottimus—S. viduus, S. ambiguus,* and *S. longiquus*—are named. The occurrence of all of these species in the Orellan show the marked diversity and regional speciation of this genus at that time. The skull of *Scottimus* shares many features with that of *Leidymys* Wood, suggesting a close relationship between these taxa. The genus *Eoeumys* Martin is not congeneric with "*Eumys*" *exiguus* because of marked differences in the skull and dentition. *Eoeumys* is referred to the Eumyinae rather than Eucricetodontinae.

A generically indeterminate cricetid is described from the Orellan of North Dakota. This specimen most closely resembles two late Oligocene cricetids from central Asia, *Aralomys* Argyropulo and *Eumysodon* Argyropulo.

Introduction

The first review of North American Oligocene rodents was included in Cope's (1884) survey of all of the Tertiary vertebrates of the western United States. He recognized 18 species from the "White River" beds. The next review of Oligocene rodents of North America was over 50 years later by Wood (1937). Wood presented a review of all of the previous literature on the White River rodents and introduced many

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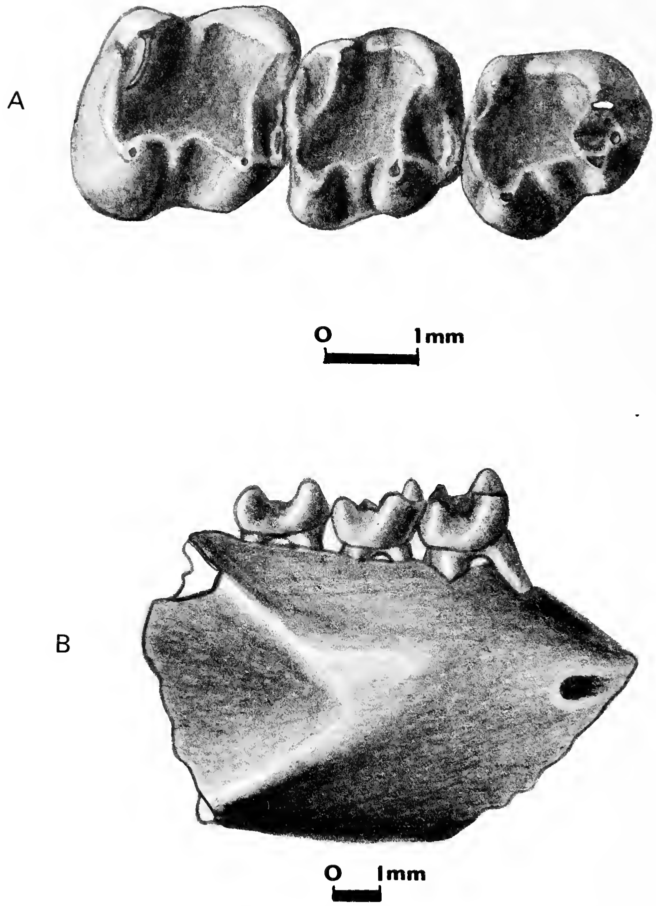

Fig. 1.—?*Protosciurus douglassi,* new species, holotype CM 38654. A, occlusal view of P_4–M_2; B, lateral view of mandible.

new genera and species. Since Wood's (1937) review, numerous new species and genera of Oligocene rodents have been described, generally as part of a faunal description of a specific locality (for example, Wilson, 1949*a*; Black, 1965; Russell, 1972; Wood, 1974).

Recently, Wood (1980) presented a summary of all previously described Oligocene rodents, in which he recognized over 80 species of rodents. Since Wood's summary, Martin (1980) has introduced 3 additional genera of Orellan rodents.

A study of unpublished specimens of Oligocene rodents in the collections of Carnegie Museum of Natural History and previously de-

Table 1.—*Measurements of the teeth of the holotype of* ?Protosciurus douglassi, *CM 38659. Measurements in millimeters.*

Teeth	A-P	tra	trp
P_4	1.91	1.54	1.93
M_1	1.87	1.95	2.05
M_2	2.24	2.23	2.30
I_1	2.87	1.39	

scribed material from other museums has yielded one new species or sciurid and three new species of cricetids from the Orellan. This new material increases the diversity of both sciurids and cricetids known from the Oligocene of North America.

Abbreviations.—AMNH, American Museum of Natural History; CM, Carneige Museum of Natural History; KU, University of Kansas Museum of Natural History; MCZ, Museum of Comparative Zoology, Harvard University; PU, Princeton University; UNSM, University of Nebraska State Museum; USNM, National Museum of Natural History, Smithsonian; A-P, anteroposterior length; tra, anterior transverse width; trp, posterior transverse width; N, number of specimens measured; M, mean; SD, standard deviation; OR, observed size range; CV, coefficient of variation. Dental terminology after Wood and Wilson (1936).

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821

Family Sciuridae Gray, 1821

?***Protosciurus douglassi,*** new species

(Fig. 1, Table 1)

Holotype.—CM 38659, right mandible with P_4–M_2.

Horizon and locality.—Orella Member, Brule Formation, Prairie Dog Creek, SE¼, T33N, R56W and W½, T33N, R55W, Sioux County, Nebraska.

Age.—Orellan (early middle Oligocene).

Hypodigm.—Holotype only.

Entymology.—Named in honor of Earl Douglass for his many contributions to vertebrate paleontology.

Diagnosis.—Small species; trigonid basins on lower cheek teeth relatively large and enclosed; entoconid separated from posterolophid by shallow groove; mesostylids distinct; partial hypolophid runs from entoconid to center of posterolophid; mesoconid and ectolophid poorly developed.

Description.—The masseteric fossa on the mandible terminates anteriorly below M_1 (Fig. 1b). A lateral swelling is present just anterior to the masseteric fossa. The mental foramen is located low on the side of the mandible below the posterior end of the diastema.

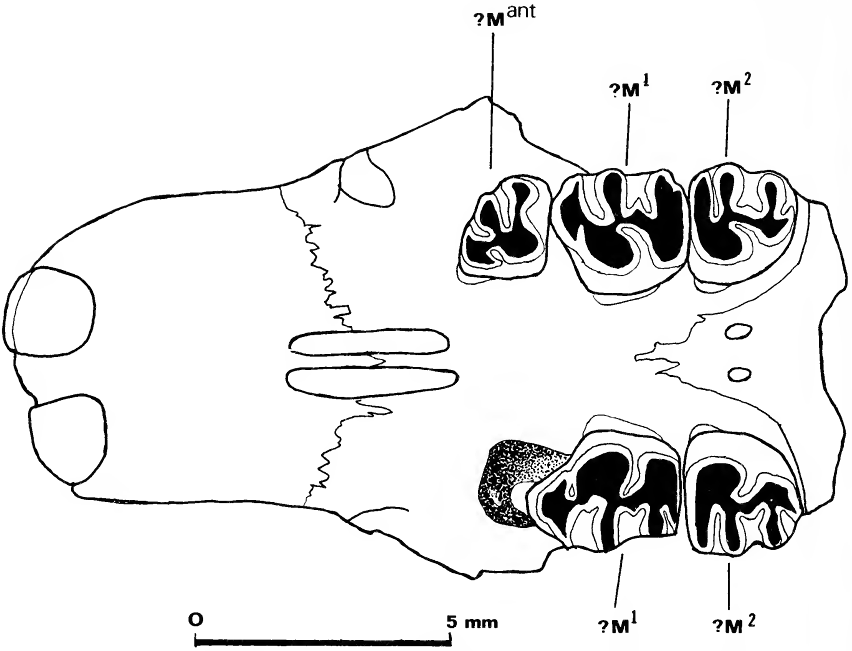

Fig. 2.—*Eumys brachyodus.* USNM 66028, ventral view of the skull.

The lower incisor is laterally compressed, flattened medially, and rounded laterally. The trigonid basins of P_4–M_2 are enclosed and relatively large, decreasing in relative size and increasing in anteroposterior compression from P_4 to M_2. M_1 and M_2 are wider than long (Table 1). A distinct hypolophid runs from the entoconid into the talonid basin, then turns posteriorly and joins the posterolophid just lingual to its center on P_4–M_2. The mesoconid is minute and the ectolophid is weak on P_4–M_2. A distinct mesostylid is present on all of the lower cheek teeth. The entoconid is separated from the posterolophid by a shallow groove, and from the mesostylid by a deeper groove. M_2 is the largest tooth preserved.

Discussion.—?*Protosciurus douglassi* most closely resembles ?*P. jeffersoni* from the early Oligocene of Pipestone Springs, Montana (Douglass, 1901; Black, 1965). It differs from all other species of *Protosciurus,* as does ?*P. jeffersoni,* in the possession of a hypolophid which extends into the talonid basin from the entoconid. Because of this structure, Black (1965) questionably referred the Pipestone Springs species to *Protoscirus.* ?*P. douglassi* is clearly referable to the same genus as ?*P. jeffersoni.* Whether these species truly represent *Protosciurus* is still questionable. Black (1965) has shown that ?*P. jeffersoni,* thus ?*P. douglassi,* is clearly not referable to the aplodontid *Cedromus* Wilson (1949*a*) as was suggested by Wood (1962, 1980).

?*P. douglassi* differs from ?*P. jeffersoni* in being 30% smaller, having cusps less bulbous and more marginally placed, having the hypolophid join the posterolophid, and having the mesoconid and ectolophid less pronounced.

?*Protosciurus douglassi* and ?*P. jeffersoni* represent a lineage of sciurids distinct from *Protosciurus* (*sensu* Black, 1963). Black (1963: fig. 7) derives the three Arikareean species of *Protosciurus* from the Orellan species, *P. mengi*. A ?*P. jeffersoni*–?*P. douglassi* lineage would originate in the Chadronian and end in the Orellan. Any common ancestor with *Protosciurus* would probably be in the late Eocene, though the earliest known species is Orellan.

A skull of ?*Protosciurus* cf. ?*P. jeffersoni* from the Chadronian of Wyoming (Emry, 1973) is currently being studied by Emry and Thorington of the National Museum of Natural History. This skull differs markedly from that of *Protosciurus* (Black, 1963), thus making ?*P. jeffersoni* and, in turn, ?*P. douglassi*, referable to a new genus (Black, personal communication)

Family Cricetidae Rocheburne, 1883
Eumys brachyodus Wood, 1937
(Fig. 2)

Referred specimen.—UNSM 66028, partial skull with complete dentition.

Horizon and locality.—Eckart Ranch locality, adjacent corners of secs. 17, 18, 19, 20, T19N, R48W, Whitney Member, Brule Formation, Morrill County, Nebraska.

Age.—Whitneyan (late middle Oligocene).

Description.—UNSM 66028 is a partial skull complete on the ventral side from the posterior margin of the palatine bones, and dorsally from the center of the orbits. The skull is nearly identical to that of *Eumys elegans* (see Wood, 1937) but is higher, with a broader snout and palate.

On the right side of the palate (Fig. 2) there are two molars. The anterior molar (?M^1) resembles M^1 of *Eumys brachyodus* (Martin, 1980). The posterior molar (?M^2) generally resembles M^2 of *E. brachyodus* but the posterior half of ?M^2 is narrower (bucco-lingually) than the anterior half. The hypocone and posterior cingulum are reduced, but not to the extent of an M^3 of *E. brachyodus*.

Anterior to ?M^1 is a deep pit. The anterior root of ?M^1 enters into the posterior end of this pit. The anterior wall of the pit is flattened and nearly vertical. There are no remnants of roots or any other indication that a tooth has occupied this pit.

Posterior to ?M^2 there is no indication of another tooth. The teeth of UNSM 66028 are heavily worn indicating that this specimen represents an old individual, thus making it impossible for an unerupted third molar to be present.

?M^1 and ?M^2 on the left side of the palate resemble those on the right. The left ?M^1 has a slightly more reduced anterocone than the right ?M^1, and the left ?M^2 is just slightly narrower posteriorly than the right ?M^2. Anterior to the left ?M^1 is a small tooth (?M^{ant}) that is triangular in outline. The only distinguishable cusp on ?M^{ant} is the ?hypocone, which is large and situated in the posterolingual corner of the tooth. Three lophs eminate from this cusp. One loph runs in a buccal direction along the posterior margin of the tooth. A second runs anteriorly, perpendicular to the first, along the lingual margin of the tooth. The third loph runs obliquely from the ?hypocone in an anterobuccal direction. Valleys separate these three lophs. A small valley lies on the posterior side of the tooth at its center, putting a slight bend in the posterior loph. A similar valley lies in the center of the lingual margin of the tooth. This lingual valley resembles, somewhat, the internal valley between the protocone and hypocone on ?M^1 and ?M^2 but is much reduced.

Discussion.—Numerous authors have discussed the reduction in the number of cheek teeth in muroid rodents (see Wilson, 1956). Most of the discussion has been centered around whether the anterior cheek teeth have been lost, leaving M^1–M^3 only, or whether the posterior teeth have been lost, leaving P^4–M^2 or dP^4–M^2.

Wilson (1956) argued strongly that reduction of the posterior teeth was highly unlikely. He stated that instances of posterior supernumerary teeth in Recent muroids was not an indication of general posterior reduction because such cases should be much more common in the early history of the family (Oligocene) but were not, and that the most likely Eocene forms ancestral to the muroids (the sciuravids) had reduced the premolars, not the posterior molars.

If the anterior molars have been reduced in UNSM 66028 leaving only the small anterior tooth on one side, it must also mean that M^2 has developed an expanded anterocone as was present on M^1, and M^3 has been enlarged posteriorly to more closely resemble an M^2. In such a case, ?M^{ant} of UNSM 66028 would be homologous to M^1, ?M^1 would be homologous to M^2, and ?M^2 would be homologous to M^3.

If UNSM 66028 is an example of the loss of the posterior molars, it would involve the loss of M^3, modification of M^2, and then introduction of a supernumerary tooth anterior to M^1. In this case, ?M^{ant} would represent a supernumerary tooth, ?M^1 would be homologous to M^1, and ?M^2 would equal M^2.

Anterior reduction would also involve an anterior movement of the tooth row. The palatine foramina of *Eumys* are always situated medial to M^2 (see Wood, 1937; Martin, 1980). In UNSM 66028, these foramina are medial to ?M^2. If ?M^2 is homologous to M^3, as would be suggested by anterior reduction, its position on the palate has been moved considerably anterior.

Conversely, posterior reduction in the tooth row would indicate a posterior movement of the tooth row, based on its relation to the skull. In *Eumys,* the palatine-maxillary suture extends anterior to the level of M^2, and the tooth row terminates anteriorly just posterior to the posterior margin of the incisive foramina. If ?M^1 is homologous to M^1 in other specimens of *Eumys,* then the teeth have moved posteriorly so that the palatine-maxillary suture now extends anteriorly to the level of M^1, and the anterior extent of the tooth row (not including ?M^{ant}) has also moved considerably posterior.

UNSM 66028 is clearly an anomalous specimen. Because the true homologies of the teeth of UNSM 66028 are uncertain, this specimen cannot be used as an example to support either theory of posterior or anterior reduction in the tooth row in muroid rodents.

Two lower jaws of *Eumys brachyodus* have been recovered from the same locality as UNSM 66028 (CM 38701, CM 38704). Neither of these specimens show a marked reduction in M_1 or M_3.

Scottimus Wood, 1937

Eumys Leidy, Wood, 1937 (in part).
Paracricetodon Schaub, Alker, 1968 (in part).
Eoeumys Martin, 1980 (in part).

Type species.—*Scottimus lophatus* Wood, 1937.

Referred species.—*S. exiguus* (Wood, 1937); *S. kellamorum* Black, 1961; *S. viduus,* new species; *S. ambiguus,* new species; *S. longiquus,* new species; *Scottimus* sp.

Emended diagnosis.—Small cricetids with low skull; slender, parallel-sided snout; incisive foramina large extending posterior to anterior margin of M^1; infraorbital foramina and palatine foramina relatively large; two parasagital crests on skull; mandible slender; upper molars decrease in size posteriorly and develop longitudinal lophs buccally between the paracone and metacone and lingually between the lingual ends of the protocone and hypocone; protoloph on M^2–M^3 joins anterior arm of the protocone or anterior cingulum; anterior cingulum on M^2–M^3 extends to the buccal and lingual margins of the tooth; transverse lophs on the lower molars tend to be oriented more anteroposteriorly; M_1–M_2 with buccal posterior cingulum; I_1^1 with minute posteriorly radiating ridges on the anterior enamel surface of primitive species and I_1 smooth on advanced species.

Range.—Chadronian (early Oligocene) of Wyoming, Orellan (early middle Oligocene) of Montana, Nebraska, South Dakota, Colorado, Whitneyan (late middle Oligocene) of Nebraska and South Dakota, and Arikareean (late Oligocene) of Wyoming and South Dakota.

Discussion.—Wood (1937) first described *Scottimus* based on a single species, *S. lophatus,* from the Whitneyan of Nebraska. He recognized *Eumys exiguus* from the Orellan of South Dakota as the probable ancestor of *Scottimus.* Galbreath (1953) referred several specimens from the Orellan of northeastern Colorado to *Eumys* near *E. exiguus* and suggested that *Leidymys vetus* Wood (1937), also from Colorado, was synonymous with *E. exiguus.* Black (1961) named a new species of *Scottimus, S. kellamorum,* from the Arikareean of Wyoming and formally synonymized *L. vetus* with *E. exiguus,* including the Colorado specimens, and transferred the species to *Scottimus.*

Alker (1968) identified over 90 specimens from Nebraska as *E. exiguus,* which he transferred to the European genus *Paracricetodon.* Dawson and Black (1970) refuted Alker and suggested that the Nebraska specimens did not represent *S. exiguus,* and were probably referable to a small species of *Eumys.*

Wood (1980) included in *Scottimus exiguus* the Colorado specimens of *Eumys* near *E. exiguus* (Galbreath, 1953) and specimens described by White (1954) as *Eumys* cf. *exiguus* from the Orellan of Montana. Wood (1980) referred the Nebraska specimens (Alker, 1968) to *Eumys* cf. *parvidens,* maintained that *Leidymys vetus* was distinct from *S. exiguus,* and retained the former in its original generic allocation.

Martin (1980) recently erected a new genus, *Eoeumys.* He recognized two species, *Eo. vetus* (including the specimens referred by Galbreath, 1953, to *Eumys* near *E. exiguus* from Colorado) and *Eo. exiguus* (including the specimens referred by Alker, 1968, to *Paracricetodon* from Nebraska). The genus *Eoeumys,* based on the type specimen of *Leidymys vetus* (AMNH 8742), is distinct from both *Scottimus* and *Leidymys,* however, none of the specimens referred to *Eumys* (or *Scottimus*) *exiguus* (Wood, 1937; Galbreath, 1953; White, 1954; Alker, 1968) can be referred to this genus.

Eoeumys vetus (restricted to the holotype) differs in morphology of the skull from *Scottimus* (described below) in 1) having a shorter snout which tapers anteriorly; 2) incisive foramina small and placed more anterior; 3) palatine foramina small; 4) infraorbital foramina smaller and restricted more dorsally on the snout; and 5) the frontal-maxillary suture on the medial wall of the orbit forms a diagonal line running from the posteroventral corner to the anterodorsal corner. The only feature of the skull of *Eo. vetus* similar to that of *Scottimus* is the possession of parasagital crests (Fig. 3f). *Eoeumys* most closely resembles *Eumys* in the above listed features except in the possession of parasagital crests, a feature shared by both *Leidymys* and *Scottimus.*

Dentally, *Eoeumys vetus* (Fig. 4) differs from *Scottimus* in 1) lack of buccal or lingual lophs on the upper molars; 2) anterior cingulum on M^2–M^3 does not extend lingually; 3) protoloph of M^2–M^3 joins posterior arm of the protocone (on M^3 the protoloph is doubled and the anterior lophule joins the anterior arm of the protocone, a feature that commonly occurs in *Eumys elegans* and is present in the holotype of *E. parvidens*); and the enamel surface of the upper incisors is smooth. The teeth of *Eoeumys* do not differ from those of *Eumys* or *Coloradoeumys* Martin (1980).

In overall cranial and dental morphology, *Eoeumys* most closely resembles *Eumys,* but differs from the latter in possessing parasagital crests, slightly narrower snout, and infraorbital foramen not as ven-

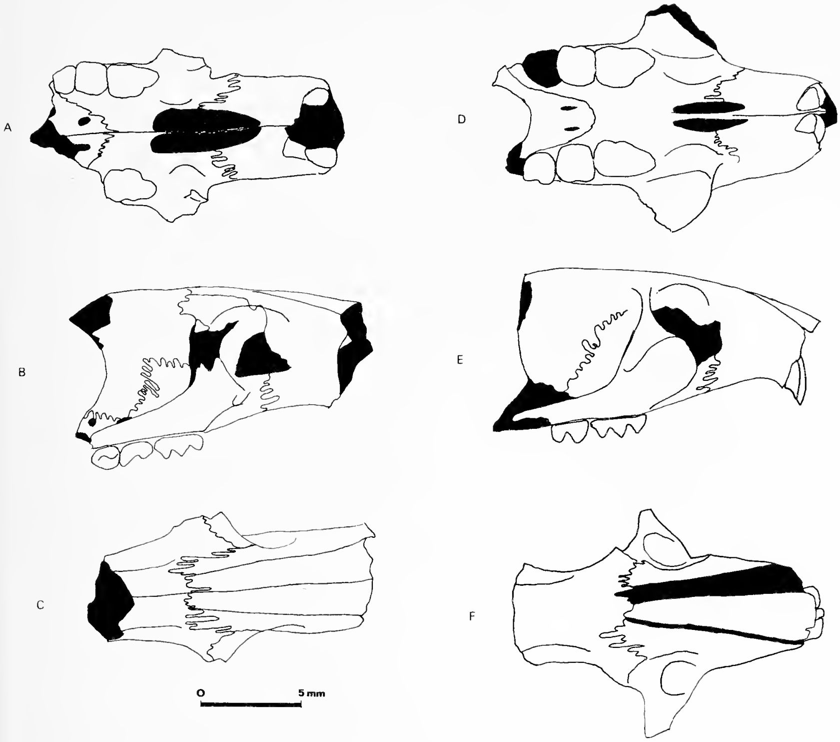

Fig. 3.—The skulls of *Scottimus* and *Eoeumys*. A–C, ventral, lateral, and dorsal view of the skull of *Scottimus viduus* (holotype) CM 10821; D–F, ventral, lateral, and dorsal view of the skull of *Eoeumys vetus* (holotype) AMNH 8742.

trally restricted. Wood (1937) noted these features as similar to the Arikareean *Leidymys*. He stated that *L. vetus* was morphologically intermediate between *Leidymys* and *Eumys* and could be referred to either genus. The relative proportions of the snout and restriction of the infraorbital foramen of "*Leidymys*" *vetus*, however, more closely resemble those of *Eumys* than those of *Leidymys* or *Scottimus*.

Martin (1980:17) mentioned a small cricetid skull from the Chadronian of Wyoming that was being described elsewhere. This specimen, according to Martin's description, is referable to *Scottimus*, and may represent the Chadronian species of *Scottimus* described below.

The uniqueness of the holotype of "*Leidymys*" *vetus* makes its retention in *Eoeumys* the most convenient allocation until more material is available.

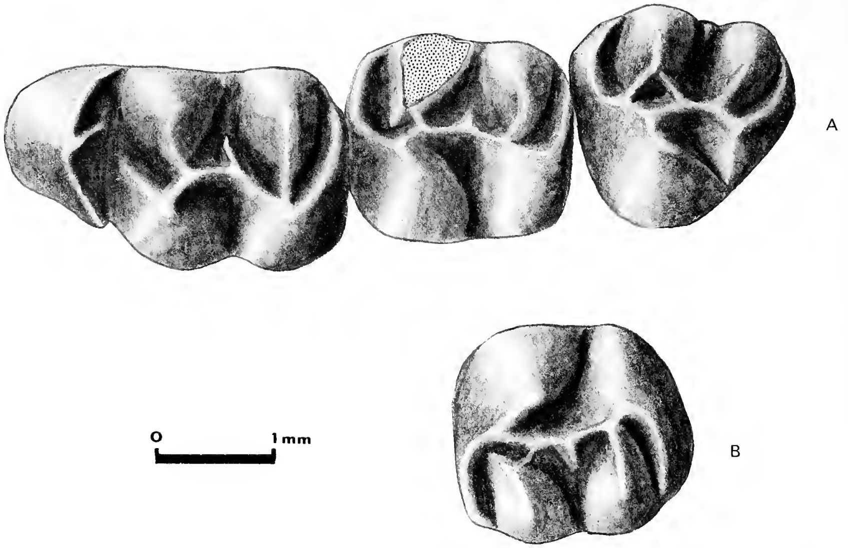

Fig. 4.—Upper teeth of *Eoeumys vetus,* holotype, AMNH 8742. A, LM^1–M^3; B, RM^2. Stippled area represents damaged area.

Alker's (1968) allocation of "*Eumys*" *exiguus* to *Paracricetodon* was based mainly on the minute multiple non-parallel ridges on the lower incisor. This type of ornamentation of the lower incisor is reported not only for the latter genus but also in species of *Eucricetodon* and *Pseudocricetodon* (Lindsay, 1978), restricting its use as the sole diagnostic feature of the genus.

Martin (1980), in separating "*Eoeumys*" (including specimens referred here to *S. ambiguus,* new species, *S. viduus,* new species, and *S. exiguus*) from *Scottimus,* cited only two differences between them—position of the anterocone on M^1 and presence of ridges on the lower incisor. He stated that the anterocone of *Scottimus lophatus* was centrally positioned and that of *Eoeumys* was buccal. The position of the anterocone on M^1 of *S. lophatus* is indeed more nearly central than that of *S. exiguus,* and the other primitive species of *Scottimus.* However, the anterocone of M^1 of *S. kellamorum* (Black, 1961: fig. 1) and "*Eumys* cf. *exiguus*" (White, 1954) is clearly intermediate. Also, the anterocone of *S. lophatus* may not be as buccal as it appears because the only published specimens with M^1 (Wood, 1937; Martin, 1980) are heavily worn, making the cusp look broader and more lingual. The minor difference in the placement of the anterocone of *S. laphatus* is more likely a specific difference than a generic one.

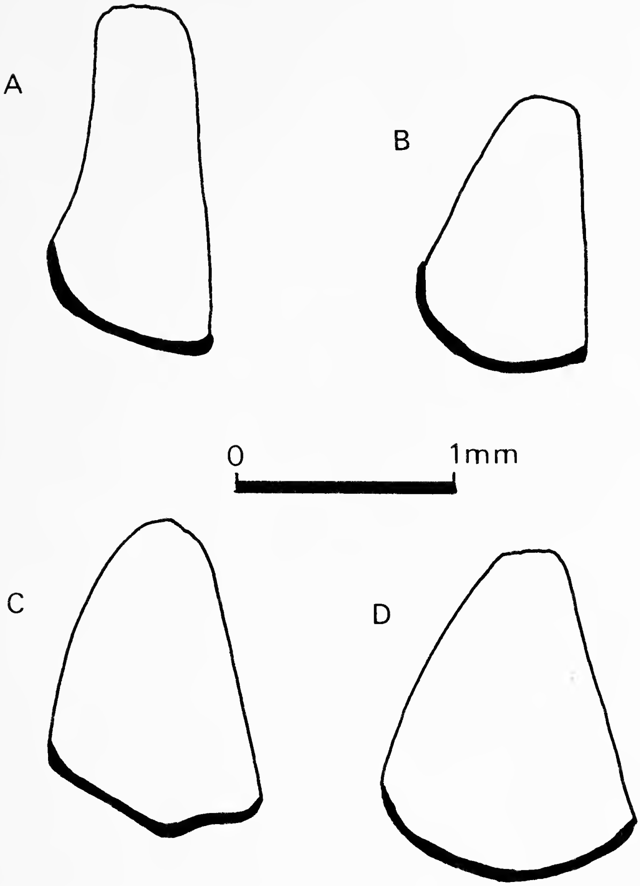

Fig. 5.—Cross-sectional shape of RI_1 of *Scottimus*. A, *S. viduus*, UNSM 65937; B, *S. ambiguus*, KU 8426; C, *S. longiquus*, USNM 18867; D, *S. lophatus*, UNSM 66167.

As is the case with the position of the anterocone, intermediate stages between ridged and smooth incisors exist within the species of *Scottimus*. Lower incisors are known for only four species of *Scottimus*—*S. viduus* new species; *S. ambiguus*, new species; *S. longiquus*, new species; *S. lophatus*. In the most primitive species (*S. viduus* and *S. ambiguus*) the fine "pinnate" ridges on I_1 are distinct. The lower incisor is laterally compressed in these species. In *S. lophatus*, I_1 is broad with a smooth enamel surface. However, in "*Eumys* cf. *exiguus*" (White, 1954; here referred to *Scottimus longiquus*, new species) from Montana, the lower incisor is broad, but not as much so

Table 2.—*Measurements of the teeth of a sample of* Scottimus viduus. *Measurements in millimeters. (Also see Tables 3 and 4.)*

							Holotype	
Teeth	Measurement	N	OR	SD	CV	M	L	R
M^1	A-P	6	2.31–2.47	.08	3.3	2.39	2.31	2.32
	tra	6	1.40–1.56	.05	3.7	1.48	1.40	1.45
	trp	6	1.47–1.59	.04	3.0	1.53	1.47	1.50
M^2	A-P	5	1.51–1.76	.10	6.1	1.60		1.51
	tra	5	1.45–1.65	.08	5.2	1.52		1.49
	trp	5	1.35–1.55	.09	5.3	1.45		1.46
M^3	A-P	4	1.08–1.28	.09	7.7	1.19		1.08
	tra	4	1.19–1.39	.10	8.1	1.30		1.19
M^1–M^3		3	4.98–5.27					4.98
M_1	A-P	19	1.92–2.24	.09	4.3	2.09		
	tra	20	0.97–1.23	.07	6.1	1.09		
	trp	20	1.18–1.45	.08	5.7	1.31		
M_2	A-P	21	1.62–1.88	.07	4.1	1.76		
	tra	20	1.32–1.60	.07	5.0	1.45		
	trp	21	1.36–1.61	.07	5.0	1.45		
M_3	A-P	18	1.47–1.88	.12	7.1	1.68		
	tra	18	1.29–1.55	.07	5.2	1.40		
	trp	18	0.92–1.18	.09	8.3	1.04		
M_1–M_3		16	5.20–5.96	.22	4.0	5.58		
I_1	A-P	14	1.25–1.66	.11	7.9	1.40		
	tra	14	0.77–1.02	.08	9.3	0.88		

as in *S. lophatus*. Minute ridges, similar to those on I_1 of the primitive species of *Scottimus*, are much reduced in size and extent on the incisor of "*Eumys* cf. *exiguus*." These ridges are confined to a narrow "keel" on I_1 of the latter species. It is evident that intermediate forms do exist between the most primitive and the most advanced forms (Fig. 5). Martin (1980) compared only the two extreme cases.

Scottimus is not the only genus to exhibit such a variety of ornamentation on the incisors. In *Leidymys*, the number of ridges is variable on the upper and lower incisors (Martin, 1980). Lindsay (1978) reported that some species of *Eucricetodon* have lower incisors with a few parallel ridges and others have multiple non-parallel ridges.

Scottimus viduus, new species
(Figs. 3a, b, c, 6, 7, Tables 2, 3, 4)

Paracricetodon exiguus (Wood) Alker, 1968.
Eumys sp. Engesser, 1979.
Eoeumys exiguus (Wood) Martin, 1980 (in part).
Eumys cf. *parvidens* Wood, 1980.

Holotype.—CM 10821, partial skull with RM^1–M^2 and LM^1–M^2.

Hypodigm.—Holotype and CM 9711, CM 38654, CM 38655, PU 23265, KU 537, KU 539, KU 540, KU 8410–8418, and UNSM 10306, 10369, 65616–65631, 65910, 65912, 65914–65916, 65927–65950, 66009, 66010, 66031, 66035, 66038, 66039, 66044–66051, 66053–66065, 66156, 66169, 66182–66192, 66197, 66198. All specimens except the holotype are whole or partial mandibles or maxillae and isolated teeth.

Horizon and locality.—Holotype and CM 9711 from Warbonnet Creek locality, N½, T33N, R56W and NW¼ T33N, R55W, Orella Member, Brule Formation, Sioux County, Nebraska. UNSM and KU specimens are from various localities in the Orella Member of the Brule Formation, Sioux County, Nebraska (precise locality data for each specimen available on file at UNSM). CM 38654 and 38655 are from Pilgrim Creek locality (formation unknown), Jackson County, Wyoming. PU 23265 is from "Head of Battle Draw" (?)SW¼ T42N, R45W, Poleslide Member, Brule Formation, Shannon County, South Dakota.

Age.—Chadronian (Pilgrim Creek), Orellan (Sioux County), and possibly Whitneyan ("Head of Battle Draw").

Etymology.—*viduus,* Latin, lacking; intended to imply the lack of many of the advanced features of the other species of the genus.

Diagnosis.—Slightly smaller than *S. exiguus*; metaloph wider than protoloph on M^1; anterocone on M^1 large, lingually placed with posterobuccal reentrant valley of the anterocone open posteriorly; buccal longitudinal lophs on upper molars very weak and variably absent; mesolophs long on M^1–M^2; metaloph joins hypocone on M^1–M^2; mesolophids long on M_1–M_2; buccal posterior cingulum on M_1–M_2 minute; hypolophid joins ectolophid posterior to the mesoconid.

Description.—The skull of *S. viduus* closely resembles that of *Leidymys* (Fig. 3). It is relatively low with a long, narrow snout. The rostrum is parallel sided and flairs anteriorly. Two low parasagital crests run along the lateral margin of the frontal bones. The nasal bones widen anteriorly and terminate posteriorly just behind the anterior margin of the orbit, on the same line as the posterior extent of the premaxillary bones.

The frontal-maxillary suture on the medial wall of the orbit (Fig. 3b) is highly crenulate. Originating above M^2, this suture runs directly dorsal midway to the top of the skull, then runs directly anterior to the infraorbital foramen. The infraorbital foramen is large. The scar for the medial masseter extends relatively far onto the rostrum, farther than that of *Eumys* or *Eoeumys vetus* (Fig. 3e).

The incisive foramina also resemble those of *Leidymys*. They are large and posteriorly placed behind the anterior margin of M^1 (Fig. 3a). The palatine foramina are large, as described for *S. exiguus* (Wood, 1937), and medial to M^2. On the medial orbital wall there are two foramina. The sphenopalatine foramen is situated above M^2 at the junction of the frontal, maxillary and palatine bones. The dorsal palatine foramen is in the center of the portion of the palatine preserved, above M^3.

On M^1, the metaloph is wider than the protoloph, in contrast to other species of *Scottimus*. The metaloph clearly joins the center of the hypocone even on worn specimens (Figs. 6, 7a, b). A buccal loph running between the paracone and metacone,

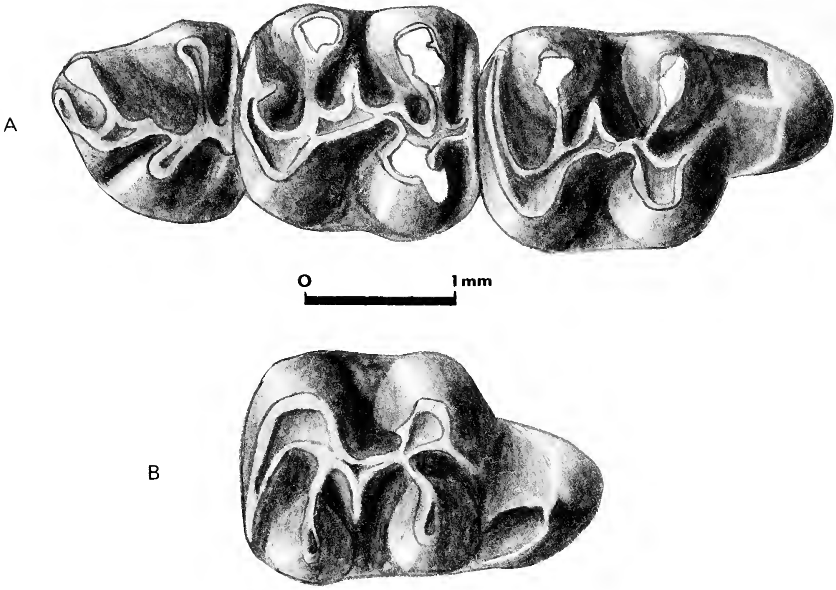

Fig. 6.—Upper teeth of *Scottimus viduus,* holotype, CM 10821. A, RM^1–M^3; B, LM^1.

present on other species, is variably present and even absent on some specimens. The anterocone is large and restricted to the buccal side of the tooth. The posterobuccal reentrant valley on the anterocone is widely open posteriorly.

M^2 is relatively broader than in *S. lophatus.* As on M^1 the metaloph runs directly to the center of the hypocone. The mesoloph is relatively long. As in all species of *Scottimus,* the anterior cingulum runs the entire width of the tooth and the protoloph joins the anterior arm of the protocone. The buccal longitudinal loph is very weak. On some specimens it appears to be nearly absent, as in M^1. The lingual margin of the protocone and hypocone have minor ridges running posteriorly and anteriorly, respectively.

The buccal longitudinal loph on M^3 is more distinct than on M^1–M^2. The anterior cingulum and protoloph are as in M^2. There is no mesoloph on M^3 and the metacone and hypocone are greatly reduced.

The lower molars are very similar to those of *Eumys* (Fig. 7c). The mesolophid on M_1–M_2 is long, approximately equal in length to the posterior arm of the protoconid, which extends lingually to the level of the apex of the metaconid. On M_2 there is a minute buccal posterior cingulum which is generally eliminated with moderate wear. This same structure is only present on unworn specimens of M_1.

The hypolophid on M_1–M_2 joins the ectolophid posterior to a distinct mesoconid. A buccal spur from the mesoconid is variably present on all molars. The posterior arm of the protoconid reaches the lingual margin of the tooth in M_3 on about half of the specimens.

The fine "pinnate" ridges on I_1 are distinct and restricted to the enamel surface. The upper incisors of the type specimen have minute ridges running obliquely across the anteromedial corner of the enamel surface.

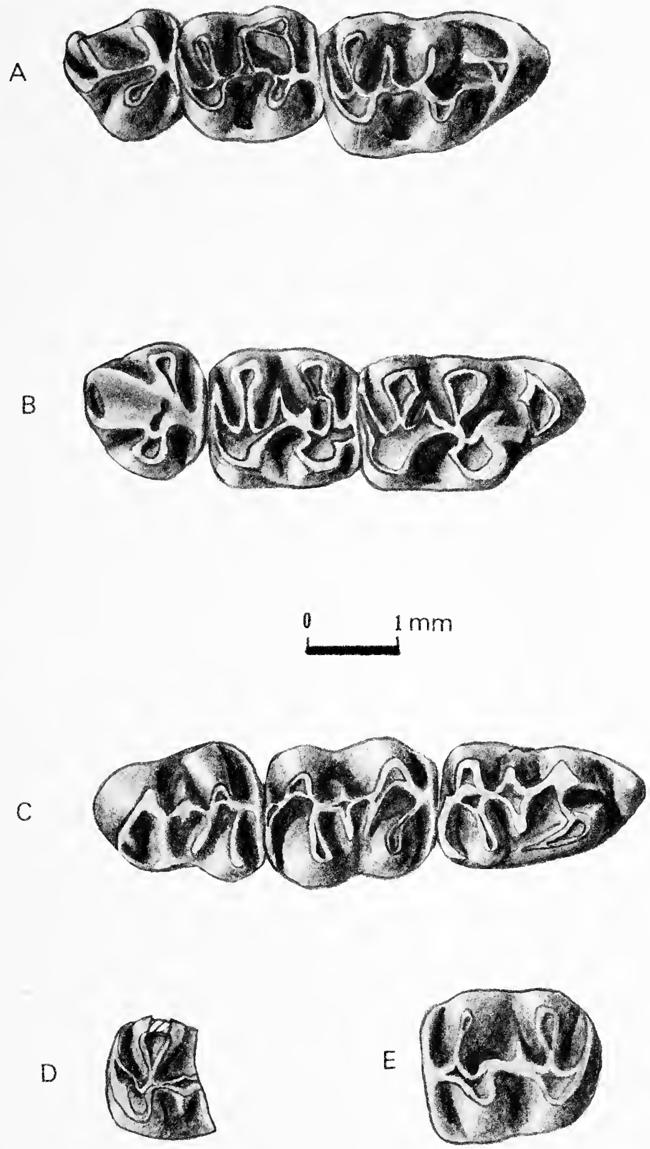

Fig. 7.—Dentition of *Scottimus viduus*. A, UNSM 65910, RM^1–M^3; B, UNSM 65939, RM^1–M^3; C, UNSM 66054, LM$_1$–M$_3$; D, CM 38654, RM$_1$; E, CM 38655, LM^2.

Discussion.—*Scottimus viduus* is the most primitive species of the genus dentally. The longitudinal lophing of the molars in *S. viduus* is quite weak and nearly absent in some specimens. The lack of many of the advanced characters of *Scottimus* led Dawson and Black (1970) to suggest that the Nebraska specimens were referable to *Eumys*.

Two isolated teeth, a partial M_1 (CM 38654, Fig. 7d) and an M^2 (CM 38655, Fig. 7e) are from the Chadronian Pilgrim Creek fauna (see Sutton and Black, 1975, for locality and age data). The longitudinal lophs on the M^2 are not developed, but the attachment of the protoloph and the lingual extension of the anterior cingulum are the same as in the topotypic material from Sioux County, Nebraska. The M_1 is worn and any trace of a buccal posterior cingulum has been removed. This tooth is referred to this species on the basis of size. The only other species of cricetid from Pilgrim Creek is *Eumys elegans*, considerably larger than CM 38654.

The M^1 on PU 23265 from South Dakota is longer than any of the specimens from Nebraska (Tables 2, 3) but in all other measurements of M^1 and M^2 it is within the range of *S. viduus*. The morphology of the molars of PU 23265 makes it clearly referable to *S. viduus*.

The skull of *Scottimus viduus* is nearly identical to that of *Leidymys* except that the former may have a slightly more restricted infraorbital foramen. It is difficult, however, to determine the exact size of the infraorbital foramen in *Leidymys* because the only known skull preserving the infraorbital foramina (AMNH 7028) is badly damaged in the area of the foramina, which has artifically enlarged them (Wood, 1936). The infraorbital foramina do not appear to be as large as the figures by Martin (1980: figs. 15, 25a) indicate. The right infraorbital foramen is partially preserved on the type specimen of *L. nematodon* (AMNH 7018) and is much smaller than has been illustrated for *L. lockingtonianus*.

Alker (1968) reported that the youngest occurrence of *S. viduus* (=*Paracricetodon exiguus*) was from the early Whitneyan. Only one specimen from the Nebraska collection (UNSM 66051) is listed from the Whitney. However, according to the field number associated with this specimen, it was recovered from the lower Orella Member, Sioux County. Several other specimens with this same field number are all listed from the lower Orella. Martin (1980:17) cited a small cricetid skull from the Chadronian of Wyoming. It may be referable to *S. viduus* based on his brief description of the specimen.

Scottimus ambiguus, new species
(Fig. 8, Table 3, 4)

Eumys near *E. exiguus* Wood, Galbreath, 1953.
Scottimus exiguus (Wood) Black, 1961 (in part).
Eoeumys vetus (Wood) Martin, 1980 (in part).

Table 3.—*Measurements of upper teeth of* Scottimus. *Measurements in millimeters.*

	M^1			M^2			M^3			
Specimen no.	A-P	tra	trp	A-P	tra	trp	A-P	tra	trp	M^1–M^3
Scottimus ambiguus										
KU 8419	2.19	1.24	1.28	1.58	1.40	1.32	1.04	1.19		4.91
KU 8420	2.19	1.31		1.56		1.39	1.34	1.30		5.17
Scottimus viduus										
PU 23265	2.65	1.48	1.57	1.75	1.59	1.58				
CM 38655				1.67	1.58	1.49				
Scottimus longiquus										
USNM 18865	2.78	1.86	1.80	1.97	1.74	1.64				
PU 23267a		1.80		2.04	1.73	1.57				
PU 23267b	2.87	1.78	1.68							
Scottimus sp.										
PU 23264				1.90	1.53	1.44		1.38		

Holotype.—KU 8419, maxilla with LM^1–M^3.

Hypodigm.—Holotype and KU 8420, LM^1–M^3; KU 8421, 8422, LM_1–M_3; KU 8423, RM_1–M_2; KU 8424, LM_2; KU 8426, LM_1–M_3.

Horizon and locality.—Holotype and all referred specimens from the Cedar Creek Member, White River Formation, Logan County, Colorado. Type and KU 8420 from SW¼ sec. 12 and SE¼ sec. 3, T11N, R54W; KU 8421 and 8422 from E½ sec. 3, T11N, R54W; KU 8423 and 8424 from W½ sec. 7, T11N, R53W; and KU 8426 from SW¼ sec. 21, T11N, R53W.

Age.—Orellan (early middle Oligocene).

Diagnosis.—Near size of *S. viduus*; upper molars narrow; protoloph narrower than metaloph on M^1; anterocone on M^1 buccal; posterobuccal reentrant valley of the anterocone of M^1 open posteriorly; buccal lophs on M^1–M^3 weak but present; metaloph joins posterior margin of hypocone on M^1 in unworn specimens, and joins the posterior cingulum with wear; hypolophid joins ectolophid at mesoconid on m_1–M_2; mesolophid on M_1–M_2 minute to absent; buccal extension of mesoconid present on M_1–M_3.

Description.—On KU 8419 (Fig. 8a), the posterior margin of the incisive foramen is preserved. This foramen is similar to those of *S. viduus* and *S. exiguus*. The upper molars most closely resemble those of *S. exiguus*. The upper molars are much narrower (buccolingually) than in *S. viduus*, but fit within the observed ranges of size of M^2 of the latter in length. The anterocone on M^1 is large and buccally situated, as in *S. viduus*. The posterobuccal reentrant valley of the anterocone, again as in *S. viduus*, is open posteriorly. On the unworn specimen (KU 8419) the metaloph of M^1 is directed posteriorly, then bends anterior just buccal to the hypocone, joining it near its center (Fig.

Table 4.—*Measurements of lower teeth of* Scottimus. *Measurements in millimeters.*

	M_1			M_2			M_3				I_1	
Specimen no.	A-P	tra	trp	A-P	tra	trp	A-P	tra	trp	M_1–M_3	A-P	tra
					Scottimus ambiguus							
KU 8421	2.07	1.11	1.39	1.73	1.47	1.49	1.58	1.44	1.06	5.54	1.14	0.82
KU 8422	1.88	1.10	1.26	1.67	1.42	1.40	1.70	1.45	0.98	5.31	1.23	0.93
KU 8423	1.98	1.05	1.23	1.79	1.37	1.44					1.29	0.83
KU 8424				1.68	1.40	1.36						
KU 8426	1.95	1.08	1.27	1.73	1.43	1.47	1.68	1.43	1.12	5.41	1.15	0.75
					Scottimus viduus							
CM 38654			1.31									
					Scottimus longiquus							
USNM 18867	2.60	1.60	1.76	2.18	1.77	1.76	2.32	1.75	1.48	7.18	1.39	0.96
USNM 18866	2.42	1.51	1.60	2.06	1.62	1.50	2.01	1.55	1.14	6.49		

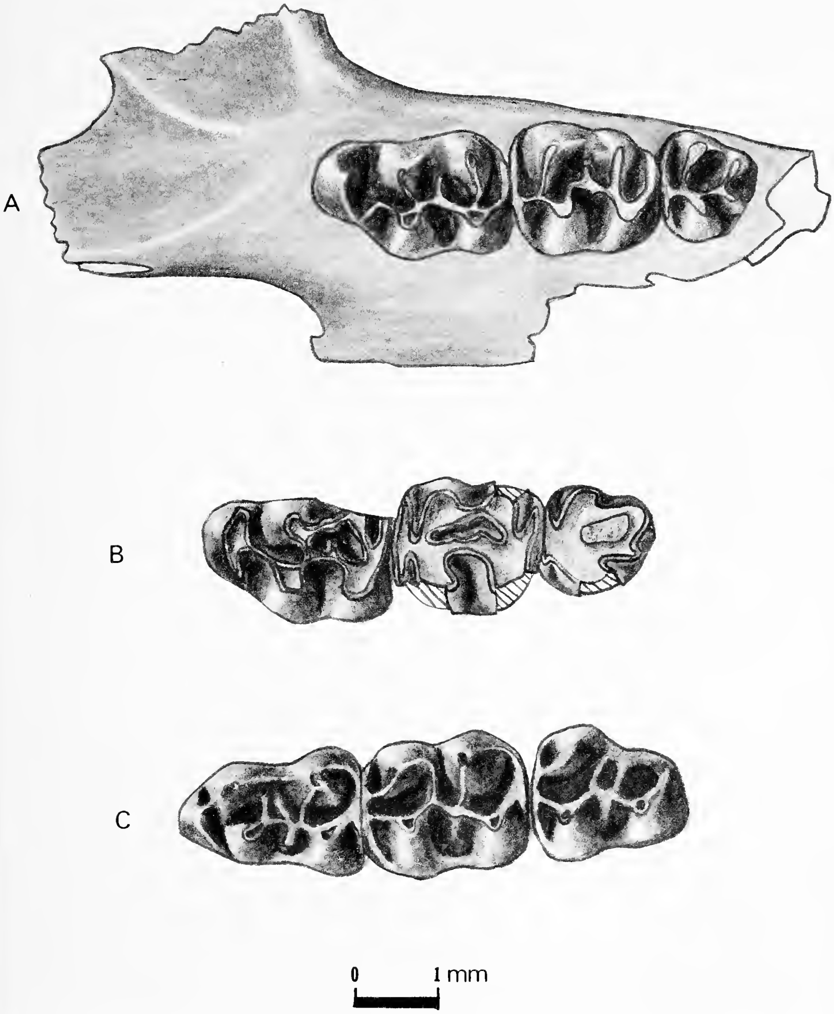

Fig. 8.—Dentition of *Scottimus ambiguus*. A, KU 8419 (holotype), LM^1–M^3; B, KU 8420, LM^1–M^3; C, KU 8421, LM_1–M_3.

8a). On KU 8420, the worn specimen (Fig. 8b), the metaloph of M^1 joins the posterior cingulum.

M^2 of *S. ambiguus* is nearly identical to that of *S. exiguus*, except that the metaloph joins the hypocone directly. In the type specimen of *S. exiguus* (AMNH 12261, Fig. 9b) the metaloph of the left M^2 clearly joins the posterior cingulum. On the right M^2 the metaloph bends anteriorly, as in the M^1 of *S. ambiguus*, just buccal to the hypocone

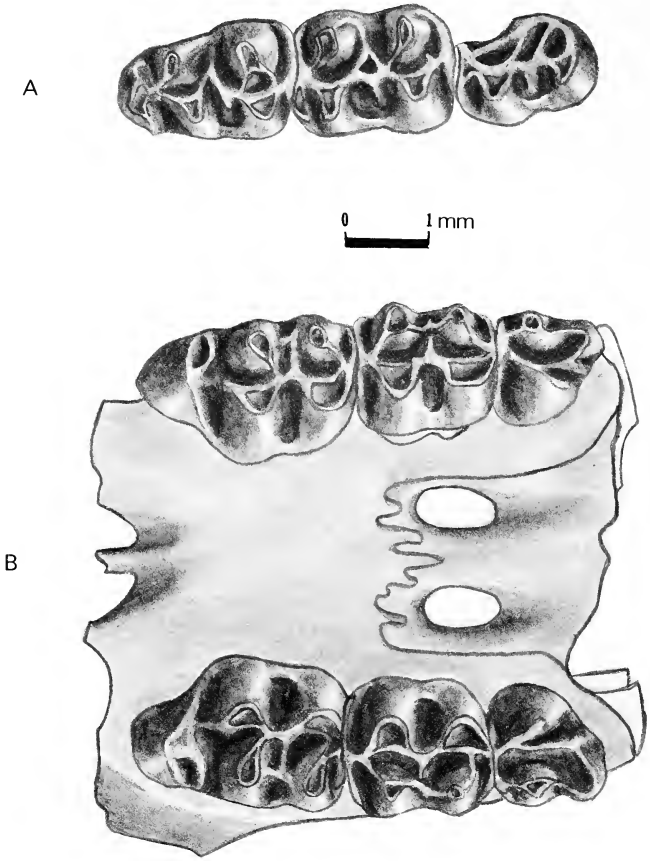

Fig. 9—Holotype of *Scottimus exiguus,* AMNH 12261. A, LM$_1$–M$_3$; B, palate with LM^1–M^3 and RM^1–M^3.

and joins it posterior to its center. It appears that after some wear, however, the metaloph on the right M^2 will merge with the posterior cingulum, as it does on the M^1 of *S. ambiguus*.

M^3 does not differ in morphology from those of other species except for the weaker development of the longitudinal lophs and smaller size relative to M^1 and M^2.

The lower molars of *S. ambiguus* more closely resemble those of *S. exiguus* than *S. viduus* (Fig. 8c) in having small but distinct buccal posterior cingulua on M$_1$–M$_2$, the hypolophid joining the mesoconid, posterior arm of the protoconid always extending to the lingual margin of the tooth on M$_3$, and having a buccal extension from the mesoconid on M$_1$–M$_3$.

The mesolophid on M$_1$–M$_2$ is minute to absent in *S. ambiguus*. In *S. exiguus,* the mesolophid is short and unites with the posterior arm of the protoconid (Fig. 9a).

On one specimen of *S. ambiguus,* KU 8426, the hypolophid on M$_1$ joins the ectolophid just posterior to the mesoconid as in *S. viduus*. All other specimens of *S. ambiguus* have the hypolophid joining the mesoconid on M$_1$.

I_1 of *S. ambiguus* is shorter (A-P) than that of *S. viduus* (Figs. 5a, b), and the minute radiating ridges are less distinct.

Discussion.—Scottimus ambiguus most closely resembles *S. exiguus* in dental morphology. The connection of the metaloph on M^2 and the position of the posterobuccal reentrant valley in the anterocone of M^1 in *S. ambiguus* are more similar to the condition in *S. viduus*. The degree of lophodonty in *S. ambiguus* is also somewhat less than that of *S. exiguus,* but slightly more than that of *S. viduus*. Martin (1980) referred the specimens assigned here to *S. ambiguus* to *Eoeumys vetus* based on size. *Eo. vetus,* however, is clearly larger than any specimens of *S. ambiguus* (Tables 3, 4; Wood, 1937:258).

Setoguchi (1978) referred an isolated M^1 (CM 32939) to *Eumys parvidens* from the Orellan Cedar Ridge fauna of Wyoming (see Korth, 1980, 1981, for age determination). This specimen is identical in morphology to *Scottimus ambiguus* but is slightly larger in size (Setoguchi, 1978: table 11). CM 32939 is here referred to *Scottimus* cf. *S. ambiguus*.

Scottimus longiquus, new species
(Fig. 10, Tables 3, 4)

Eumys exiguus Wood, 1937 (in part).
Eumys cf. *exiguus* Wood, White, 1954.
Scottimus exiguus (Wood) Wood, 1980 (in part).

Holotype.—USNM 18865, partial maxilla with LM^1–M^2.

Hypodigm.—Type and USNM 18866, partial mandible with RM_1–M_3; USNM 18867, mandible with RM_1–M_3; PU 23267a, maxilla with LM^1–M^2; PU 23267b (listed as PU 11385 by Wood, 1937:254), RM^1.

Horizon and locality.—Type and USNM specimens from the Canyon Ferry Reservoir area, locality 24LC17, "Toston beds" (Douglass, 1901), Lewis and Clark County, Montana. PU specimens from "Head of Battle Draw" (?)SW¼, T42N, R45W, Poleslide Member, Brule Formation, Shannon County, South Dakota.

Age.—Orellan (Montana) and possibly Whitneyan (South Dakota).

Etymology.—longiquus, Latin, long; in reference to the higher, longer lophs on the molars.

Diagnosis.—Large size, just slightly smaller than *S. lophatus*; molars highly lophate; M^1 with protoloph wider than metaloph, and anterocone predominantly buccally situated; posterobuccal reentrant valley on anterocone of M^1 opens bucally with a restricted opening; metaloph joins posterior cingulum on M^1–M^2; mesoconid and mesolophid minute or absent on M_1–M_3; posterior arm of protoconid short on lower molars and does not extend to the lingual margin of the tooth on M_3; minute ridges on I_1 reduced and restricted to a low central keel along the center of the anterior surface of the tooth.

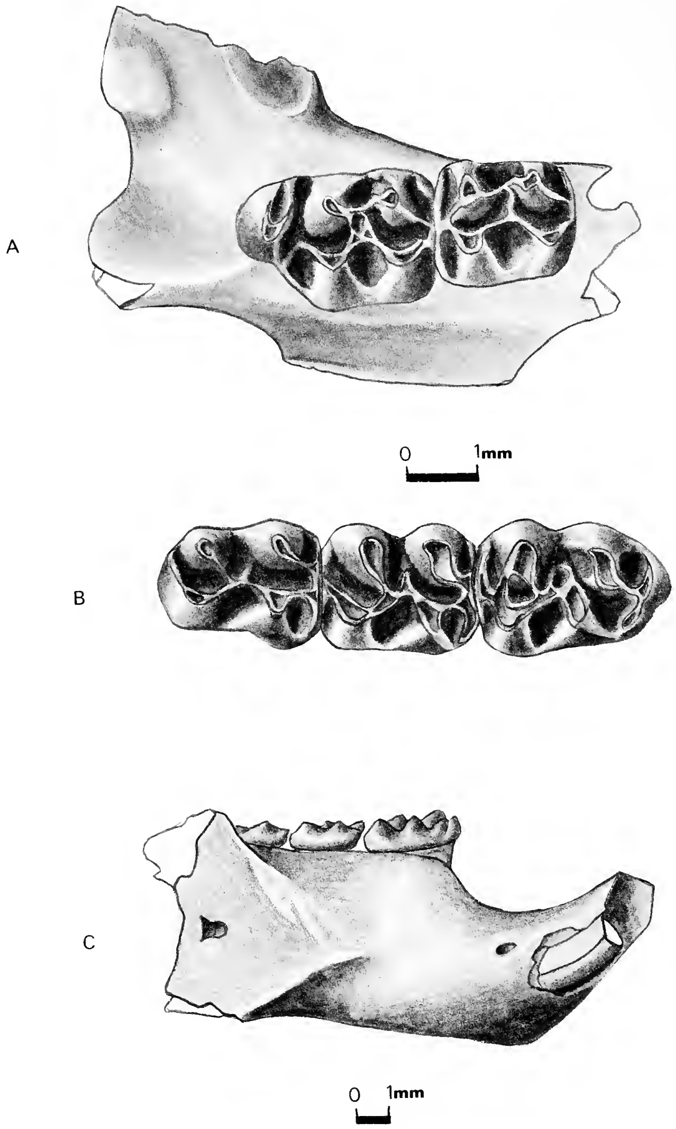

Fig. 10.—Dentition of *Scottimus longiquus*. A, USNM 18865 (holotype), LM^1–M^2; B, USNM 18867, LM$_1$–M$_3$; C, USNM 18867, lateral view of mandible.

Description.—The posterior margin of the incisive foramen is farther posterior than in other species of *Scottimus,* nearly to the level of the protocone of M^1 (Fig. 10a). The upper molars are highly lophate with well developed buccal and lingual longitudinal lophs. M^1 differs from that of *S. lophatus* only in having an anterocone less anteroposteriorly compressed and more restricted to the buccal half of the tooth. The posterobuccal reentrant valley of the anterocone is oriented buccolingually, and opens buccally through a restricted opening.

M^2 differs from that of *S. lophatus* only in the length of the mesoloph which extends bucally to the buccal longitudinal loph, and in being relatively broader (buccolingually). On both M^1 and M^2, the metaloph joins the posterior cingulum far behind the hypocone.

The lower molars of *S. longiquus* strongly resemble those of *S. lophatus* (Fig. 10b). The mesoconid and mesolophid are absent on all of the lower molars. The posterior protoconid arm on M_1–M_2 is greatly reduced. The posterior protoconid arm on M_3 fails to reach the lingual margin of the tooth, unlike that in *S. lophatus.*

The ectolophid is nearly in the center of the lower molars of *S. longiquus* as in *S. lophatus.* The lower molars of *S. longiquus,* as in the upper molars, are broader than those of *S. lophatus.* The buccal posterior cingulum on M_1–M_2 of *S. longiquus* is short, comparable to that of *S. exiguus.* An accessory loph is present on the talonid of M_1 on USNM 18867 (Fig. 10b). It runs lingually from the hypoconid toward the entoconid, bisecting the valley bounded by the posterior cingulum and hypolophid.

The lower incisor of *S. longiquus* differs from that of *S. viduus* and *S. ambiguus* in being much wider (tra) and having a low central keel that runs the entire length of the tooth. The minute radiating ridges present on I_1 of *S. viduus* and *S. ambiguus* are weakly developed on *S. longiquus,* and restricted to the surface of the central keel.

Discussion.—The development of lophs on the molars of *S. longiquus* exceeds that of the Arikareean species *S. kellarmorum* (Black, 1961). *S. longiquus* is distinguished from *S. lophatus* in the morphology of the anterocone on M^1, the length of the mesoloph on M^2, relative width of the molars, smaller size, cross-sectional shape of I_1, and shorter buccal posterior cingulum on M_1.

S. longiquus differs from the other Orellan species previously described in its larger size and greater development of lophs on the molars.

Scottimus sp.
(Fig. 11, Table 3)

Scottimus lophatus Wood, 1937 (in part).

Referred specimen.—PU 23264 (listed as PU 11385 by Wood, 1937:256 and Macdonald, 1963:200), partial maxilla with LM^2–M^3.

Horizon and locality.—"Head of Battle Draw," (?)Sw¼, T42N, R45W, Poleslide Member, Brule Formation, Shannon County, South Dakota.

Age.—Late Orellan or early Whitneyan.

Description.—M^2 of PU 23264 more nearly approaches that of *S. lophatus* in morphology than of any other species. M^2 is narrower in relation to length than all other Orellan species, and comparable in proportions to *S. lophatus* and *S. kellamorum.* The degree of lophodonty of M^2–M^3 of *Scottimus* sp. equals that of *S. lophatus.* The only

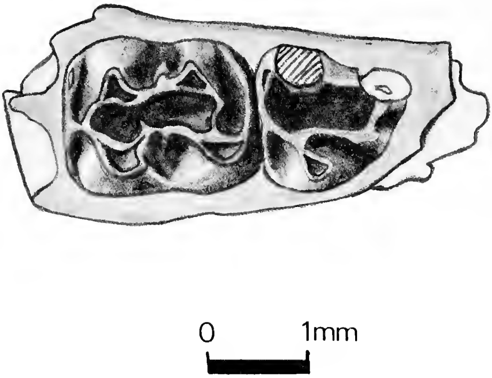

Fig. 11.—*Scottimus* sp., PU 23264, LM^2–M^3.

difference in morphology of M^2 of *Scottimus* sp. from *S. lophatus* is the connection of the metaloph to the hypocone in PU 23264 (Fig. 11). *S. kellamorum* has a similar connection, but it is much less distinct and does not have the obvious bend seen in PU 23264. The bend in the metaloph of M^2 of PU 23264 is similar to that in the right M^2 in the holotype of *S. exiguus* (Fig. 9b) and M^1 of the holotype of *S. ambiguus* (Fig. 8a). In all of these cases it appears that the metaloph will join the posterior cingulum after the tooth is moderately worn.

M^3 of PU 23264 is quite similar to that of *S. lophatus* in the height and arrangement of the lophs.

Scottimus sp. is smaller than *S. lophatus*.

Discussion.—Wood (1937:256) listed a specimen of *Scottimus lophatus* from South Dakota in his tables (listed as PU 11385), but suggested that this specimen might represent a distinct species which was intermediate between *S. lophatus* and its probable ancestor "*Eumys*" *exiguus*. PU 23264 clearly differs from *S. exiguus* in size, relative width of the upper molars, absence of a mesoloph on M^2, and degree of lophodonty. It more closely resembles *S. lophatus* in all of these features, but differs from the latter in size and connection of the metaloph to the hypocone on M^2.

PU 23264, though distinct from all other species of *Scottimus,* is too poorly known to establish a new species. If *Scottimus* sp. is accepted as a distinct species, there are three species of *Scottimus* known from the "Head of Battle Draw," South Dakota. This is unusual because no more than one species of *Scottimus* is known from any other locality. The other two species present at "Head of Battle Draw," *S. longiquus* and *S. viduus,* are readily separable from PU 23264, and are otherwise only known from Orellan deposits in Montana and Nebraska (also Chadronian of Wyoming), respectively. All of the specimens from "Head of the Battle Draw" were collected in 1893 by J. B. Hatcher for Princeton University. In his original field notes, Hatcher described this locality as "Upper *Oreodon* beds, White River, Miocene" (D. Baird, personal communication). In the Big Badlands area of South Dakota, however, there is no "Battle Draw," though there is a Battle Creek Draw. This appears to be the location Hatcher intended in his original field notes.

Both Wanless (1923) and Clark et al. (1967) have mapped this area. The head of Battle Creek Draw is just to the north of Cuny Table, SW¼, T42N, R45W, Shannon County. Wanless (1923: Pl. 1, fig. 1 and text fig. 5) provided a photograph and stratigraphic section of this area. He recognized two lithologic units in this area—the "Upper *Oreodon* beds" below, and the "*Leptauchenia* beds" above. Clark et al. (1967: fig. 52) also provided a measured section from the area near Battle Creek Draw. They recognized Wanless' "Upper *Oreodon*" and "*Leptauchenia*" beds in this area as being equivalent to the Poleslide Member of the Brule Formation which contains Orellan (lower) as well as Whitneyan (upper) faunas (see Harksen, 1969). It is not unlikely that Hatcher's collection was made over the entire area and Orellan and Whitneyan faunas were mixed. Therefore, the three species recognized from "Head of Battle Draw" cannot be definitely assigned to an Orellan or Whitneyan age in this area.

Macdonald (1963) reported two isolated M^2s from the Arikareean Sharps Formation of South Dakota, which he referred to *Scottimus* sp. These two specimens are near the size of *Scottimus* sp. described above, but are wider than PU 23264 (Macdonald, 1963: 200) and may not be assigned to the same species. The two Sharps specimens may well represent a distinct Arikareean species of *Scottimus* but more material is needed to determine their specific allocation.

Species of Scottimus

In all, seven species of *Scottimus* are recognized here. One species, *S. viduus,* appears in the Chadronian and persists into the Orellan. Hough and Alf (1956) reported specimens of "*Eumys*" *exiguus* from Chadronian ant hills in Nebraska. However, Guthrie and Allen (1974) have shown that these ant hills contained predominately Orellan species and that this occurrence of Orellan forms should not be considered as Chadronian.

During the Orellan, *Scottimus* attained its greatest diversity, as does *Eumys*. Besides *S. viduus* from Nebraska and South Dakota, four species of *Scottimus* are known from the Orellan—*S. ambiguus* from Colorado, *S. exiguus* from South Dakota, *S. longiquus* from Montana and South Dakota, and *Scottimus* sp. also from South Dakota. Any one, or all, of the species present at the "Head of Battle Draw" (*S. viduus, S. longiquus, Scottimus* sp.) may also be from the Whitneyan.

Wood (1937, 1980) cited *S. lophatus* from the Orellan of Nebraska. However, the only known specimens of *S. lophatus* from Nebraska (MCZ 5067, UNSM 66168, UNSM 66167—listed as UN 8-4-8-33-SP by Wood, 1937:255) are from the Whitney Member of the Brule Formation (Martin, 1980). *S. lophatus* is the only species of the genus definitely known from the Whitneyan.

Scottimus kellamorum and the two Sharps specimens (not referable to *S. kellamorum*) are the only Arikareean representatives of the genus.

Martin (1980) considered that *Eoeumys* represented the basal stock from which all later Oligocene and early Miocene cricetids were derived. The specimens of *Scottimus* that he included in *Eoeumys* were already too specialized to be considered as ancestors of later cricetids. However, *Eoeumys,* if restricted to the holotype, may represent the basal eumyine if Martin is correct in assuming the presence of parasagital crests as primitive for cricetids.

Cricetid genus and species indeterminate
(Fig. 12)

Referred specimen.—CM 2290, right mandible with I_1, M_2.

Horizon and locality.—?White River Formation, White Butte, Billings County, North Dakota.

Age.—Orellan (early middle Oligocene).

Description.—The mandible of CM 2290 is deep and heavy (Fig. 12b). The masseteric fossa is bounded by a heavy ridge originating from the posteroventral margin of the mandible, and a less well developed ridge originating from the anterior edge of the ascending ramus. These two ridges unite anteriorly below M_1. The diastema is shallow and relatively short. The mental foramen lies at mid-depth of the mandible below the center of the diastema. A broad, deep valley separates the tooth row from the ascending ramus.

The lower incisor is broad, rounded anteriorly, and asulcate, with enamel extending slightly onto the medial and lateral sides of the tooth.

From the alveolae present, the molars increase in size from M_1 to M_3. M_2 is lophate and rectangular in outline (Fig. 12a). The anterior cingulum extends nearly the entire width of the tooth, but is more pronounced buccally. It is joined at its center by the anterior arm of the protoconid and the metalophid. Posterior to the metaconid is a distinct mesostylid. It is an elongate convex cusp which bends toward the center of the tooth and blocks the anterior ¾ of the valley between the metaconid and entoconid. The posterior arm of the protoconid runs obliquely across the tooth to the entoconid. There is no sign of an ectolophid. On the posterior arm of the protoconid, midway to the entoconid, are two short "spurs" eminating from it. The shortest projects lingually into the valley between the metaconid and entoconid. The longer spur extends buccally into the valley between the protoconid and hypoconid, about halfway to the buccal margin of the tooth.

The posterior cingulum is broad and arises as the posterior arm of the hypoconid. A deep wide valley separates the posterior cingulum from the entoconid.

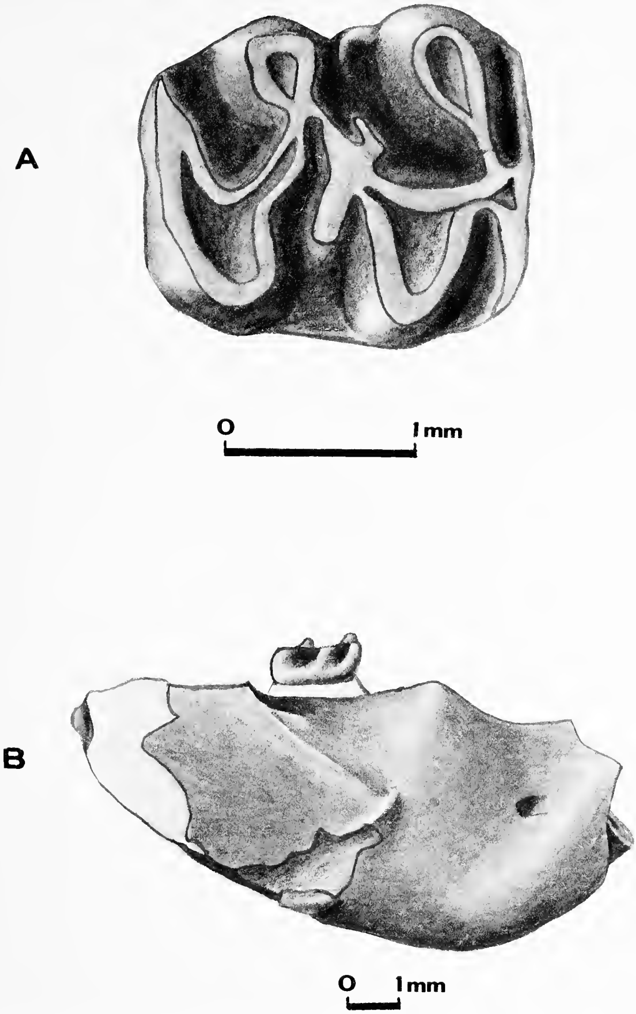

Fig. 12.—Cricetid genus indeterminate, CM 2290. A, occlusal view of RM_2; B, lateral view of mandible.

Discussion.—CM 2290 closely resembles *Eumys elegans* in size and morphology of the mandible and lower incisor. The only difference in the mandible of *Eumys* and CM 2290 is the breadth of the valley separating the tooth row from the ascending ramus. In CM 2290, this valley is no deeper than in *Eumys elegans*, but is much wider.

The most striking difference from *Eumys* in the occlusal pattern of M_2 of CM 2290 is the lack of an ectolophid and the posterior arm of the protoconid joining the entoconid. The posterior arm of the protoconid joins the entoconid in one species *Eumys, E. obliquidens* Wood (1937), later considered a variation of *E. elegans* (Galbreath, 1953). However, all specimens with this connection in *E. "obliquidens,"* maintain an ectolophid.

The valley between the posterior cingulum and entoconid of CM 2290 is wider than that in *Eumys*. The mesostylid in CM 2290 differs from that in *Eumys*. In large populations of *E. elegans,* several specimens may have mesostylids, but they are minute, round cuspules, unlike the mesostylid in CM 2290. The buccal spur on the posterior arm of the protoconid in CM 2290 also differs from that of *Eumys. E. elegans* has a strong mesoconid but there is no buccal extension of this cusp. A lingual spur is present but smaller on some specimens of *E. brachyodus*.

Any one of these differences between CM 2290 and *Eumys* could well be considered only a minor variation in a population. However, the combination of all of these differences makes this possibility very unlikely.

The ectolophid on M_2 of *Wilsoneumys planidens* runs obliquely across the tooth, in some cases, and joins the hypolophid buccal to the entoconid. On some specimens a minute lingual and buccal spur are present on the ectolophid (Wilson, 1949*a*; Galbreath, 1953; Setoguchi, 1978; Martin, 1980). This arrangement somewhat resembles that of CM 2290. However, CM 2290 is less lophate than *Wilsoneumys* and differs in a number of other features of M_2. No other North American Oligocene cricetid has the unique morphology of the posterior arm of the protoconid of M_2 of CM 2290.

Two late Oligocene genera from central Asia, *Aralomys* and *Eumysodon* Argyropulo (1939) share many similarities with CM 2290. In both Asian genera, the posterior arm of the protoconid joins the entoconid on M_2. In *Aralomys,* it is directly connected and in *Eumysodon* a short hypolophid joins the posterior arm of the protoconid just buccal to the entoconid.

The valley separating the entoconid and posterior cingulum is wider in CM 2290 than in either Asian genus. Some specimens of *Eumysodon* have a lingual spur on the posterior arm of the protoconid (Argyropulo, 1939: fig. 1). Neither *Aralomys* nor *Eumysodon* have a buccal spur on the posterior arm of the protoconid of M_2. The relative sizes of the molars in *Aralomys* and *Eumysodon* do not increase from M_1–M_3 as in CM 2290.

CM 2290 appears to represent a distinct cricetid. It is still possible, but unlikely, that it may represent a variation of *Eumys elegans*. Specimens showing intermediate stages must be found in order to establish this. In overall appearance of the M_2, CM 2290 most closely resembles *Aralomys* and *Eumysodon* from Asia, but is clearly distinct from both.

Measurements of M_2 of CM 2290 are as follows: A-P, 2.04 mm; tra, 1.70 mm; trp, 1.58 mm. Measurements of I_1 are as follows: A-P, 1.83 mm; tra, 1.44 mm.

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RESULTS OF THE ALCOA FOUNDATION-SURINAME EXPEDITIONS. V. NOTEWORTHY RECORDS OF SURINAMESE MAMMALS

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Abstract

The occurrence of seven species of mammals previously unknown in Suriname is documented. The new taxa recorded include *Didelphis albiventris, Peropteryx macrotis, Lonchorhina aurita, Micronycteris hirsuta, Vampyrodes caraccioli, Furipterus horrens,* and *Thyroptera discifera*. Additional information is provided on several species already known to occur in Suriname, including *Metachirus nudicaudatus, Peronymus leucopterus, Mimon bennettii, Tonatia carrikeri, T. schulzi, Anoura geoffroyi, Choerniscus intermedius, Mesophylla macconnelli, Neacomys guianae, Holochilus brasiliensis,* and *Potos flavus*.

Introduction

Recent field work in Suriname has resulted in collection of specimens of 18 species of mammals that were unknown previously from there or known only by a few specimens. Records of two species of

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marsupials are included, one of which was not previously recorded, bringing the number of marsupials known from the country to 11. We have significant new records of two rodents and one carnivore, but none of these represents species new to the fauna.

Currently, 86 species of bats are known to occur in Suriname (Husson, 1978; Genoways and Williams, 1979, 1980; Williams and Genoways, 1980*a*, 1980*b*). Six species are herein reported for the first time from the country. Significant new information also is provided for seven previously recorded species of bats. The number of species of Chiroptera now known to occur in Suriname is 92.

METHODS AND MATERIALS

All specimens collected were prepared as standard museum skins accompanied by skulls, or were preserved in fluid. Supplemental data recorded for most of these specimens included standard karyotypes, live tissue for chromosomal banding, and frozen tissue for electrophoretic analysis. The specimens are deposited in the Section of Mammals of Carnegie Museum of Natural History and a synoptic series will be returned to Suriname in care of Stichting Natuurbehoud Suriname (STINASU) for deposition in their reference collection.

Forearm and cranial dimensions were taken by means of dial calipers accurate to 0.1 mm. External measurements, recorded in millimeters, are those of the collector and were taken in the field. Forearm and cranial measurements were taken as described by Genoways and Williams (1979).

Field weights in grams were taken with Pesola spring scales. The reproductive condition of standard museum specimens was determined by gross dissection in the field, whereas fluid-preserved specimens were dissected in the laboratory. Crown-rump length of fetuses and testes length of males are recorded in millimeters.

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SPECIES ACCOUNTS

Didelphis albiventris Lund

Specimen examined (1).—BROKOPONDO: Brownsberg Nature Park, 3 km S, 20 km W Afobakka, 4°58′N, 55°10′W, 1.

The geographic distribution of *Didelphis albiventris* in South America is shaped like a large "U" (Hershkovitz, 1969). An arm of the range extends along the Andes from western Venezuela (Handley, 1976) and Colombia southward and eastward into the northern half of Argentina and then northward into the eastern half of Brazil. In north-central South America, Hershkovitz (1969) reports this species from one area of Brazil and three in southern Venezuela. In this area, the species evidently is confined to isolated "tepuis" or eroded tablelands of the pre-Cambrian Guianan shield. Hershkovitz (1969) pointed out that mammalian fauna of Guianan Highlands consists only of wide ranging species with two exceptions, *Didelphis albiventris* and *Podoxomys roraimae*. Therefore, obtaining a specimen of *D. albiventris* on the Brownsberg Plateau is of considerable interest and indicates that, even though this area is not a "tepui," it does possess one of the unique species of the Guianan faunal complex.

Our specimen is a subadult male (age class 3 of Gardner, 1973) trapped on the night of 7 July 1977. It was taken in a trap set on the ground in an area of mature rainforest. There was little ground cover in the area. Other species of mammals taken in the area were *Monodelphis brevicaudata, Oryzomys capito,* and *Proechimys guyannensis*. Testes of the specimen were 21 long.

Hershkovitz (1969) gave the reasons for the use of the name *D. albiventris* in place of *D. azarae,* which was used previously for this species. *D. albiventris* currently is considered to be monotypic. External and cranial measurements of our specimen are as follows: total length, 690; length of tail, 268; length of hind foot, 53; length of ear, 56; greatest length of skull, 79.8; condylobasal length, 79.0; zygomatic breadth, 41.0; mastoid breadth, 23.7; postorbital breadth, 10.1; length of maxillary toothrow (C-M3), 31.1; breadth across upper molars, 26.8. The specimen weighed 564.

Metachirus nudicaudatus nudicaudatus (É. Geoffroy-St. Hilaire)

Specimen examined (1).—SURINAME: Powaka, 5°26′N, 55°04′W, 1.

As pointed out by Husson (1978), it is difficult to assess early records of this opossum from Suriname because it often was confused with *Philander opossum*. Husson (1978) was able to verify only three specimens from the country. One of these was taken near Republiek and the other two near Zanderij. The specimen listed above is from this same part of the country.

Our specimen is an adult male (length of testes, 9) that was trapped on 9 August 1977. It was taken in a swampy area adjacent to a small stream in a trap that was placed on the branch of a fallen tree about 2 m above the ground. The vegetation in the area was secondary gallery forest. Other marsupials obtained here were *Didelphis marsupialis* and *Philander opossum*. A specimen of *P. opossum* was taken in a trap set within 10 m of the one in which our *M. nudicaudatus* was taken.

The type locality of *M. n. nudicaudatus* is Cayenne, French Guiana; therefore, we assign our specimen to that subspecies. External and cranial measurements of our specimen are as follows: total length, 602; length of tail, 336; length of hind foot, 47; length of ear, 38; greatest length of skull, 58.3; condylobasal length, 57.8; zygomatic breadth, 28.7; mastoid breadth, 17.5; postorbital breadth, 9.7; length of maxillary toothrow (C-M3), 24.1; breadth across upper molars, 17.5. The specimen weighed 410.

Peronymus leucopterus leucopterus (Peters)

Specimen examined (1).—PARA: Zanderij, 5°27′N, 55°12′W, 1.

The only specimens of this species previously recorded from Suriname were the type series, which probably came from near Albina (Husson, 1978). The one here reported is from about 130 km west of Albina.

Our specimen is an adult male in which the testes measured 3 when obtained on 18 May 1980. This individual was taken in a mist net set in an area of tall secondary forest with some areas being cleared beneath the canopy. Uncleared areas had moderately dense stands of undergrowth. The net was placed across a relatively wide (4 m) trail near a dry culvert. Other species of bats taken in the same area included *Cormura brevirostris, Saccopteryx leptura, Phyllostomus discolor, P. elongatus, Tonatia silvicola, Trachops cirrhosus, Artibeus* sp., and *Eptesicus brasiliensis*.

Measurements of our specimen are as follows: length of forearm, 41.2; greatest length of skull, 15.1; condylobasal length, 13.8; zygomatic breadth, 9.6; mastoid breadth, 7.7; postorbital breadth, 3.3; length of maxillary toothrow, 5.9; breadth across upper molars, 6.8.

Peropteryx macrotis macrotis (Wagner)

Specimens examined (10).—SARAMACCA: Voltzberg, 4°40′N, 56°12′W, 10.

Although this species is known from most of the northern half of South America (Sanborn, 1937), it has not been reported previously from Suriname (Husson, 1978). We found this bat to be abundant in small caves and crevices along the steep slope of the Voltzberg. Some individuals were seen during the day roosting near the entrances to the caves where it was not necessary to use headlamps to see them. Other *P. macrotis* also were located deep in caves where there was little light. Some individuals were captured during the day with nets set inside the caves. Nets set at night at the entrances to the caves and crevices captured additional specimens.

Of the 10 specimens that we collected on the nights of 11 to 13 May 1980, six were males and four were females. Recorded testes lengths for males are 3, 3, 3, and 4. A female taken on the night of 12 May was carrying a single fetus that measured 18 in crown-rump length. The other three females evinced no gross reproductive activity.

The measurements of our specimens agree with those given by Sanborn (1937) for this subspecies. *P. macrotis* is distinctly smaller than *P. kappleri* which was recorded previously from Suriname by Husson (1978). Both Husson and Sanborn discussed other characteristics of these species. External and cranial measurements for three males and one female, respectively, are as follows: length of forearm, 40.2, 44.2, 42.8, 45.9; greatest length of skull, 13.9, 14.5, 14.4, 14.9; condylobasal length, 12.2, 13.1, 12.9, 13.3; zygomatic breadth, 7.9, 8.4, 8.2, 8.5; mastoid breadth, 7.2, 7.4, 7.2, 7.3; postorbital breadth, 2.6, 2.7, 2.6, 2.6; length of maxillary toothrow, 5.3, 5.8, 5.7, 5.9; breadth across upper molars, 5.9, 6.0, 6.1, 6.4.

Lonchorhina aurita aurita Tomes

Specimens examined (3).—NICKERIE: Avanavero, 4°52′N, 57°21′W, 3.

These three specimens represent the first record of this unique species from Suriname. The species was known previously from Colombia, Venezuela, Trinidad, and Brazil in northern South America (Cunha Vieira, 1942; Goodwin and Greenhall, 1961; Handley, 1976; Hernández and Cadena, 1978; Jones and Carter, 1976; Linares and Ojasti, 1971).

The three specimens are adult females. One, taken on 26 May 1980, was pregnant with a fetus that measured 18 in crown-rump length. The other two females, taken on 24 May, evinced no gross reproductive activity. Nets in which these individuals were taken were set across a path through old secondary tropical forest. Other bats taken at this place were *Cormura brevirostris, Pteronotus parnellii, Micronycteris minuta, M. nicefori, Glossophaga soricina, Lonchophylla thomasi, Carollia perspicillata, Artibeus* sp., *Sturnira lilium, Uroderma bilobatum, Vampyrops helleri,* and *Vampyrodes carraccioli.*

Hernández and Cadena (1978) recognized two subspecies of *L. aurita* in South America, of which *L. a. aurita* is the one found in the northeastern part of the continent. External and cranial measurements of two of these specimens are as follows: length of forearm, 54.5, 53.9; greatest length of skull, 22.3, 22.7; condylobasal length, 20.5, 20.7; zygomatic breadth, 11.4, 11.6; mastoid breadth, 11.2, 11.5; postorbital breadth, 5.0, 5.3; length of the maxillary toothrow, 7.6, 7.5; breadth across upper molars, 7.8, 7.8.

Micronycteris hirsuta (Peters)

Specimens examined (3).—NICKERIE: Kabalebo, 4°51′N, 57°24′W, 1. PARA: Zanderij, 5°27′N, 55°12′W, 2.

These are the first specimens of the species to be reported from Suriname. Our records are about 200 km and 350 km, respectively, east and probably slightly south of the nearest record, which is in Guyana (Hill, 1964). Elsewhere in South America, this species is known from Venezuela, Trinidad, and Colombia (Handley, 1976; Goodwin and Greenhall, 1961; Jones and Carter, 1978).

The specimen from Kabalebo is an adult female that revealed no gross reproductive activity. It was taken on the night of 30 May 1980 along the edge of a small hill in an area of mixed secondary and primary lowland rainforest. The following species of bats were taken from that area: *Saccopteryx leptura, Pteronotus parnellii, Phyllostomus elongatus, P. hastatus, Tonatia silvicola, Trachops cirrhosus, Carollia perspicillata, Artibeus* sp., *Uroderma bilobatum*, and *Vampyrops helleri*. The specimens from Zanderij were taken on 18 May. One is an adult female that evinced no reproductive activity; the other is an immature female with unfused phalangeal epiphyses. The vegetation in the vicinity of Zanderij was secondary lowland rainforest. The area in which the specimens were taken was bisected with small secondary roads; much of the undergrowth had been cleared for planting rubber trees. Numerous species and individuals of bats were taken in this area, including *Cormura brevirostris, Saccopteryx bilineata, Phyllostomus discolor, P. elongatus, P. hastatus, Tonatia carrikeri, Lonchophylla thomasi, Carollia perspicillata, Rhinophylla pumilio, Artibeus* sp., *Chiroderma trinitatum, Mesophylla macconnelli, Sturnira lilium, Desmodus rotundus, Eptesicus brasiliensis, Myotis nigricans, Molossus ater*, and *M. molossus*.

Micronycteris hirsuta is considered to be a monotypic species. However, Baker et al. (1973) demonstrated that Central American and Trinidadian representatives differed chromosomally. Our specimens have a karyotype like those from Central America (Baker et al., 1981). External and cranial measurements of the adult female from Zanderij are as follows: length of forearm, 44.4; greatest length of skull, 23.6; condylobasal length, 20.4; zygomatic breadth, 11.2; mastoid breadth, 10.2; postorbital breadth, 4.9; length of maxillary toothrow, 8.9; breadth across upper molars, 7.1.

Mimon bennettii (Gray)

Specimens examined (5).—SARAMACCA: Voltzberg, 4°40′N, 56°12′W, 5.

According to Husson (1978), *Mimon bennettii* is known from Suriname by three specimens all lacking exact provenance.

Of our specimens, three were adult females that appeared to be reproductively inactive and two were adult males. Testes of the males measured 4 and 6. All specimens were taken along the northwestern side of the Voltzberg monolith on 12 May 1980. In this area huge boulders of granite formed numerous caves and crevices. These were intermixed along the steep slopes with relatively low primary rainforest. The first specimen obtained was knocked from the wall of a small crevice by throwing a small stone at the bat. The remaining four were taken in mist nets at the mouths of small caves as they emerged from their daytime roosts or in nets set among the boulders. Three of the four specimens preserved as standard museum specimens evinced molt over much of the dorsum.

Some recent authors have considered *M. bennettii* to be conspecific with *M. cozumelae* of Middle America (Schaldach, 1965; Jones, 1966; Goodwin, 1969). However, we have chosen to consider the two as distinct species (see also Husson, 1978; Jones and Carter, 1976), because no intergradation has been shown and because there are karyotypic differences between them (Baker et al., 1981). As presently understood, *M. bennettii* is known only from Brazil (Dalquest, 1957; Handley, 1960), Guyana (Hill, 1964), and Suriname. External and cranial measurements of one male and three females, respectively, are as follows: length of forearm, 53.5, 54.6, 54.0, 52.4; greatest length of skull, 25.9, 25.9, 25.7, 25.9; condylobasal length, 22.3, 22.3, 21.7, 22.5; zygomatic breadth, 14.2, —, 13.7, 14.0; mastoid breadth, 11.6, 11.7, 11.1, 11.8; postorbital breadth, 4.7, 4.6, 4.7, 4.5; length of maxillary toothrow, 9.2, 9.1, 8.9, 9.1; breadth across upper molars, 9.6, 9.4, 9.3, 9.2.

Tonatia carrikeri (J. A. Allen)

Specimen examined (1).—PARA: Zanderij, 5°27′N, 55°12′W, 1.

Our specimen is evidently the third record of this rare species to be reported from Suriname. Husson (1978) examined one specimen without precise locality data; Williams and Genoways (1980*a*) took one at Voltzberg.

The new specimen is an adult female that was lactating when obtained on 18 May 1980. It was taken in a mist net set across a road in a rubber plantation. Vegetation in the area was secondary forest as described in the account for *Micronycteris hirsuta*.

Tonatia carrikeri is considered to be monotypic. External and cranial measurements of our specimen are as follows: length of forearm, 46.3; greatest length of skull, 25.8; condylobasal length, 20.6; zygomatic breadth, 11.6; mastoid breadth, 11.9; postorbital constriction, 13.7; length of maxillary toothrow, 8.2; breadth across upper molars, 8.0.

Tonatia schulzi Genoways and Williams

Specimens examined (2).—NICKERIE: Kayserberg Airstrip, 3°06′N, 56°29′W, 1. SARAMACCA: Raleigh Falls, 4°44′N, 56°12′W, 1.

These individuals represent the third and fourth known specimens of this recently described species (Genoways and Williams, 1980). They extend the known range about 100 km to the north and 85 km to the south-southeast from the type locality.

The specimen from Raleigh Falls was an adult male with testes measuring 7 when taken on 10 May 1980. It was taken on an island in the Coppename River that serves as the headquarters for the Raleigh Falls Nature Reserve. Mist nets were placed across a trail leading along the western side of the island. The local vegetation consisted of near-mature tropical forest with only a little understory. Other species of bats taken in this series of nets were *Saccopteryx bilineata, S. leptura, Pteronotus parnellii, Chrotopterus auritus, Phyllostomus elongatus, Tonatia silvicola, Lonchophylla thomasi, Carollia perspicillata, Rhinophylla pumilio, Artibeus* sp., *Sturnira tildae,* and *Myotis nigricans.* The specimen from the vicinity of the Kayserberg Airstrip was a male (preserved in fluid) taken on 6 May 1980. It was captured in a mist net set across a trail in an area of mature lowland rainforest. Other bats taken on this date include *Saccopteryx leptura, Pteronotus parnellii, Phyllostomus elongatus, P. hastatus, Carollia perspicillata, Artibeus* sp., and *Eptesicus brasiliensis.*

Length of forearm for the specimens as listed above are 42.7 and 44.0. Cranial measurements for the specimen from Raleigh Falls are as follows: greatest length of skull, 23.4; condylobasal length, 18.9; zygomatic breadth, 11.3; mastoid breadth, 12.1; postorbital breadth, 3.8; length of maxillary toothrow, 7.8; breadth across upper molars, 7.3. The size and other characteristics of these newly acquired specimens closely agree with those of the holotype and paratype. The unique wart-like granulations characteristic of this species are evident on the forearms, digits, hind limbs, ears, and noseleaf of the new specimens.

Anoura geoffroyi geoffroyi Gray

Specimens examined (9).—SARAMACCA: Voltzberg, 4°44′N, 56°12′W, 9.

Husson (1978) only reported specimens of *Anoura geoffroyi* from the vicinity of Tafelberg in central Suriname. Our specimens are from approximately 90 km north of that locality.

We found *A. geoffroyi* to be relatively abundant in the caves and crevices along the northwestern slope of the Voltzberg (see account for *Mimon bennettii*). Our specimens were taken during the daytime of 12 May 1980 by setting mist nets inside some of the larger caves and driving the bats from their roosts. The only other two species of bats taken, *Pteronotus parnellii* and *Carollia perspicillata,* proved to be more abundant than *A. geoffroyi.* All of the specimens were adult males. Testes length for one specimen measured 6, for five measured 7, and for two measured 8.

Choeroniscus intermedius (J. A. Allen and Chapman)

Specimen examined (1).—PARA: Zanderij, 5°27′N, 55°12′W, 1.

This is the second locality record from Suriname for this species. It was first reported by Williams and Genoways (1980*a*) from Grassalco, approximately 190 km southwest of the new locality.

The present specimen is an adult female that showed no gross reproductive activity when taken on 20 May 1980. The specimen was collected in savannah bordering a forested area. Nets were placed in open grassland and near savannah shrubbery. Other bat species collected in the same area included *Saccopterx bilineata, S. leptura, Chiroderma villosum, Rhinophylla pumilio, Artibeus* sp., *Sturnira lilium, S. tildae, Eptesicus brasiliensis, Myotis nigricans,* and *Molossus molossus.*

There is considerable confusion surrounding the systematics of members of this genus. However, until more data are available, we follow Koopman (1978) in recognizing two species in the *minor-inca-intermedius* complex. The measurements of our specimen match those of the smaller species to which the name *intermedius* is applicable. External and cranial measurements of the present specimen are as follows: length of forearm, 34.6; greatest length of skull, 22.9; condylobasal length, 22.2; mastoid breadth, 8.3; postorbital breadth, 3.6; length of maxillary toothrow, 7.7; breadth across upper molars, 4.2.

Mesophylla macconnelli macconnelli Thomas

Specimen examined (1).—PARA: Zanderij, 5°27′N, 55°12′W, 1.

Our specimen is the third of *Mesophylla macconnelli* to be recorded from Suriname. Williams and Genoways (1980*a*) reported single specimens from the extreme northern (Nieuwe Grond Plantation) and the extreme southern (Sipaliwini Airstrip) parts of the country. The present specimen is from about 50 km to the south of the northernmost locality. It is a nonpregnant adult female that was taken on 18 May 1980. Conditions under which this specimen was taken are described in the account for *Micronycteris hirsuta.*

Two subspecies of *M. macconnelli* currently are recognized. All mainland specimens are assigned to the nominate race with the type locality in Guyana. External and cranial measurements of our specimen are as follows: length of forearm, 30.7; greatest length of skull, 17.4; condylobasal length, 15.7; zygomatic breadth, 10.0; mastoid breadth, 9.1; postorbital breadth, 4.4; length of maxillary toothrow, 5.8; breadth across upper molars, 7.1.

Vampyrodes caraccioli caraccioli (Thomas)

Specimens examined (2).—NICKERIE: Avanavero, 4°52′N, 57°21′W, 1. SARAMACCA: Raleigh Falls, 4°44′N, 56°12′W, 1.

These specimens represent the first recorded occurrence of *V. caraccioli* in Suriname. This species, which originally was described from Trinidad, is found elsewhere in northern South America (Jones and Carter, 1976) and as far south as northern Brazil and eastern Peru.

The specimen from Raleigh Falls is a nonpregnant female obtained with our specimen of *Thyroptera discifera* on 14 May 1980. The individual from Avanavero is an immature male with the phalangeal epiphyses still unfused. The pelage of this specimen is much grayer and darker than the pale brown of the adult. Length of testes of the immature specimen was 3. See the account of *Lonchorhina aurita* for the conditions under which this specimen was taken.

Length of forearm of the immature male from Avanavero is 54.3. External and cranial measurements of the female from Raleigh Falls are as follows: length of forearm, 56.5; greatest length of skull, 28.3; condylobasal length, 24.5; zygomatic breadth, 17.1; mastoid breadth, 13.2; postorbital breadth, 6.6; length of maxillary toothrow, 9.8; breadth across upper molars, 12.8.

V. caraccioli and *V. major* are considered by recent authors to be conspecific (Handley, 1966; Jones and Carter, 1976). We have followed this action and have assigned our specimens to the nominate subspecies on geographic grounds. Their measurements are much larger, however, than those given by Swanepoel and Genoways (1979) for specimens from Trinidad (type locality of *caraccioli*) and more nearly approach those from Central American specimens. Clearly, geographic variation in this species is in need of review.

We follow Carter and Dolan (1978) for the spelling of the specific name *caraccioli*.

Furipterus horrens (Cuvier)

Specimen examined (1).—SARAMACCA: Voltzberg, 4°40′N, 56°12′W, 1.

Only three specimens of this rare species have been reported previously from Suriname. One of the records is from near Kaaimanston (Sanborn, 1941), another from Ligolio (Husson, 1978), and the precise locality of the third record is unknown (Husson, 1978).

Our specimen is an adult female that evinced no gross reproductive activity when taken on 12 May 1980. The bat was obtained in the same area in which we caught *Mimon bennettii*. It was trapped in a net placed across the entrance of a small cave and crevice where our first specimen of *M. bennettii* was obtained. The bat was taken on the cave side of the net; a light rain was falling when the specimen was caught.

This species is considered to be monotypic. External and cranial measurements of our specimen are as follows: length of forearm, 35.8; greatest length of skull, 11.9; condylobasal length, 11.0; zygomatic breadth, 7.2; mastoid breadth, 6.3; postorbital breadth, 2.9; length of maxillary toothrow, 4.5; breadth across upper molars, 4.5.

Thyroptera discifera discifera (Lichtenstein and Peters)

Specimen examined (1).—SARAMACCA: Raleigh Falls, 4°44′N, 56°12′W, 1.

A male *Thyroptera discifera* taken on the night of 14 May 1980 is the first specimen of this species to be recorded from Suriname. The species is known from French Guiana (Thomas, 1928) and elsewhere in northern South America (Wilson, 1976, 1978). The other member of this genus and family, *T. tricolor,* has been recorded from Suriname previously (Husson, 1978; Honeycutt et al., 1980).

This male had testes that were 2 in length and was netted in the same area as *T. schulzi* (collected 10 May), near the headquarters of Raleigh Falls Nature Reserve. Other species of bats taken on the same night as our specimen of *T. discifera* were as follows: *Tonatia silvicola, Trachops cirrhosus, Carollia perspicillata, Rhinophylla pumilio, Artibeus* sp., and *Vampyrodes caraccioli.*

Wilson (1976) recognized two subspecies of *T. discifera* with only the nominate race occurring in South America. Husson (1978) gives characteristics to distinguish *T. discifera* and *T. tricolor.* External and cranial measurements of our specimen are as follows: length of forearm, 32.4; greatest length of skull, 14.2; condylobasal length, 13.1; zygomatic breadth, 6.8; mastoid breadth, 6.7; postorbital breadth, 2.4; length of maxillary toothrow, 5.5; breadth across upper molars, 4.6.

Holochilus brasiliensis guianae Thomas

Specimens examined (5).—NICKERIE: Sipaliwini Airstrip, 2°02′N, 56°07′W, 5.

Husson (1978) believed that this species occurred only along the coastal plain of Suriname. However, on 19 and 20 August 1979, we took this species in the extreme southern part of the country, far from the coastal plain. Our specimens were taken in a ditch along the edge of the airstrip at Sipaliwini. The vegetation of the area consisted of thick grass that was no more than a meter tall. The only other species taken along this ditch was *Oryzomys delicatus.*

Three of the specimens were adult females, one was a subadult female, and the other was an adult male. One of the adult females was found to be carrying three fetuses (crown-rump length, 4) when trapped on 20 August. The other two adult females taken on 19 August were lactating.

We have assigned our specimens to the subspecies *guianae* (type locality Kanuko Mountains, Guyana) tentatively until further study can elucidate the relationship among populations of this species (Hershkovitz, 1955). External and cranial measurements of the four adult specimens (male followed by three females) are as follows: total length, 342, 315, 338, 300; length of tail, 145, 143, 161, 133; length of hind foot, 41, 38, 39, 38; length of ear, 20, 20, 20, 20; greatest length of skull, 37.9, 35.6, 38.4, 36.3; condylobasal length, 35.7, 34.0, 35.4, 33.9; zygomatic breadth, 21.2, 19.7, 20.1, 20.2; interorbital constriction, 4.4, 4.5, 4.2, 4.4; mastoid breadth, 14.2, 13.8, 14.0, 13.4; length of nasals, 14.7, 13.7, 13.7, 14.7; length of maxillary toothrow, 7.2, 6.8, 6.8, 7.5; length of palatal bridge, 8.1, 7.3, 7.9, 8.3.

Neacomys guianae Thomas

Specimens examined (21).—BROKOPONDO: Brownsberg Nature Park, 5 km S, 21.5 km W Afobakka, 4°56′N, 55°09′W, 1; Brownsberg Nature Park, 7 km S, 18.5 km W Afobakka, 5°55′N, 55°11′W, 8; Brownsberg Nature Park, 8 km S, 2 km W Brownsweg, 4°55′N, 55°11′W, 5; 1 km N Rudi Kappelvliegveld, 300 m, 3°48′N, 56°08′W, 1. NICKERIE: 24 km S, 60 km E Apoera, 4°41′N, 56°07′W, 1; 38 km S, 27 km E Apoera, 4°46′N, 56°55′W, 1; Grassalco, 4°46′N, 56°46′W, 1; Sipaliwini Airstrip, 2°02′N, 56°07′W, 2. SURINAME: Powaka, 5°26′N, 55°04′W, 1.

Husson (1978) reported only three specimens of this spiny mouse from Suriname. We have found the species to be widespread throughout the country but nowhere abundant. Most of our specimens were trapped in seral stages of vegetation dominated by low bushes and small secondary-growth trees. Typical areas were along the sides of roads, around the edges of gardens, and at the edges of savannas. We have not taken the species in grassy areas of savannas or under mature rain forest.

Testes lengths of three adult males taken 8 July were 6, 7, and 10, and one taken on 20 August was 6. Testes lengths of males taken in September were 6, 6, 6, 6, 7, 7, and 7. An adult female containing three fetuses with crown-rump lengths of 5 was trapped on 24 September. A lactating female was taken on 20 July. Nonpregnant adult females were taken on the following dates: 8 July; 20 July (2); 24 July; 9 August.

External and cranial measurements of two adult males and an adult female, respectively, from the Brownsberg Nature Park are as follows: total length, 155, 147, 144; length of tail, 77, 70, 70; length of hind foot, 20, 20, 18; length of ear, 13, 13, 13; greatest length of skull, 20.5, 20.1, 19.9; condylobasal length, 17.9, 18.0, 17.3; zygomatic breadth, 11.1, 11.2, —; interorbital constriction, 4.5, 4.5, 4.4; mastoid breadth, 9.4, 9.3, 9.5; length of nasals, 7.7, 7.9, 7.2; length of maxillary toothrow, 2.6, 2.6, 2.7; length of palatal bridge, 3.3, 3.5, 3.1.

Potos flavus flavus (Schreber)

Specimen examined (1).—BROKOPONDO: 1 km N Rudi Kappelvliegveld, 300 m, 3°48′N, 56°08′W, 1.

Husson (1978) only reported six specimens of kinkajous from Suriname. Of those, only three were known from precise localities, which were all in the northern part of the country. Our specimen is an adult female that was taken in the Tafelberg Nature Reserve in central Suriname. The specimen was shot as it climbed a tree in an area of mature lowland tropical forest. An adult female, it carried a single embryo when taken on 30 September 1979. Crown-rump length of the embryo was 73.

The type locality of *Potos flavus* is Suriname as corrected by Thomas (1902), and thus we have assigned our specimen to the nominate subspecies. Cranial measurements of our specimen are as follows: greatest length of skull, 75.5; condylobasal length, 69.2; zygomatic breadth, 49.1; interorbital constriction, 15.5; postorbital constriction, 22.2; mastoid breadth, 37.4; length of the maxillary toothrow, 19.7; breadth across upper molars, 22.2.

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RESULTS OF THE ALCOA FOUNDATION-SURINAME EXPEDITIONS. VI. ADDITIONAL CHROMOSOMAL DATA FOR BATS (MAMMALIA: CHIROPTERA) FROM SURINAME

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Abstract

As part of ongoing studies of the bats of Suriname, karyotypic information is presented for 17 species. Chromosomal data are presented for the first time for *Peronymus leucopterus, Peropteryx macrotis, Mimon bennettii, Artibeus concolor, Furipterus horrens,* and *Thyroptera discifera*. Additional chromosomal data are presented for 11 other species of bats for which some information was available previously.

Introduction

As part of an ongoing study of the mammalian fauna of Suriname, we have examined the karyotypes of 17 species of bats (Table 1). No

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karyotypic data have been published for six of the species. Of the other 11 species, these are the first karyotypic data based upon Surinamese specimens for six species and we have additional information for five species discussed by Honeycutt et al. (1980). The specimens reported herein are part of the sample which formed the basis for the report by Genoways et al. (1981) on bat records for Suriname. They discuss the reasons for conclusions concerning specific identification. In those cases where our data are indistinguishable from those in the literature, we have simply presented the information on Table 1 and Specimens Examined. Accounts are given for those species where the data warrant them.

METHODS AND MATERIALS

Standard karyotypes were prepared from *in vivo* bone marrow techniques (Baker, 1970). A minimum of five spreads were examined per specimen. G-banded karyotypes were prepared from fibroblast cultures (Patton and Baker, 1978).

SPECIES ACCOUNTS

Cormura brevirostris (Wagner)

$2n = 22$; $FN = 40$

Karyotype of a male of this species from Leticia, Colombia, was reported by Baker and Jordan (1970). The karyotype of this single individual was unique among bats in that the total size of the X-chromosome was over 30% of the haploid genome, and in that the largest pair of autosomes was heteromorphic in the length of the short arm. We have examined six males and one female of this species from Suriname and find this uniquely large X-chromosome to be characteristic of all individuals. The autosomal heteromorphism noted in the Colombian specimen was also present in our sample.

Peronymus leucopterus (Peters)

Fig. 1, $2n = 48$; $FN = 62$

This species has the highest diploid number thus far reported for an emballonurid (Baker, 1970; Baker and Jordan, 1970). If many of the short arms in the autosomal complement are assigned fundamental values, the fundamental number could be as high as 78. Unlike the karyotype of most other emballonurids, there is little variation in size of the chromosomes in the karyotype of this species, with the 23 pairs of autosomes consisting of a gradated series of medium-sized elements. The largest pair of autosomes are approximately the size of the X-chromosome. The X-chromosome is a medium-sized submetacentric and the Y-chromosome can not be identified unequivocally. However, it is probably one of the smaller elements. A comparison of Figs. 1 and 2 will quickly reveal that the karyotype of *Peronymus* would have to

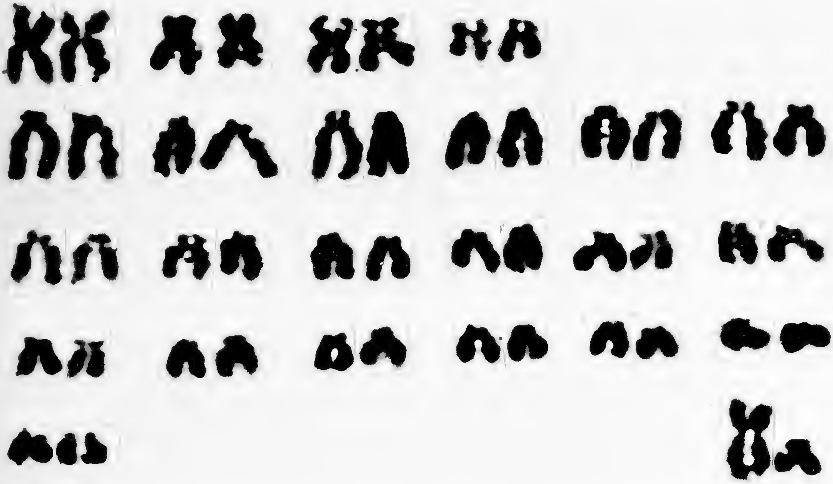

Fig. 1.—Representative karyotype of a male *Peronymus leucopterus* from Suriname: Para; Zanderij.

undergo many chromosomal rearrangements to become like that of *Peropteryx macrotis*. For example, in the karyotype of *Peronymus*, all autosomes are essentially the same size or smaller than the X-chromosome, whereas in *Peropteryx* all autosomes are equal to or larger

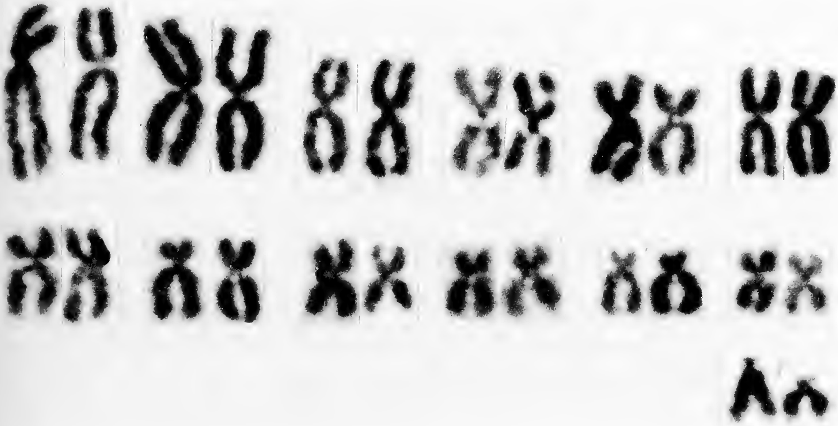

Fig. 2.—Representative karyotype of a male *Peropteryx macrotis* from Suriname: Saramacca; Voltzberg.

than the X-chromosome. This means that if the X-chromosome is the same size in the two karyotypes then essentially all elements would need to be rearranged to relate the two karyotypes.

Peropteryx macrotis (Wagner)
Fig. 2, 2n = 26; FN = 48

The autosomes of this species are composed of 11 pairs of metacentric or submetacentric elements plus one pair of subtelocentric elements. The pair of autosomes in Fig. 2 that are fourth from left in the top row have a secondary constriction proximal to the centromere on the lower arms. The X-chromosome is a medium-sized, near acrocentric chromosome and the Y-chromosome is also a near acrocentric chromosome that is about half the size of the X-chromosome. The published karyotypic data for other emballonurids (Baker, 1970; Baker and Jordan, 1970; RayChaudhuri and Pathak, 1966) fail to reveal a karyotype that is grossly similar to either *Peropteryx* (Fig. 2) or *Peronymus* (Fig. 1). See also the account for *Peronymus* for discussion of the relationships of *Peronymus* and *Peropteryx*.

Lonchorhina aurita Tomes
2n = 32; FN = 60

Karyotype of this species has been reported by Baker and Hsu (1970) and Baker (1973). The karyotype is essentially like that reported by these authors, except that in a smaller pair of autosomes the short arm is reduced to a point where the element may appear acrocentric in overcontracted spreads. Whether or not this represents geographic variation is unclear at this point.

Micronycteris hirsuta (Peters)
2n = 30; FN = 32

There are two karyotypes reported for *Micronycteris hirsuta* (Baker et al., 1973; Baker, 1979). Specimens from Middle America have a diploid number of 30, whereas specimens from Trinidad have a diploid number of 28. The three specimens from Suriname have a karyotype like that reported for Middle American specimens. The fact that the 2n = 30 karyotype has been reported northwest of Trinidad in Middle America and southeast of Trinidad in Suriname would suggest the strong possibility that the 2n = 28 karyotype may be restricted to Trinidad.

Micronycteris minuta (Gervais)
2n = 28; FN = 52

There does not appear to be much difference between the karyotype of our specimen and the specimen figured by Baker (1979: Pl. 6), ex-

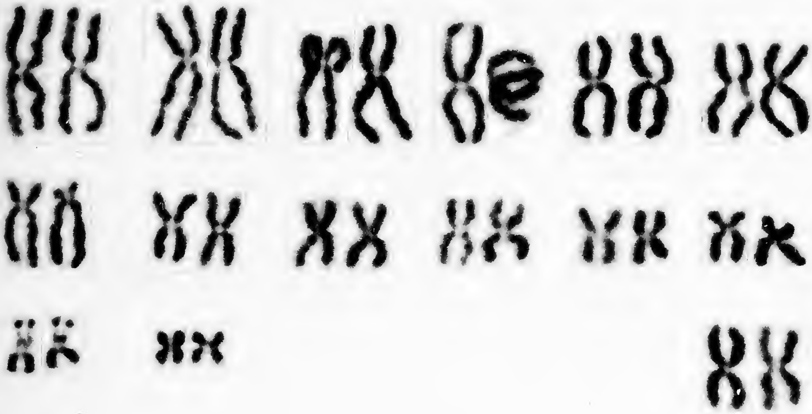

Fig. 3a.—Representative karyotype of a female *Mimon bennettii* from Suriname: Saramacca; Voltzberg.

cept that the smallest pair of autosomes is distinctly biarmed in the Suriname specimen, whereas the homologous pair in the specimen from Trinidad was more acrocentric in nature.

Mimon bennettii (Gray)

Fig. 3, 2n = 30; FN = 56

The autosomal complement of this species consists of a gradated series of biarmed elements ranging from large to medium. The X-chromosome is a medium-sized metacentric element and Y-chromosome is minute. All autosomes except the pair discussed below are submetacentric or metacentric. Each chromosome of one of the three smallest pairs has two secondary constrictions. This particular chromosomal configuration of secondary constrictions has not been recorded in any other phyllostomid species thus far studied.

In the seventh largest pair of autosomes there is a chromosomal polymorphism. Both chromosomal morphs are subtelocentric; however, one morph clearly has a more telomeric placement of the centromere than does the other, which might be called subtelocentric or submetacentric depending upon the spread available. This polymorphism is shown in Fig. 3a as the first pair on the second row. The G-banding pattern and nature of the polymorphism are shown in Fig. 3b. The rearrangement which has resulted in this polymorphism is probably a pericentric inversion (Fig. 3b). Based on standard karyotypes, all four individuals examined possessed this polymorphism. It is of interest to note that a similar polymorphism (involving three morphs)

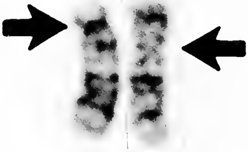

Fig. 3b.—G-banded preparation of the seventh largest pair of autosomes of the *Mimon bennettii* to show the nature of the chromosomal polymorphism in this species. Arrows indicate the positions of the centromeres.

has been reported for *Mimon crenulatum* (Baker et al., 1972); however, in *M. crenulatum* the polymorphism involves the fifth largest pair of autosomes.

Some authors have considered *Mimon bennettii* and *Mimon cozumelae* to be conspecific (Schaldach, 1965; Jones, 1966; Goodwin, 1969), whereas others have considered them to be distinct species (Carter et al., 1966; Gardner et al., 1970; Jones and Carter, 1976; Husson, 1978). Minimally the karyotype of one species must go through two rearrangements to be converted to the karyotype of the other (see Baker, 1979, for chromosomal data for *M. cozumelae*). As chromosomal races are uncommon in phyllostomid bats these data indirectly suggest that *M. bennettii* and *M. cozumelae* will prove to be specifically distinct.

Tonatia carrikeri (J. A. Allen)
Fig. 4, 2n = 26; FN = 46

A diploid number of 26 and fundamental number of 46 were reported by Gardner (1977) for this species based upon material from Peru. Our specimen, a female, has these same values. As a karyotype of this species has not been published, one is shown in Fig. 4.

Choeroniscus intermedius (J. A. Allen and Chapman)
2n = 20; FN = (36)

The karyotype of this species is figured in Honeycutt et al. (1980: Fig. 7). The karyotype of another female from Zanderij is essentially like the one figured except that in the third largest pair of autosomes there is a polymorphism. One element is subtelocentric as previously figured, whereas the other element is submetacentric. One of us (Baker) has examined the karyotypes of several specimens of this species from Trinidad and has found a similar polymorphism in the third largest pair of autosomes. Other polymorphisms were also found in the Trinidadian specimens.

Table 1.—*Chromosomal data for bats from Suriname. Symbols are 2n, diploid number; FN, fundamental number; M, metacentric; SM, submetacentric; ST, subtelocentric; A, acrocentric.*

Taxon	2n	FN	X	Y	Source of photograph of karyotype	Number of specimens reported in this study ♂	♀
Emballonuridae							
Cormura brevirostris	22	40	M	A	Baker and Jordan, 1970	5	2
Peronymus leucopterus	48	62	SM	SM	This paper	1	
Peropteryx macrotis	26	48	ST	ST	This paper	4	3
Saccopteryx leptura	28	38	SM	M	Baker and Jordan, 1970	1	
Phyllostomidae							
Phyllostominae							
Lonchorhina aurita	32	60			Baker, 1979		3
Micronycteris hirsuta	30	32			Baker, 1979		3
Micronycteris minuta	28	52	ST	A	Baker, 1979	1	
Micronycteris nicefori	28	52	SM	A	Baker, 1979	1	
Mimon bennettii	30	56	SM	A	This paper	1	3
Tonatia carrikeri	26	46			This paper		1
Tonatia schulzi	28	36	A	A	Honeycutt et al., 1980	2	
Glossophaginae							
Choeroniscus intermedius	20	(36)			Honeycutt et al., 1980		1
Glossophaga soricina	32	60			Baker, 1979		1
Carolliinae							
Rhinophylla pumilio	34	64	SM	A	Honeycutt et al., 1980	1	3
Stenodermatinae							
Artibeus concolor	31	56	ST	A-A	This paper	1	
Furipteridae							
Furipterus horrens	34	62			This paper		1
Thyropteridae							
Thyroptera discifera	32	38	SM	A	This paper	1	

Artibeus concolor Peters
Fig. 5, 2n = 31; FN = 56

Artibeus concolor has a diploid number of 31 in our male specimen, which is not unexpected because most other species of *Artibeus* have

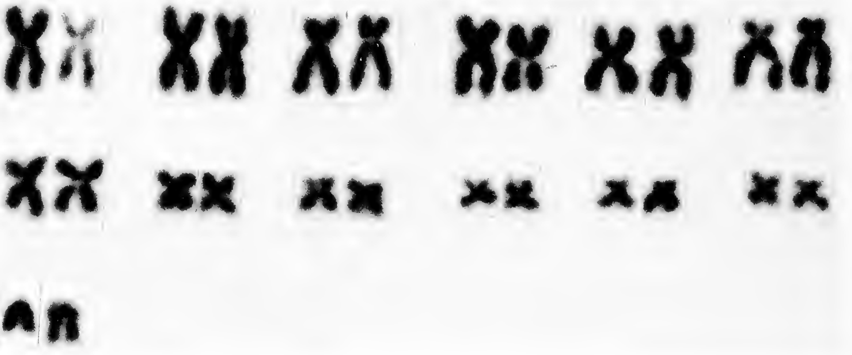

Fig. 4.—Representative karyotype of a female *Tonatia carrikeri* from Suriname: Para; Zanderij.

a diploid number of 31 in males. Autosomally, *A. concolor* is similar to other species in this genus with 10 pairs of submetacentric or metacentric elements and four pairs of subtelocentric elements. The two Y-chromosomes are acrocentric. There are currently 12 species recognized in the genus *Artibeus* (Baker, 1979); of these all but *A. phaeotis* and *A. watsoni* have two Y-chromosomes in males. The single biarmed Y-chromosome of *A. phaeotis* and *A. watsoni* appears to be a valuable taxonomic character. With the addition of data from *A. concolor,* all currently recognized species of *Artibeus* are known karyotypically.

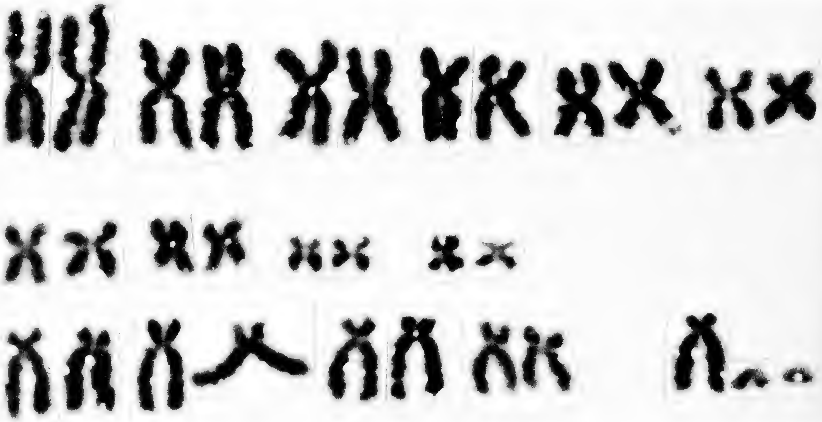

Fig. 5.—Representative karyotype of a male *Artibeus concolor* from Suriname: Para; Zanderij.

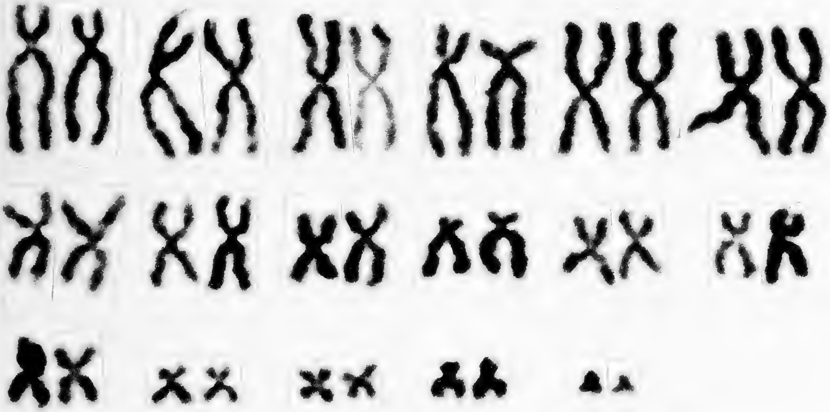

Fig. 6.—Representative karyotype of a female *Furipterus horrens* from Suriname: Saramacca; Voltzberg.

Furipterus horrens (Cuvier)
Fig. 6, 2n = 34; FN = 62

The karyotype of this species consists of a gradated series of biarmed elements ranging from large to small plus a pair of small acrocentric chromosomes. Three of the larger pairs are subtelocentric in nature (large arm is more than twice the length of the short arm). The remainder of the biarmed elements are submetacentric or metacentric chromosomes. As only a female was examined the sex elements could not be determined.

These are the first chromosomal data reported for this family. The diploid, fundamental values, and karyotypic characteristics are well within the range of values for other bats.

Thyroptera discifera Lichtenstein and Peters
Fig. 7, 2n = 32; FN = 38

The autosomes of this disk-winged bat consist of four pairs of biarmed elements plus a gradated series of 11 pairs of acrocentric elements. Of the biarmed autosomes, the second largest pair approaches a subtelocentric placement of the centromere. The other three pairs of biarms have a submetacentric or metacentric centromere placement. The X-chromosome is a metacentric element which is larger than any biarmed autosome. The Y-chromosome is tentatively identified as an acrocentric element about half the size of the X-chromosome.

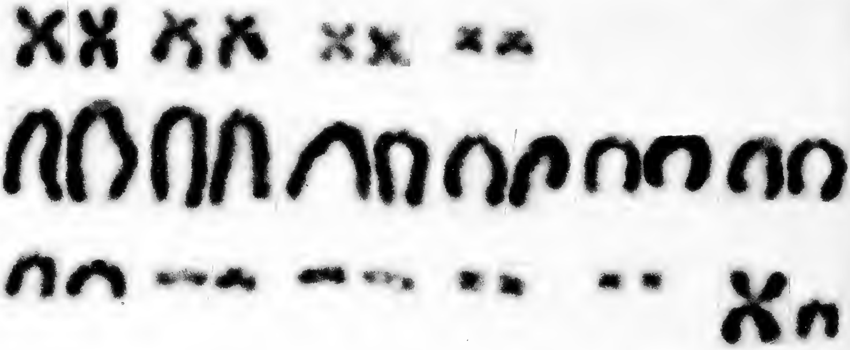

Fig. 7.—Representative karyotype of a male *Thyroptera discifera* from Suriname: Saramacca; Raleigh Falls.

The karyotype of the only other species in the family Thyropteridae, *T. tricolor,* was reported by Baker (1970) and Honeycutt et al. (1980). The karyotype of *T. discifera* can be derived from that of *T. tricolor* by four centric fusions, plus events which would change the acrocentric X-chromosome to a biarmed element and an enlargement of the Y-chromosome. Baker and Bickham (1980) reviewed the magnitude of change that generally distinguishes congeneric species and found that most differ by fewer than six chromosomal rearrangements. However, some congeneric species were distinguished by as many as 20 rearrangements. If the standard karyotypes in this case are reflective of the magnitude of chromosomal evolution that distinguishes these two species (see Haiduk et al., 1981), then we interpret this variation between *T. discifera* and *T. tricolor* as being well within the range which characterizes congeneric species of bats thus far studied.

SPECIMENS EXAMINED

Cormura brevirostris.—NICKERIE: Avanavero, 4°52′N, 57°21′W (♀, CM 68554); PARA: Zanderij, 5°27′N, 55°12′W (5♂, CM 68370–73, 68555; ♀, CM 68556).

Peronymus leucopterus.—PARA: Zanderij, 5°27′N, 55°12′W (♂, CM 68374).

Peropteryx macrotis.—SARAMACCA: Voltzberg, 4°40′N, 56°12′W (4♂, CM 68377–80; 3♀, CM 68376, 68557–58).

Saccopteryx leptura.—SARAMACCA: Voltzberg, 4°40′N, 56°12′W (♂, CM 68383).

Lonchorhina aurita.—NICKERIE: Avanavero, 4°52′N, 57°21′W (3♀, CM 68385–86, 68637).

Micronycteris hirsuta.—NICKERIE: Kabalebo, 4°51′N, 57°24′W (♀, CM 68638). PARA: Zanderij, 5°27′N, 55°12′W (2♀, CM 68387–88).

Micronycteris minuta.—SARAMACCA: Voltzberg, 4°40′N, 56°12′W (♂, CM 68391).

Micronycteris nicefori.—NICKERIE: Kabalebo, 4°51′N, 57°24′W (♂, CM 68643).

Mimon bennettii.—SARAMACCA: Voltzberg, 4°40′N, 56°12′W (♂, CM 68663; 3♀, CM 69393–95).

Tonatia carrikeri.—Para: Zanderij, 5°27′N, 55°12′W (♀, CM 68400).

Tonatia schulzi.—Nickerie: Kayserberg Airstrip, 3°06′N, 56°29′W (♂, CM 68706). Saramacca: Raleigh Falls, 4°44′N, 56°12′W (♂, CM 68409).

Choeroniscus intermedius.—Para: Zanderij, 5°27′N, 55°12′W (♀, CM 68413).

Glossophaga soricina.—Para: Zanderij, 4°27′N, 55°12′W (♀, CM 68414).

Rhinophylla pumilio.—Para: Zanderij, 5°27′N, 55°12′W (♀, CM 68869). Saramacca: Raleigh Falls, 4°44′N, 56°12′W (♀, CM 68887); Voltzberg, 4°40′N, 56°12′W (♂, CM 68891; ♀, CM 68890).

Artibeus concolor.—Para: Zanderij, 5°27′N, 55°12′W (♂, CM 68421).

Furipterus horrens.—Saramacca: Voltzberg, 4°40′N, 56°12′W (♀, CM 68439).

Thyroptera discifera.—Saramacca: Raleigh Falls, 4°44′N, 56°12′W (♂, CM 68440).

Acknowledgments

Our fieldwork in Suriname was supported by a grant from the Alcoa Foundation, Charles L. Griswold, President. We gratefully acknowledge this support. Laboratory phases of the study were supported by NSF grant DEB-80-04293 to Baker.

We would like to thank Henry A. Reichart, STINASU, for his assistance during our work and for making the many facilities of STINASU available to us. Without his help, our work in Suriname would have been impossible. Ferdinand L. J. Baal, Department of Forestry, issued our permits. Mr. Leo Roberts, STINASU, proved to be an excellent field guide, and most congenial companion. The personnel of Surinaams Museum of Natural History, particularly Marga Werkhoven and Mr. I. Douglas, were helpful in making housing and laboratory facilities available for our use. Mr. E. W. Kensmil of the Airports and Civil Aviation was very helpful in providing some of our air transportation to the country's interior. Dr. Robert Power of the Universiteit van Suriname assisted in acquiring chemicals for our karyological studies. Jane A. Groen and Stephen L. Williams assisted with the collection and preparation of specimens. Lynn W. Robbins prepared the G-banded preparation from which Fig. 3b was made.

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BAT RECORDS FROM MAURITANIA, AFRICA (MAMMALIA: CHIROPTERA)

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Abstract

The occurrence of seven species of bats previously unknown in Mauritania are documented, making a total of 11 species of bats recorded from the country. The new records include *Taphozous perforatus, Nycteris hispida, Hipposideros caffer, Asellia tridens, Pipistrellus rueppelli, Scotophilus leucogaster,* and *Tadarida condylura.* Additional information is provided on three species of bats (*Rhinopoma hardwickei, R. microphyllum,* and *Nycticeius schlieffeni*) already known to occur in Mauritania.

Introduction

Mauritania is situated in northwestern Africa, bounded in the north by Algeria and Morocco, in the east by Mali, in the south by Senegal and Mali, and in the west by the Atlantic Ocean. Very few published reports deal with the bat fauna of Mauritania. Those few existing reports, particularly the old ones, are diverse in scope and attention (Rochebrune, 1883; Dekeyser and Villiers, 1952, 1956; and Poulet, 1970).

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Submitted 20 December 1980.

This report is based primarily on a collection of specimens made as part of the African Mammal Project of the Division of Mammals, National Museum of Natural History, Smithsonian Institution. In addition, a single specimen of *Asellia tridens* in the mammal collection of Carnegie Museum of Natural History is included.

The senior author is involved in a major study of the distribution, systematics, and zoogeographical relationships of the bats of North Africa north of the 18°N latitude line. Because of the paucity of bat records from Mauritania and because the country, and the few records available, straddle the 18°N latitude line, this summary paper was completed so that the information might be available.

The following is a list of localities with coordinates from which the bats reported were collected. The coordinates are those given in the Official Standard Names Gazetteer, United States Board on Geographic Names. Species collected and dates of collection are given for each locality.

1) Akjoujt, Mogrein Copper Mine (19°45′N, 14°23′W). *Rhinopoma hardwickei* and *R. microphyllum*. 18, 21, 22 November 1966.
2) 8 km N Boghe (16°39′N, 14°17′W). *Taphozous perforatus* and *Nycticeius schlieffeni*. 6 May 1967.
3) Garak (16°33′N, 15°46′W), *Nycteris hispida, Hipposideros caffer,* and *Pipistrellus rueppelli*. 16, 18 April 1967; 1, 2 May 1967.
4) 3 km S Aleg (17°02′N, 13°55′W). *Asellia tridens, Nycticeius schlieffeni,* and *Scotophilus leucogaster*. 12, 16 May 1967.
5) Tiguent (17°16′N, 16°01′W). *Nycticeius schlieffeni*. 12, 13 April 1967.
6) Passe de Soufa (15°56′N, 12°01′W). *Nycticeius schlieffeni*. 30 May 1967.
7) Rosso (16°31′N, 15°49′W). *Hipposideros caffer* and *Tadarida condylura*. 28 April 1967; 1 May 1967.

The accounts are listed phylogenetically with measurements and natural history notes given under the species. We would like to thank Charles O. Handley, Jr., Richard W. Thorington, Jr., and Michael D. Carlton for allowing us to study the North African bats, including these Mauritanian specimens.

ACCOUNTS OF SPECIES

Family Rhinopomatidae

Rhinopoma hardwickei Gray, 1831

Specimens examined.—Akjoujt, Mogrein Copper Mine, 27 skins with skulls (11 ♂♂, 16 ♀♀), 8 in alcohol (2 ♂♂, 6 ♀♀).

Remarks.—Kock (1969) showed that the *Rhinopoma* reported as *R. microphyllum* from Grotte de Lapin and Adrar by Dekeyser and Villiers (1952, 1956) were instead *R. hardwickei.* Kock (1969) also listed material from Fort Gouraud. Poulet (1970) recorded *R. hardwickei* from Akjoujt with specimens from Mogrein Copper Mine. The taxonomic status of Saharan *R. hardwickei* is unclear at this time. Kock (1969) referred specimens from south of the Sahara to *R. h. sennaariense* and those from Niger and southern Algeria to *R. h. cystops*. Hill (1977) referred all Moroccan and Mauritanian material to *R. h.*

Table 1.—*External and cranial measurements of selected specimens of three species of bats from Mauritania.*

Catalog no. and sex	Locality	Length of fore-arm	Con-dylo-basal length	Zygo-matic breadth	Post-orbi-tal breadth	Breadth of brain-case	Mastoi-dal breadth	Length of maxil-lary tooth-row	Breadth across upper molars
		Taphozous perforatus							
USNM 401331 ♀	8 km N Boghe	62.5	18.7	11.6	4.5	9.6	10.4	8.1	8.0
		Pipistrellus rueppelli							
USNM 401420 ♀	Garek	33.7	—	—	—	—	—	4.6	—
		Scotophilus leucogaster							
USNM 401431 ♂	3 km S Aleg	49.1	18.1	14.3	5.1	9.7	12.9	6.5	—
USNM 401432 ♂	3 km S Aleg	50.6	18.0	13.8	4.8	9.5	12.0	6.7	8.6

arabium and pointed out that the name *sennaariense* Fitzinger, 1866, was listed with no description. Hill (1977) regarded all material from North Africa except Upper and Central Egypt as belonging to the slightly larger Arabian peninsula subspecies *R. h. arabium.* A detailed study of geographic variation throughout the range of the species is needed to better understand subspecific limits.

Rhinopoma microphyllum (Brunnich, 1782)

Specimens examined.—Akjoujt, Mogrein Copper Mine, 29 skins with skulls (16 ♂♂, 13 ♀♀), 12 in alcohol (7 ♂♂, 5 ♀♀).

Remarks.—The large mouse-tailed bat was first reported in Mauritania from Grotte de Lapin and Adrar by Dekeyser and Villiers (1952, 1956) but Kock (1969) showed these to be *R. hardwickei.* Subsequently, Poulet (1970) reported both species from Mogrein Copper Mine at Akjoujt. We concur with Hill (1977) that Mauritanian specimens are closer to the nominate subspecies than to the larger *R. m. tropicalis* from Sudan and Nigeria. As Hill (1977) showed in the Sudan, we believe there is still a need for a critical examination of geographic variation in this species before subspecific limits will be understood.

Family Emballonuridae

Taphozous perforatus (E. Geoffroy, 1818)

Specimen examined.—8 km N Boghe, 1 skin with skull (1 ♀).

Remarks.—This specimen is the first record of this species from Mauritania. *T. perforatus* has been reported from Senegal (Rochebune, 1883) and Mali (Aellen, 1957). The recognition of subspecies in *T. perforatus* is controversial (Rosevear, 1965; Hayman and Hill, 1971; Corbet, 1978), and little can be added based on a single specimen.

The single adult female was collected on 6 May 1967 and carried a single embryo measuring 18 mm in crown-rump length in the right horn of the uterus.

Measurements.—See Table 1.

Family Nycteridae

Nycteris hispida (Schreber, 1774)

Specimens examined.—Garak, 52 skins with skulls (26 ♂♂, 26 ♀♀), 125 in alcohol (47 ♂♂, 78 ♀♀).

Remarks.—This is the first report of this widespread African species for Mauritania. The closest record of occurrence to Garak is at Rosso, just south of the Senegal River in Senegal (Adam and Hubert, 1977). The Mauritanian locality thus represents the northwesternmost record of the hairy slit-faced bat in Africa. The range of this species seems limited by the Sahara, although *Nycteris thebaica* occurs widely in northern Africa.

Sixteen females collected on 16 April 1967 each carried a single embryo in the right uterine horn. The embryos, ranging from 11 to 18 mm in crown-rump length, averaged 14.2 mm in length.

Family Hipposideridae

Hipposideros caffer (Sundevall, 1846)

Specimens examined.—Garak, 4 skins with skulls (1 ♂, 3 ♀♀); Rosso, 1 in alcohol (1 ♀).

Remarks.—The Mauritanian specimens, the first reported for the country, are referable to *H. c. tephrus,* the Saharan subspecies of this widespread African species. Hayman and Hill (1971) listed the species from Senegal; Aellen (1956) reported specimens of *H. c. guineensis* (=*H. ruber guineensis*) from Badi, Senegal.

Asellia tridens (E. Geoffroy, 1818)

Specimens examined.—3 km S Aleg, 33 skins with skulls (18 ♂♂, 15 ♀♀).

Remarks.—*Asellia tridens* occurs in a patchy distribution from Pakistan through southwestern Asia and across northern Africa as far south as Gambia, Senegal, Sudan, and Somalia (Corbet, 1978). These specimens are the first reported for Mauritania. Within the species there is much local variation in pelage color, with individuals ranging from gray to reddish in color. The Mauritanian specimens exhibit this typical variation. The name *A. t. diluta,* reported from the Algerian Sahara, is available for the Mauritanian material. However, a detailed study of geographic variation within the species is needed.

Five females collected on 16 May 1967 each had one embryo in the left horn of the uterus. These embryos measured 7, 8, 12, 13, and 13 mm in crown-rump length.

Family Vespertilionidae

Nycticeius schlieffeni (Peters, 1859)

Specimens examined.—Tiguent, 4 skins with skulls (2 ♂♂, 2 ♀♀), 1 in alcohol (1 ♀); 8 km N Boghe, 1 skin with skull (1 ♂); 3 km S Aleg, 2 skins with skulls (2 ♂♂), 2 in alcohol (2 ♂♂); Passe de Souffa, 2 skins with skulls (1 ♂, 1 ♀).

Remarks.—The Mauritanian specimens are referable to *N. s. albiventer* Thomas and Wroughton, 1908, the subspecies considered by Hayman and Hill (1971) to include the western African material. This species is widespread in the savanna regions of Africa. In Mauritania, it seems to be restricted to the southern Sahel savanna region. In his review of West African bats, Rosevear (1965) listed records from Trarza Country, the southwestern coastal corner of Mauritania.

Pipistrellus rueppelli (Fischer, 1829)

Specimens examined.—Garak, 2 skins with skulls (1 ♂, 1 ♀), 1 in alcohol (1 ♀).

Remarks.—Although widely distributed in Africa, Rueppell's bat does not appear to be locally common. These specimens, the first reported for Mauritania, are assigned to *P. r. senegalensis* Dorst, 1960, known only from Richard Toll, Senegal (Adam and Hubert, 1972). But, as pointed out by Hayman and Hill (1971), the subspecies limits of the species are not clear.

The single male collected on 2 May 1967 was a juvenile with unfused epiphyses and weighed 4 grams. The forearm length was 31.9 mm, and had nearly reached the adult length. Both females were collected on 18 April 1967 and were not pregnant when captured.

Measurements.—See Table 1.

Scotophilus leucogaster (Cretzschmar, 1830)

Specimens examined.—3 km S Aleg, 2 skins with skulls (2 ♂♂).

Remarks.—These two specimens are the first record of *S. leucogaster* from Mauritania. The small species of *Scotophilus* are in a confused state of taxonomy (Kock, 1969; Koopman, 1975; Koopman et al., 1978; Robbins, 1978; Hill, 1980; Robbins, 1980). In West Africa there seems to be three species—the largest *S. dinganii* or *S. nux,* the middle-sized *S. leucogaster* (although Koopman et al., 1978, seem to recognize three taxa but at the same time suggest placing both the large and middle-sized taxa together under *S. leucogaster*), and the small *S. nigritellus*. Hill (1980) has shown that *S. viridis* of southern Africa is predated by *S. borbonicus* (E. Geoffroy,

1803) and thus if *S. viridis* is a junior synonym of *S. leucogaster* as suggested by some, both would be known by *S. borbonicus*. We prefer to call the medium-sized, savanna inhabiting species in West Africa *S. leucogaster* until a revision of the genus in Africa clarifies the taxonomic relationships.

Measurements.—See Table 1.

Family Molossidae

Tadarida condylura (A. Smith, 1833)

Specimens examined.—Rosso, 70 skins with skulls (50 ♂♂, 20 ♀♀), 33 in alcohol (27 ♂♂, 6 ♀♀).

Remarks.—The Angola free-tailed bat is a common inhabitant of dwellings and other buildings throughout its widespread range in Africa. These specimens, the first records for Mauritania, represent the northwestern limits of the geographic distribution of *T. condylura* in this region.

Five females examined on 28 April 1967 evidenced reproductive activity. Each carried a single embryo in the right horn of the uterus. Crown-rump lengths of the five embryos were 12, 16, 17, 17, and 18 mm.

DISCUSSION

Eleven species of bats are now known from Mauritania. Ten of these 11 are covered in this paper with seven species reported for the first time for the country. *Taphozous nudiventris* was reported previously by Panouse (1951) and Aellen (1957) and is not covered in the present paper.

Judging from the records of bats known from adjacent countries (Morocco, Algeria, Senegal, and Gambia), as many as 36 additional species could be found to occur in Mauritania. Thirty of these species are predominantly sub-Saharan in distribution and are known from Senegal (27) and Gambia (3). Of these 30, seven are Pteropodids which may occur in Mauritania although some such as *Hypignathus montrosus,* known from Gambia, will certainly be found only along the Senegal River in extreme southern Mauritania if it occurs in the country. Of the remaining species, *Hipposideros cyclops,* reported from Senegal, also is generally a forest block species and may occur only along the Senegal River in Mauritania. Others such as *Myopterus daubentoni* from Senegal are poorly known and probably occur in woodland only. *Nycteris thebaica* is a widespread African species that is known as far north as Morocco and so will certainly occur in Mauritania.

Three species of bats that are Palaearctic in distribution are known from Algeria and Morocco so may occur in Mauritania. These are *Pipistrellus kuhli, Otonycteris hemprichi,* and *Tadarida teniotis*. An additional Palaearctic species, *Plecotus austriacus*, is known from Senegal and Cape Verde Islands so should be found in Mauritania.

Judging by the number of species known from surrounding countries but not yet recorded from Mauritania, it is probable that the list of species of bats for this country could increase to as many as 47 species. Most of these species should be found to occur in southern Mauritania but some additional species with primarily Palaearctic distributions may be found in the north.

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ECOLOGY AND REPRODUCTION OF THE PARTHENOGENETIC LIZARD *CNEMIDOPHORUS UNIPARENS* (TEIIDAE)

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Abstract

A population of *Cnemidophorus uniparens* was studied in the vicinity of Portal, Cochise County, Arizona, in summer 1977 and 1978. Daily activity was distinctly bimodal with peak activity occurring in the morning. Frequency of tail breakage (a measure of predation) increased with size, but overall tail breakage was low (15.6%). Reproduction began in mid-May and extended to the end of July. Peak reproduction occurred in late June and early July. Clutch size ranged from one to four eggs and was positively correlated with snout-vent length. There was no correlation between individual egg size and body size. Relative clutch mass was low (mean = 14.4%). Mean home range size differed significantly between years and appeared to be related to differences in prey availability between years. Home ranges overlapped and there was no evidence for territoriality or agonistic behavior. Average growth rate was 0.17 mm/day. Growth rate was negatively correlated to snout-vent length. Population size and structure remained relatively constant between years.

Introduction

The lizard genus *Cnemidophorus* is large and widespread, ranging from the eastern United States to central Argentina (Peters and Donoso-Barros, 1970). Greatest species diversity within the genus is found in the southwestern United States and northwestern Mexico. The ge-

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nus contains a large number of parthenogenetic species. Of the 16 species inhabiting the southwestern United States nine (58.8%) are all-female parthenospecies (Conant, 1975; Lowe and Wright, 1964; McKinney et al., 1973; Scudday, 1973; Stebbins, 1966).

In recent years an increased interest in the biology of *Cnemidophorus* has resulted in a number of ecological papers dealing with the group. Most of these have been concerned with the biparental species (Parker, 1972; Turner et al., 1969; Vitt and Ohmart, 1977, among others). Less attention has been devoted to the uniparental forms. In the present paper I present data on the ecology, reproduction, and population structure of a uniparental species, *Cnemidophorus uniparens,* from southeastern Arizona.

MATERIALS AND METHODS

Cnemidophorus uniparens was studied during summer (late May to the end of August) 1977 and 1978 at a site approximately 2 km W of the Arizona-New Mexico border along the Portal Road, Cochise County, Arizona. The study site consisted of a pitfall trap grid composed of 100 number 10 cans (155 mm by 170 mm) buried flush with the ground and covered with slightly elevated plywood boards designed to prevent the lizards from escaping and to provide shade during the heat of the day. The cans were set in 10 rows of 10 cans each spaced 10 m apart, so that the grid covered an area of 1 ha. The cans were checked twice daily (ca 1200 h and 1900 h). These times roughly corresponded to the end of morning and evening activity periods for the lizards.

Upon initial capture lizards were given a permanent identification number by toe clipping (Tinkle, 1967). Originally each animal was also marked with a unique color code to allow for easy visual identification from a distance, however, this procedure proved impractical and was soon abandoned due to unequal paint loss, fading, and partial shedding. Later the animals were simply marked with a single dot of paint at the base of the tail. The color of paint was changed weekly. Upon initial capture and all subsequent recaptures the following data were recorded: grid location, snout-vent length (mm), length of tail base (= unregenerated portion of the tail), length of regenerated portion of the tail (mm), weight (measured with a Pesola spring balance to 0.1 g), reproductive condition (determined by palpation), and shedding.

In addition to work on the grid, lizards were sampled weekly from similar habitat near the grid (less than 0.5 km) for detailed information on thermal relations, feeding, and reproduction. Feeding and thermal relations will be reported on in separate papers. Lizards were collected using blowguns constructed of steel or plastic conduit with 12 or 20 gauge shotgun wads as projectiles. This proved to be very effective in collecting *Cnemidophorus* at distances up to 10 m. Immediately upon capture lizards were placed on ice and transported to the laboratory for analysis. In the lab they were measured to the nearest mm and weighed to the nearest 0.01 g on a Mettler top-loading balance. Ovaries were removed and trimmed of superfluous tissue and then weighed to the nearest 0.01 g. Ovarian follicles and corpora lutea were counted and measured in the fresh state to the nearest 0.1 mm with an ocular micrometer attached to a dissecting microscope. Condition of the oviducts was noted and any oviducal eggs removed, weighed, and measured to the nearest 0.1 mm with dial calipers. The liver and fat bodies (if present) were removed and weighed to the nearest 0.01 g.

DESCRIPTION OF THE STUDY SITE

The study site was located along the Portal Road at the eastern foot of the Chiricahua Mountains in the San Simon Valley at an elevation of approximately 1500 m. The soil on the grid site was sandy with some scattered large rocks. The entire region was dissected by numerous shallow, often poorly defined watercourses (washes). One large wash on the extreme southern portion of the grid drastically affected the density of the vegetation in that region.

Dominant plant species on the grid were mesquite (*Prosopis glanduosa*) and Mormon tea (*Ephedra trifurca*). Subdominants were white thorn acacia (*Acacia albicans*), tarbush (*Flourensia cernua*), snakeweed (*Gutierrezia* sp.), and cowweed (*Boutela* sp.). Total ground cover was sparse, comprising about 15 to 20% except along the southern border in the vicinity of a large wash where *Prosopis glandulosa* formed a dense border. Ground cover on the grid increased slightly (30 to 35%) during late summer due to the appearance of summer annuals after heavy July and August rains.

A dominant aspect of the area in general and the grid in particular was the presence of large earthen mounds produced by the activity of banner-tailed kangaroo rats (*Dipodomys spectabilis*). These mounds were abundant, often exceeding 30/ha. The tunnels within the mounds were a major source of nocturnal retreats and daytime refugia for *Cnemidophorus uniparens* and other lizards on the grid. The site also contained numerous tunnels and burrows of other small heteromyid rodents (*Dipodomys merrami* and *Perognathus* sp.) which were also used as retreats and refugia by the lizards.

Several other species of lizards occurred on the grid with *C. uniparens*. They were *Holbrookia maculata, Phrynosoma cornutum, Phrynosoma modestum, Sceloporus undulatus, Urosaurus ornatus, Uta stansburiana, Crotaphytus wislizenii,* and *Eumeces obsoletus*.

RESULTS AND DISCUSSION

Activity

During the course of the study the daily activity pattern of *Cnemidophorus uniparens* was distinctly bimodal with the majority of the activity being concentrated in early morning (from sunrise to about 1130 h) and with a lesser peak in late afternoon (1730 to 1930 h). Morning and afternoon grid capture data show that 75% of all animals were collected during the morning activity period. Virtually no lizards were active during the middle of the day, except on overcast days when midday temperatures were reduced. On such days the bimodal pattern broke down and lizards were active throughout the day. Rainfall depressed activity. Lizards were never active during rain storms and the strength and duration of the storms affected subsequent activity. *Cnemidophorus uniparens* would become active almost immediately after light showers, but heavy rainfall (>3 cm) would often depress activity for as much as 24 to 36 h. The reason for this refractory period remains unclear, however, it may have to do with the difficulty in foraging in rain soaked soil.

Table 1 shows grid capture success during the summers of 1977 and

Table 1.—*Summary of seasonal activity in* Cnemidophorus uniparens *as measured by capture success (average number of animals captured/100 trap days during the time period).*

Date	1977	1978
16–31 May	No sample	4.4
1–15 June	8.8	3.7
16–30 June	16.8	4.5
1–15 July	8.9	4.3
16–31 July	5.6	3.5
1–15 August	5.2	4.3
16–31 August	3.5	2.5

1978. In 1977 capture success reached a peak in the second half of June and then gradually declined. Even with this decrease, activity remained fairly high until the termination of field work in late August. In 1978 overall capture success was reduced, but activity remained fairly constant throughout the summer, with only a slight decrease in late August.

Daily activity in *C. uniparens* was similar to that reported by other workers for *Cnemidophorus* (for example, Echternacht, 1967; Medica, 1967; Milstead, 1957*a*; Vitt and Ohmart, 1977). These authors mention the bimodal activity period and cessation of activity with rainfall, but none of them noted a refractory period depending upon amount of rainfall as was seen in *C. uniparens*. Most workers (Christiansen, 1971 and Medica, 1967, among others) have noted a sharp decline in activity of post-reproductive adults, however, prolonged activity after cessation of reproductive activity has been reported for *C. tigris* (Parker, 1972; Vitt and Ohmart, 1977).

Predation and Tail Breakage

The following species of birds were observed successfully preying on *Cnemidophorus uniparens*: Roadrunners (*Geococcyx californianus*), Burrowing Owls (*Speotyto cunicularia*), and Loggerhead Shrikes (*Lanius ludovicianus*). In addition to these direct observations there are a number of potential avian and reptilian predators on the site. The potential avian predators are Swainson's Hawk (*Buteo swainsoni*), Red-tailed Hawk (*Buteo jamaicensis*), and the American Kestrel (*Falco spaverius*). Potential reptilian predators include *Masticophis flagellum, Salvadora derserticola, Arizona elegans, Rhinocheilus leconti, Lampropeltis getulus,* and juveniles of *Pituophis melanoleucus, Crotalus atrox,* and *Crotalus scutulatus*. With the exceptions of *M. flagellum* and *S. derserticola* (both active diurnal species) most snakes probably encounter whiptails while they are in nocturnal retreats. *Cro-*

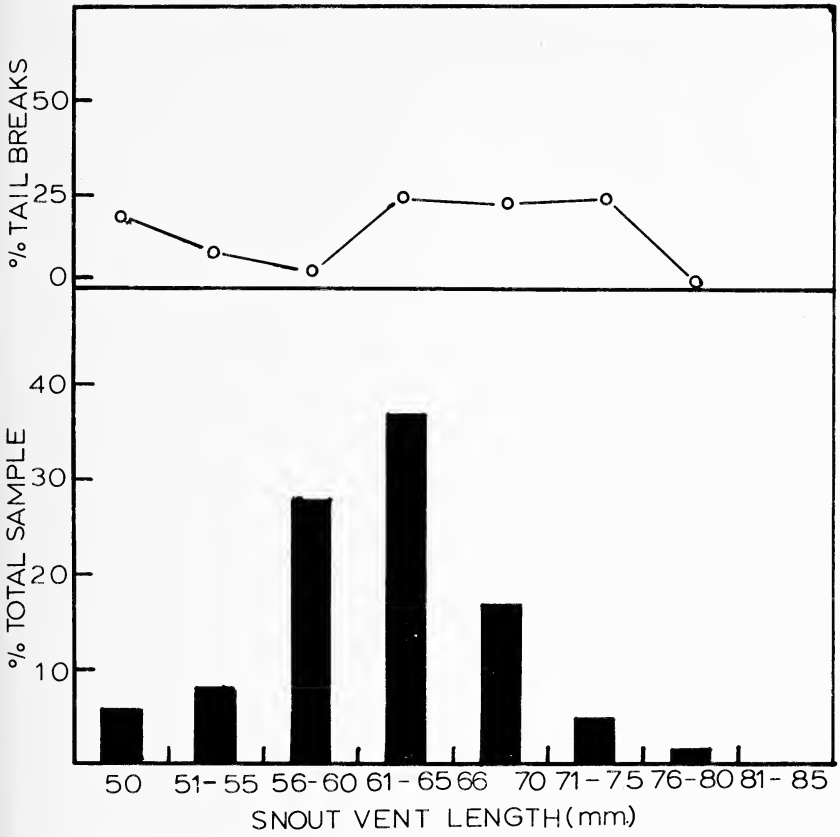

Fig. 1.—Size composition and relative tail breaks by size class for *Cnemidophorus uniparens* (N = 472).

taphytus wislizenii also occurs on the grid and the remains of a *C. uniparens* was found in the stomach of a *C. wislizenii*.

Fig. 1 compares population percentage by size class and percent tail breakage within size class. Frequency of tail breakage has been used by many investigators as an indication of relative predation pressure (Tinkle and Ballinger, 1972; Parker and Pianka, 1973; Vitt and Ohmart, 1977) or predation pressure in conjunction with intraspecific aggression (Vitt et al., 1974). The probability of an individual lizard having at some time had an encounter with a predator should increase with increasing age (snout-vent length) and this should then be reflected in increased frequency of tail breakage in the larger size classes. The tail

Table 2.—*Summary of seasonal reproductive cycle in* Cnemidophorus uniparens *by percent of sample possessing the character. Data are pooled for 1977 and 1978.*

Date	N	Enlarged follicles	Oviducal eggs	Corpora lutea	Enlarged oviducts
16–31 May	6	16.6	16.6	33.3	66.6
1–15 June	23	60.8	21.7	43.4	95.6
16–30 June	32	62.5	21.8	40.6	96.8
1–15 July	34	52.9	26.4	55.8	100.0
16–31 July	16	18.7	18.7	68.7	100.0
1–15 August	25	0.0	0.0	24.0	0.0
16–31 August	9	0.0	0.0	0.0	0.0

breakage data for *C. uniparens* conforms to the expected prediction. Combined tail breakage for all size classes is 15.6%, and is considerably lower than frequencies reported by Parker (1972) and Vitt and Ohmart (1977) for *Cnemidophorus tigris*. This initially suggests that predation pressure might be lower on *C. uniparens* than on *C. tigris*; however, two other factors, adult body size and demographic structure, might differentially affect tail breakage frequencies in *C. uniparens*. Tail breakage data are actually a measure of unsuccessful predation attempts. A higher success to attack ratio on the part of a predator would potentially reduce the proportion of a population exhibiting regenerated tails. Due to its small size it is probable that *C. uniparens* is less likely to escape a predation event, especially from an avian predator. If this is the case tail breakage frequency is low not because of a reduction in predation but rather to the greater success on the part of the predators. Demographic structure might also affect the frequency of tail breakage. Because frequency of regenerated tails is assumed to be a time related phenomenon, one would expect higher frequencies of tail breakage in populations of long lived organisms. Several studies have shown *C. tigris* to be long lived (McCoy, 1965; Parker, 1972; Turner et al., 1969), whereas the present study suggests that *C. uniparens* is short lived, with few if any animals attaining an age of three years (see section on Population Structure, Density, and Turnover).

Reproduction and Fat Body Cycles

Females were judged to be reproductively mature if they possessed any of the following: oviducal eggs; corpora lutea; enlarged ovarian follicles; or enlarged, distended oviducts. The smallest mature female collected was 58 mm snout-vent length and the largest immature was 59 mm; however, four other 59 mm animals were mature, having either enlarged ovarian follicles or corpora lutea. All animals over 59 mm

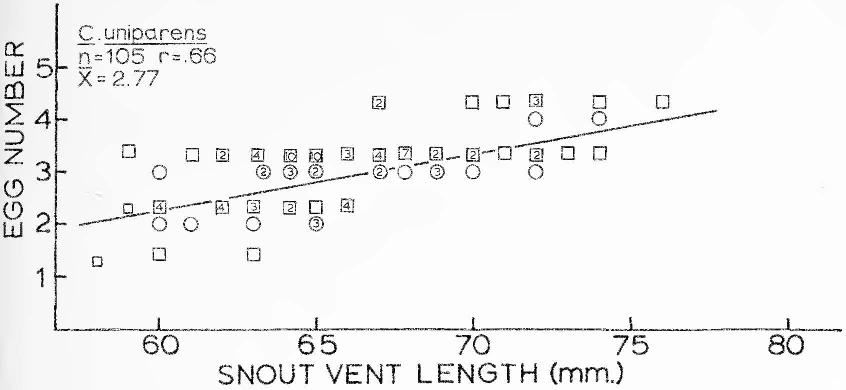

Fig. 2.—Relationship between egg number and snout-vent length for *Cnemidophorus uniparens*. Open circles are oviducal eggs and open squares ovarian follicles near ovulatory size. Numbers in open symbols denote number of individuals sharing a point.

were mature. Minimum size at maturity apparently varies from 58 to 59 mm. Mature females ranged from 58 to 77 mm (mean = 65.5 ± 3.9 mm, N = 145).

The annual reproductive cycle is summarized in Table 2. Samples were not collected before 16 May in either year, but due to the small percentage of animals with either ovarian follicles or oviducal eggs in late May it would seem that little reproductive activity occurs earlier in the year. By early June virtually all animals possessed enlarged oviducts and either actively yolking follicles or oviducal eggs. This heightened reproductive activity continued through the first half of July, rapidly dropped off in the second half of July and stopped by early August. No animals collected in August contained enlarged follicles or oviducal eggs, indicating that reproduction had ceased for the year. Cessation of reproductive activity in late July and early August is further supported by the small or regressing condition of the oviducts of all animals collected in August.

Clutch size was determined from counts of oviducal eggs, enlarged ovarian follicles, or corpora lutea. Clutch size ranged from one to four eggs (mean = 2.77 ± 0.06, N = 105). There was a significant correlation between clutch size and snout-vent length (Fig. 2, $P < 0.001$) with greater than 40% ($r^2 = .44$) of the variation in clutch size being attributable to increase in snout-vent length. The slope of the regression line indicated that an additional egg would be added to the clutch with every 7 mm increase in snout-vent length. *Cnemidophorus uniparens* produced multiple clutches of eggs in a year, as was demonstrated by the presence of both corpora lutea and ovarian follicles near ovulatory size in several animals. Individual mark-recapture data confirm multiple clutches with females collected while gravid, spent, and gravid again. Time between clutches in these individuals varied from 21 to 28 days. It is probable that most, if not all, females lay two clutches per year and that some could produce three clutches due to the relatively short time between clutches and the extended reproductive season (late May to early August).

Egg size was variable in *C. uniparens*. Mean egg size for 66 shelled oviducal eggs was 13.1 mm ± 1.3 mm by 7.1 mm ± 0.8 mm with a range of 11.5 to 16.4 mm for egg length and 5.7 to 8.2 mm for egg width. Egg weight varied from 0.30 to 0.52 g (mean = 0.38 ± 0.05 g). There was no significant correlation between snout-vent length and either egg size or egg weight.

Relative clutch mass (sensu Vitt and Congdon, 1978) as used here refers to the ratio of total clutch weight of shelled oviducal eggs to total body weight. No attempt was made to determine either dry weight ratios or caloric ratios. Ballinger and Clark (1973) have demonstrated that wet weight ratios are comparable to both dry weight and caloric ratios (but see Vitt and Congdon, 1978). Relative clutch mass was low, ranging from 9.6% to 20.0% (mean = 14.4 ± 0.24). Using the Wilcoxon's two sample test (Sokal and Rohlf, 1969) there was no significant difference in relative clutch mass between 1977 and 1978 samples, between early and late season clutches, or between small ($\leq$65 mm) and large ($\geq$66 mm) animals.

Reproductive potential refers to the total number of eggs produced by an average female during a single breeding season. As a result it is a function of both clutch size and number of clutches. Mean clutch size for *C. uniparens* was 2.77 eggs and lizards laid from two to three clutches per season. Therefore average annual reproductive potential for *C. uniparens* varies from 5.5 to 8.7 eggs.

The importance of fat bodies to lizard reproduction has been experimentally demonstrated by Hahn and Tinkle (1965). No clear picture of fat body cycling was obtained in the present study, but this is probably a function of sampling time, rather than the biology of the animals. Fat bodies were either absent or very small from the initial samples in May through the end of July. In August fat bodies began to appear and became progressively larger until the termination of the study in the end of August. It is probable that by the time sampling was initiated in mid-May the fat body lipids had already been mobilized for reproduction. With the end of the reproductive season in late July, energy that would earlier have been allocated for reproduction could be shunted into fat body storage, presumably to be used both as a source of energy during brumation and to initiate vitellogenesis in the following spring.

Home Range

Home range size in *Cnemidophorus uniparens* was detemined by the convex polygon method. Only animals with five or more captures, with none of the capture points occurring on the border of the grid were used in the analysis. These restrictions were placed on the analysis to prevent unrealistically small home ranges being generated either from animals with too few captures, or from lizards that had some or most of their home ranges outside the confines of the study grid. It was assumed that an animal that was never captured along the margin of the grid had its total home range within the study site. A total of 47 animals met these requirements.

Much debate has arisen concerning both the methods utilized in determining home range size and the meaning of home range data (Turner, 1971; Wieazlowska, 1975; Waldschmidt, 1979, among others). I have chosen the convex polygon method rather than statistical probabilistic methods such as the recapture radii method (Tinkle and Woodward, 1967) or the probability ellipse method (Jennrich and Turner, 1969), because it measures home range only in regions where the animals have been captured, rather than measuring the home range as some probability function. Methods such as recapture radii and probability ellipse consistently over-estimate home ranges compared to the convex polygon method (Wieazlowska, 1975; Waldschmidt, 1979).

Size of the home range was not significantly correlated with either number of captures ($r = .28$, $P < 0.1$) or with snout-vent length of the animals ($r = .12$, $P > 0.1$). Combined size of home range for both years varied from a minimum of 120 m^2 to a maximum of 2386 m^2 (mean = 728 m^2 ± 77 m^2). For 1977 home range varied from 120 m^2 to 2386 m^2 (mean = 815 m^2 ± 88 m^2, N = 39). In 1978 home range size varied from 240 m^2 to 746 m^2 (mean = 417 m^2 ± 62 m^2, N = 8). The difference between mean home range size in the two years is highly significant (t-test, $P < 0.001$). This difference in home range size between 1977 and 1978 is probably a function of different invertebrate prey availability during the two summers. A correlation has been shown between increased rainfall in desert regions and increased primary productivity, which in turn produces higher densities of invertebrate herbivores and detritivores (Dunham, 1978; Whitford and Creusere, 1977). Summer 1977 was preceded by a year of average rainfall, whereas heavy rains preceded summer 1978, greatly increasing the density of spring annuals and their invertebrate herbivores. Apparently *C. uniparens* responded to this increased prey availability by reducing average size of home range. In a widely foraging species such as *C. uniparens* home range size should be inversely related to prey density, with animals having to forage further during times of prey paucity than during times of prey abundance. The upper limit on home range size is set by the trade-off between energy expended in foraging and energy gained from increased foraging area (home range).

Cnemidophorus uniparens exhibited no signs of territoriality. Home ranges greatly overlapped and in some cases the home range of one individual was completely encompassed by that of another. I did not observe any sign of agonistic behavior among the lizards, even when they were close to each other. It was not unusual to find two individuals foraging within 20 to 30 cm of each other, or to find two or more individuals taking refuge under the same shrub. As many as four animals have been found in the same pit trap, resting on top of each other with no sign of aggression. This lack of aggression between individuals would be predicted from the parthenogenetic mode of reproduction where all animals within a population should theoretically share the same genotype. Congdon et al. (1978) have also reported a lack of agonistic behavior in the uniparental *Cnemidophorus* that they studied. However, this appears to not always be the case. Milstead (1957*b*) found *C. tesselatus* to exhibit some intraspecific aggression and Cole and Townsend (1977) alluded to possible intraspecific aggression in various uniparental species under laboratory conditions. In addition Congdon et al. (1978) referred to intraspecific aggression in the "unisexual *C. perplexus*" as reported by Milstead (1957*b*), however, in a reassessment of the nomenclature used in his 1957 study Milstead (1965) equated *C. perplexus* with *C. inornatus,* a biparental species.

The occurrence of agonistic behavior in some populations of uniparentals is puzzling considering the supposed genetic make-up of the populations. It would be interesting to analyze the genetic make-up of those populations that exhibit agonistic behavior to determine if they really are genetically homogeneous.

Growth and Tail Regeneration

Growth rates were determined for all lizards exhibiting growth with a minimum of 10 days between captures. Using these criteria growth rates could be calculated for 80 *Cnemidophorus uniparens*.

Growth rates were variable, ranging from 0.03 mm/day to 0.6 mm/day, with an average growth rate of 0.17 mm/day for both years. There was no significant difference in mean growth rates between years (1977, mean = 0.171 mm ± 0.017 mm, and 1978, mean = 0.176 mm ± 0.023 mm). Dunham (1978) noted a direct correlation between prey availability and rate of growth in *Sceloporus merriami,* with growth

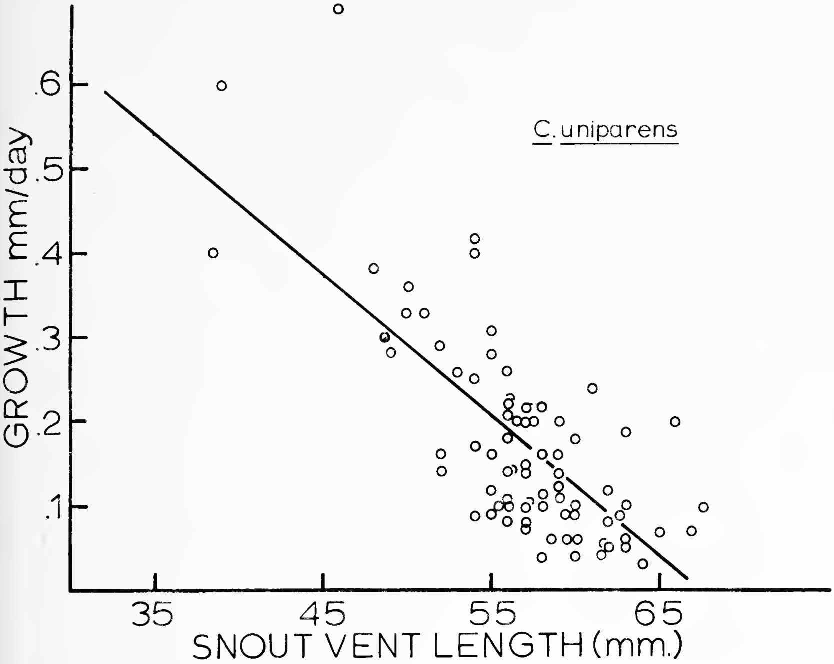

Fig. 3.—Relationship between growth rate and snout-vent size in *Cnemidophorus uniparens*.

rate being greater in years of high prey availability. However, he also noted that prey capture success was positively correlated with prey availability. In *C. uniparens* differences in prey availability between years did not influence volume of prey consumed (Hulse, personal observation). As a result of this growth rates remained unchanged even in years of varying prey availability.

Growth rate was negatively correlated with snout-vent length (Fig. 3, r = .7, $P < 0.001$), with animals below 60 mm having significantly higher growth rates than those greater than 60 mm. Highest growth rates were found among hatchlings between 32 and 50 mm (mean = 0.46 ± 0.07 mm/day, N = 6). Lowest growth rates were found for reproductively mature animals (mean = 0.098 ± 0.01 mm/day).

Growth of regenerated tails was rapid with rates ranging from 0.16 to 1.6 mm/day (mean = 0.757 ± 0.16, N = 8). There was a significant negative correlation between rate of regenerated tail and length of tail

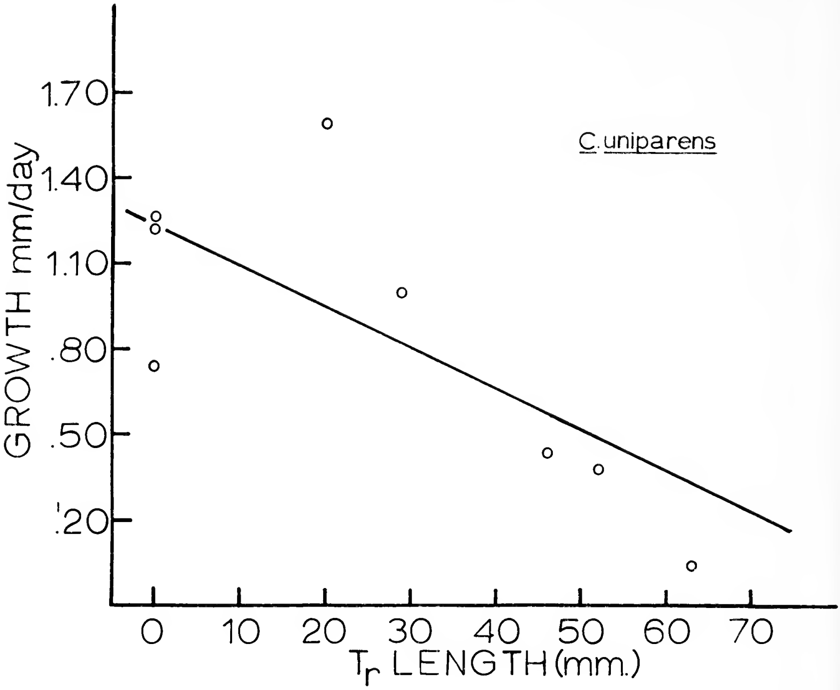

Fig. 4.—Relationship between growth of regenerated tail and length of tail already regenerated.

already regenerated (Fig. 4, r = .72, $P < 0.05$), indicating that initial growth is very rapid, but quickly tapers off as regeneration proceeds to maximum tail length.

The only other work on growth rates in *Cnemidophorus* is that of Fitch (1958) for *C. sexlineatus*. He found growth rates of approximately 0.5 mm/day for hatchling lizards from 32 to 52 mm. Larger animals grew at reduced rates, 0.22 mm/day (55–68 mm) and 0.18 mm/day (66–73 mm). His results are very similar to mine.

Energy assimilated by animals may be used for growth, maintenance, and reproduction. Apportionment of energy for growth and reproduction should be a trade-off between increased fitness through increased body size and increased reproductive effort. A sharp decline in growth rate of *C. uniparens* occurs with attainment of reproductive size, at which point most energy above the maintenance level is shunted into reproduction. One would predict that the majority of growth

Table 3.—*Population density estimates for* Cnemidophorus uniparens.

Year	Total marked	Total with two or more captures	Lincoln-Peterson estimate
1977	135	98	103 ± 6
1978	138	82	78 ± 12

in adults should occur after the reproductive season, unfortunately my data are not extensive enough to show whether or not this occurs.

Population Density, Structure, and Turnover

Population size was estimated by computing Lincoln-Peterson Indices during the middle of the collecting season (mid-June to mid-July), with a two week precensus period and a 2 week census period. Results of these estimates are listed in Table 3. Because estimates were made during mid-season, the population densities exclude hatchlings. The differences in estimates for *C. uniparens* in 1977 and 1978 are not significant. Total number of adults marked (135 and 138) was nearly identical for the 2 years. The difference between total animals marked and the density estimates is probably a function of single captures of individuals along the margin of the grid. For these animals, it may be assumed that the majority of their home range occurs off of the site and that their capture along the margin was a rare event. The number of animals captured two or more times was 98 and 82 for 1977 and 1978, respectively. These numbers are very similar to the Lincoln-Petersen Indices for those years.

Few studies have examined population densities in *Cnemidophorus*. Fitch (1958) reported densities of *C. sexlineatus* that varied from 96 to 172 animals per hectare over a 4-year period in Kansas. Clark (1976) reported population estimates ranging from 15 to 24/ha in an east-central Texas population of *C. sexlineatus*. Mitchell (1979) found *C. uniparens* to be the most abundant of four species of *Cnemidophorus* that he studied in southeastern Arizona, with a minimum density of 18 animals per hectare. Fitch's densities are most likely over-estimates caused by the long and narrow (7.6 m by 304 m) shape of his study area. The estimate of Mitchell is an underestimate because he determined densities simply by line transect counts. He suggests that actual densities are between two and three times his estimates.

Fig. 5 illustrates population structure by size class for *C. uniparens*. The data are pooled for both years, because no significant differences were noted between years. Population size structure changes with time, with the smaller size classes becoming less common as the sea-

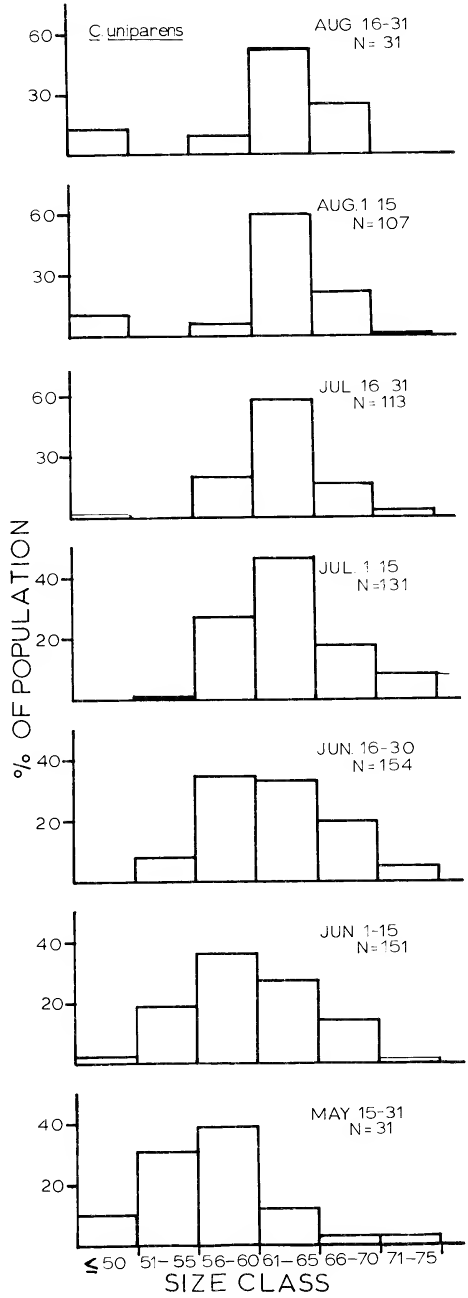

Fig. 5.—Change in size structure of *Cnemidophorus uniparens* population with time.

son progresses, until the end of the sampling periods when all individuals were either large adults or hatchlings. The data strongly suggest an annual cycle with hatchlings appearing from mid-July through August (possibly into September), rapid growth of the hatchlings in the autumn and following spring and the achievement of maturity by the beginning of the reproductive season in late May. Less than 10% of the population consisted of the larger size classes in late May, further supporting the presence of an annual turnover. Of the 135 individuals marked during the 1977 field season, only 12 (8.8%) were recaptured the following year, suggesting a very high mortality over winter in the second year animals. This assumes that all animals marked remain on the study site. There is some evidence that certain individuals have a mobile home range and that the range changes from year to year. Three of the 12 animals recaptured in 1978 had shifted home ranges to other areas of the site, in addition a few marked specimens from 1977 were collected off the site in 1978. This mobility should however, have little effect on the over-all proportion of size classes, assuming that in a homogeneous environment, such as that found in the vicinity of the study area, movement of home ranges is a random event.

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SYSTEMATICS OF *ANTROZOUS DUBIAQUERCUS* (CHIROPTERA: VESPERTILIONIDAE), WITH COMMENTS ON THE STATUS OF *BAUERUS* VAN GELDER

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Don E. Wilson[2]

Abstract

Geographic variation within *Antrozous* (*Bauerus*) *dubiaquercus* is reviewed based on examination of pelage and multivariate analyses of external and cranial measurements of 29 specimens from the Islas Tres Marias, Nayarit, Mexico, and five specimens from the mainland of Middle America. As much variation exists among mainland specimens as is found between the nominal mainland subspecies (*A. d. meyeri*) and that from the Islas Tres Marias (*A. d. dubiaquercus*), and the species is regarded as monotypic. Systematic relationships between the subgenera *Antrozous* and *Bauerus* are discussed based on several suites of characters. Differentiation between these taxa equals that found among most genera of vespertilionid bats and *Bauerus* is accorded generic rank. The karyotype of *B. dubiaquercus* is reported for the first time.

Introduction

Evolutionary relationships within and among American nyctophiline bats are poorly understood. One Recent genus, *Antrozous,* comprising two subgenera, *Antrozous* and *Bauerus,* and three species, *A.* (*A.*) *pallidus, A.* (*A.*) *koopmani,* and *A.* (*B.*) *dubiaquercus,* is recognized

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in the New World (Koopman and Jones, 1970; Pine et al., 1971; Martin, 1974; Jones et al., 1977).

Geographic variation in mensural characters of *A. pallidus* was reviewed by Martin (1974). Variation within the rare Cuban bat, *A. koopmani,* was described by Silva Taboada (1976). Although the nomenclature of populations of *A. dubiaquercus* has been in a state of flux since Van Gelder (1959) described the taxon, a review of variation among populations has not been possible because this species is rare in collections. Two nominal subspecies have been recognized—*A. d. dubiaquercus* from the Islas Tres Marias off the coast of Nayarit in western Mexico and *A. d. meyeri* from Veracruz and Honduras on the mainland of Middle America (Pine et al., 1971).

Since the description of *A. dubiaquercus* (Van Gelder, 1959) and reports of three mainland specimens by Pine (1966, 1967) and Pine et al. (1971), we have collected 42 specimens from the Islas Tres Marias and two specimens from mainland Mexico. This additional material, including karyotypic data from some specimens, led us to review variation within *A. dubiaquercus* and reevaluate systematic relationships within *Antrozous*.

MATERIALS AND METHODS

In the morphological analysis, we used 34 specimens of *A. dubiaquercus* housed in the National Museum of Natural History (USNM), Carnegie Museum of Natural History (CM), and the Texas Cooperative Wildlife Collection, Texas A&M University (TCWC) from the following localities: MEXICO. *Nayarit*: Islas Tres Marias, Maria Cleofas, 6 ♂, 8 ♀ (USNM); Maria Magdalena, 5 ♂, 7 ♀ (USNM), Maria Madre, 2 ♂, 1 ♀ (USNM). *Jalisco*: 12.5 mi SW (by road) Talpa de Allende, 4200 ft, 1 ♂ (CM). *Veracruz*: Ojo de Agua del Rio Atoyac, 1400 ft, 1 ♀ (TCWC); Rio Quezalapan, 2 mi E Lago Catemaco, 1 ♀ (TCWC). HONDURAS. 40 km E Catacamas, 1 ♂, 1 ♀ (TCWC). All specimens are adults (as defined by the fusion of the epiphyses of the metacarpals and phalanges) except the holotype of *A. d. meyeri* which is a subadult female. We also examined 13 specimens (USNM) preserved in fluid or as skeletons, and the holotype and three paratypes in the American Museum of Natural History.

The following measurements are those taken by field collectors: total length (TL) and lengths of tail (LT), hindfoot (LHF), and ear (LE). We measured length of forearm (LFA) according to Handley (1959). The following cranial measurements were taken as defined by Cockrum (1962): greatest length of skull (GLS); condyle-premaxillae length (CPL); postpalatal length (PPL); length of maxillary toothrow (LMT); zygomatic breadth (ZB); mastoid breadth (MB); least interorbital constriction (LIC); and greatest width across upper molars (GWM).

The 29 specimens from the Islas Tres Marias were combined as a single sample to test for differentiation between the sexes using the TTEST procedure of the Statistical Analysis System (SAS; Goodnight, 1979). Two multivariate programs of the Numerical Taxonomy System (NT-SYS; Rohlf and Kishpaugh, 1972) were used to assess the phenetic affinities of individual specimens. Cluster and principal components analyses were chosen because neither program requires any *a priori* assumptions concerning the within sample variation (Rohlf, 1971). Samples of *A. dubiaquercus* from the mainland are so small that calculation of within group variation is impossible. Accordingly, each specimen was considered an Operational Taxonomic Unit (OTU).

Correlation and distance matrices among OTU's were generated from standardized character values. The unweighted pair-group method based on arithmetic averages (UPGMA) was used to cluster each matrix and the results were summarized as dendrograms. In all analyses the coefficient of cophenetic correlation (a measure of the distortion of the original matrix in producing the phenogram) was larger for the distance phenogram and only these results are presented.

Principal components analysis (PCA) was performed on the correlation matrix to obtain vectors, which indicate the major trends of variation among the OTU's. Standardized values of the OTU's were then projected onto the first three axes to depict the variation among OTU's relative to the total variation within the group.

We karyotyped four specimens from Maria Madre, Maria Magdalena, and Maria Cleofas, Islas Tres Marias, and the one specimen from Jalisco. Karyotypes were prepared in the field from bone marrow cells obtained from the humeri of bats according to methods modified from Patton (1967) and Baker (1970). Terminology regarding placement of the centromere is that of Patton (1967).

RESULTS

External and Cranial Morphology

Results of the TTEST procedure for secondary sexual variation in the Islas Tres Marias sample are summarized in Table 1. Females averaged larger than males in all cranial characters except LIC (which varies inversely with size of skull) and in all external characters except LT and LE. Females were significantly larger than males ($P < 0.05$) in five of eight cranial measurements (GLS, ZB, MB, CPL, GWM) and the sexes were separated in subsequent analyses. Specimens from the Islas Tres Marias and from Veracruz are similar in external and cranial dimensions and are unlike the individuals from Honduras (especially the female) and Jalisco (Table 1).

Multivariate analyses for each sex using external and cranial characters and using cranial characters only yielded similar results. Results derived from the entire set of characters are illustrated in Figs. 1 and 2. Analyses of cranial characters are discussed only when they differ from analyses using all characters.

Cluster analyses of the distance matrices of females and males are illustrated in Fig. 1A and Fig. 1B, respectively. The respective coefficients of cophenetic correlation were 0.918 and 0.897. Most of the females are arranged in one large cluster of similar-sized bats from the Islas Tres Marias and the two individuals from Veracruz (designated as group a in Fig. 1A). When only cranial characters are analyzed the Veracruz specimens fall near the center of the main cluster. No pattern of variation corresponding to the distribution of specimens among Maria Magdalena, Maria Cleofas, and Maria Madre of the Islas Tres Marias is apparent. The female from Honduras is smaller in most cranial characters (Table 1) than the island specimens or those from Veracruz and is a distant outlier (designated as b in Fig. 1A) of group a.

Cluster analysis of males yielded three groups (designated a, b, and

Table 1.—*Measurements and summary statistics for samples of* Antrozous dubiaquercus. *T statistics given for the Islas Tres Marias sample were used to test for sexual dimorphism and asterisks indicate levels of significance (**P < 0.05; **P < .01*). Abbreviations of characters are defined in text. Values in the Veracruz sample are for specimens from localities near Lago Catemaco and Ojo de Agua del Rio Atoyac, respectively. N = 12 for zygomatic breadth of males in the Islas Tres Marias sample.*

	Islas Tres Marias		Jalisco	Veracruz	Honduras	
Character	Females (N = 16) mean ± 1 SD (range)	Males (N = 13) mean ± 1 SD (range)	Male (N = 1) value	Females (N = 2) values	Female (N = 1) value	Male (N = 1) value
TL	122.1 ± 3.05 (115–126)	121.8 ± 3.14 (117–126)	104	107, 120	115	115
	T = −.31					
LT	50.9 ± 1.77 (47–53)	52.2 ± 2.58 (49–57)	46	46, 55	48	47
	T = 1.50					
LHF	12.8 ± .75 (12–14)	12.5 ± .66 (12–14)	11	12, 13	10	10
	T = −1.03					
LE	24.9 ± 2.45 (20–27)	25.5 ± 1.33 (23–27)	22	24, 25	23	22
	T = .93					
LFA	55.2 ± 1.51 (50.50–57.05)	54.3 ± 1.43 (50.55–55.80)	50.20	52.00, 55.90	50.70	47.90
	T = −1.67					
GLS	21.01 ± .24 (20.55–21.50)	20.67 ± .27 (20.25–21.25)	19.25	21.20, 21.50	20.55	19.90
	T = −3.66**					
ZB	13.11 ± .23 (12.65–13.45)	12.86 ± .21 (12.50–13.20)	12.50	13.05, 12.90	12.85	12.40
	T = −2.88**					
MB	10.04 ± .15 (9.75–10.35)	9.86 ± .15 (9.50–10.10)	9.60	10.00, 9.95	9.65	9.40
	T = −3.17**					
CPL	18.75 ± .22 (18.35–19.15)	18.42 ± .31 (17.95–19.15)	17.65	18.90, 18.70	18.20	17.70
	T = −3.35**					
PPL	6.73 ± .18 (6.20–7.00)	6.62 ± .14 (6.30–6.85)	6.30	6.50, 6.20	6.20	5.80
	T = −1.65					
LIC	3.98 ± .08 (3.85–4.10)	4.01 ± .10 (3.85–4.20)	4.05	3.95, 3.90	4.20	4.15
	T = .79					
LMT	7.16 ± .08 (7.05–7.30)	7.09 ± .13 (6.90–7.40)	6.60	7.15, 7.25	7.05	6.95
	T = −1.64					
GWM	8.09 ± .14 (7.75–8.25)	7.94 ± .11 (7.80–8.15)	8.00	8.30, 8.20	7.75	7.75
	T = −2.40*					

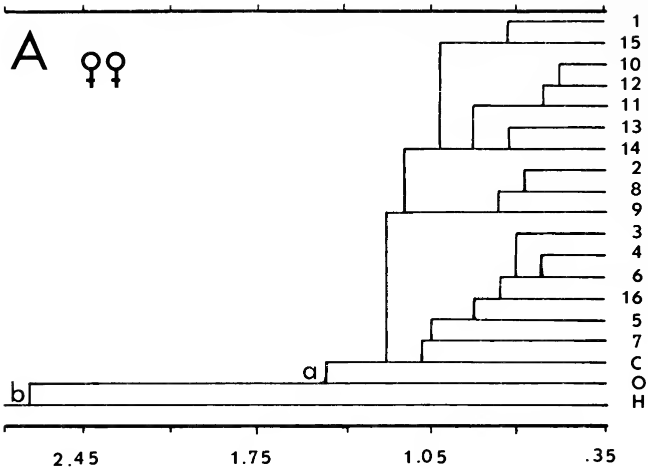
c in Fig. 1B). Group a comprises the specimens from Maria Madre and Honduras, which are slightly smaller in external and cranial dimensions than those from Maria Cleofas and Maria Magdalena. Group b consists of a mixture of specimens from Maria Cleofas and Maria Magdalena. The male from Jalisco (group c) is smaller in most cranial measurements than any other specimen analyzed (see Table 1). In cranial dimensions, this individual is most similar to the female specimen from Honduras but appears proportionately smaller in several characters (most notably GLS, CPL, LMT). Although morphologically adult, the sagittal crest of the Jaliscan specimen is less developed and the skull is more delicate than in any other bat examined.

Results of the PCA are given in Table 2 and Fig. 2. Each character, except least interorbital constriction, is highly and positively correlated with principal component I in all analyses, causing OTU's to be dispersed along this component on the basis of overall size.

Along principal components I and II, females (Fig. 2A) from the Islas Tres Marias and Veracruz form one group and the single OTU from Honduras appears as a distant outlier, paralleling the results of the cluster analysis. The position of the specimen from Honduras on principal component I reflects the small size of this individual. The two specimens from Veracruz separate slightly from the remainder of the OTU's along principal component III which is most correlated with the characters TL, LFA, PPL, LIC, and GWM. When cranial characters alone are considered, only the specimen from near Lago Catemaco, Veracruz, can be differentiated along the third axis.

In males (Fig. 2B), the island OTU's form one diffuse cluster along principal component I and the specimens from Honduras and Jalisco appear as outliers. The males from Jalisco and Maria Madre separate from one another and from the remaining OTU's along principal component II (highly correlated with TL, LHF, GLS, ZB, MB, and GWM), whereas the specimen from Honduras is distinct along principal component III (highly correlated with GLS, ZB, PPL, LIC, and LMT).

When cranial characters alone are considered for males, positions among the island OTU's with respect to the first three principal components are similar to those obtained using all characters; however, the specimen from Honduras does not separate from the island OTU's along principal components I or III but groups with the Isla Maria Madre specimen along all three principal components. Cranial similarities between these specimens probably account for their close association in the cluster analysis (Fig. 1B). The position of the Jaliscan specimen is similar in both PCA runs but its distinctness along principal components I and II is emphasized when only cranial characters are considered.



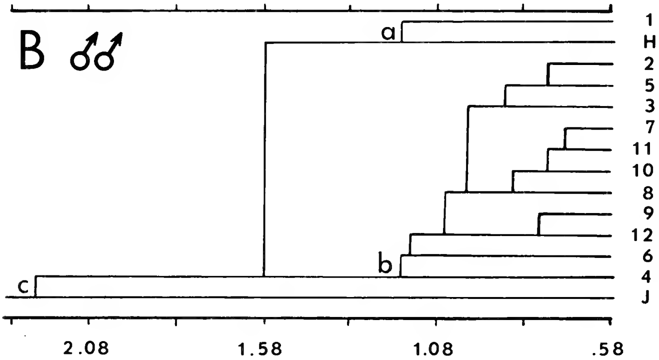


Fig. 1.—Distance phenograms resulting from cluster analyses of females and males of *Antrozous dubiaquercus,* considering each specimen as an OTU. Lower case letters indicate clusters mentioned in text. A) Females; localities of specimens numbered 1 =

Table 2.—*Eigenvalues, percentage of total variance, and character loadings for the first three components resulting from Principal Components Analyses of females and males of* Antrozous dubiaquercus. *Percentage of total variance is cumulative. Abbreviations of characters are defined in text.*

Statistics and characters	Females Components I	Females Components II	Females Components III	Males Components I	Males Components II	Males Components III
Eigenvalue	6.8	1.9	1.3	6.6	1.7	1.5
% total variance	52.4	67.4	77.3	50.9	64.0	75.6
TL	0.46	−0.26	0.70	0.79	−0.43	0.09
LT	0.50	−0.54	0.19	0.71	−0.03	0.27
LHF	0.87	−0.29	−0.07	0.55	−0.34	0.28
LE	0.47	−0.58	−0.21	0.68	0.03	0.09
LFA	0.71	0.10	0.31	0.73	0.08	−0.09
GLS	0.92	0.02	−0.27	0.87	−0.33	−0.30
ZB	0.83	0.45	0.12	0.64	0.48	−0.45
MB	0.86	0.37	0.10	0.81	0.49	−0.14
CPL	0.94	0.11	−0.12	0.88	−0.14	−0.10
PPL	0.57	0.00	0.48	0.80	0.17	0.42
LIC	−0.43	0.70	0.32	−0.55	−0.14	−0.75
LMT	0.86	−0.05	−0.23	0.75	−0.27	−0.52
GWM	0.68	0.56	−0.35	0.32	0.82	−0.01

Karyology

The diploid number (2n) of *A. dubiaquercus* is 44 and the number of autosomal arms (FN) equals 52 (Fig. 3). The autosomal complement comprises two large, one medium-sized, and two small pairs of metacentric chromosomes and a graded series of 16 pairs of medium-sized to small acrocentrics. The X chromosome is a medium-sized submetacentric and the Y is a small acrocentric. No chromosomal variation was found among individuals.

DISCUSSION

Geographic Variation

As noted by Bogan (1978), variation between populations of bats inhabiting the Islas Tres Marias and those inhabiting the mainland is

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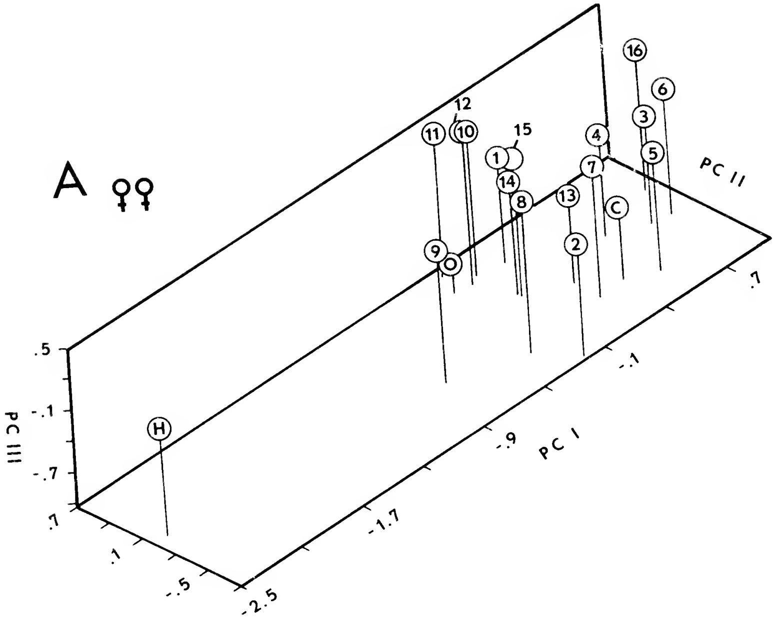
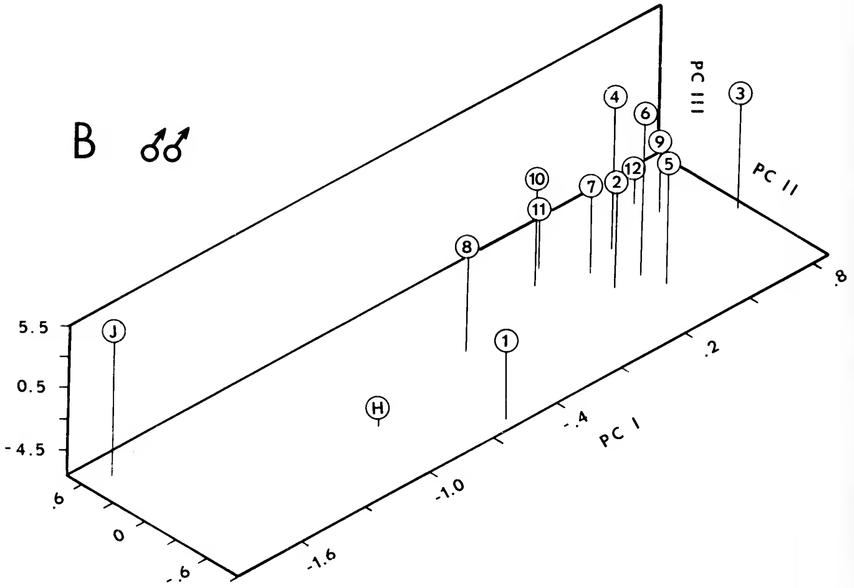
Maria Madre, 2–8 = Maria Magdalena, and 9–16 = Maria Cleofas, Islas Tres Marias. Abbreviated localities of specimens designated as C = Lago Catemaco, Veracruz, O = Ojo de Agua, Veracruz, and H = Honduras. B) Males; localities of specimens numbered 1 = Maria Madre, 2–6 = Maria Magdalena, and 7–12 = Maria Cleofas, Islas Tres Marias. Abbreviated localities of specimens designated as J = Jalisco and H = Honduras.


A ♀♀
16
6
12
3
11
10
15
4
5
1
7
PC II
14
13
8
C
2
9
O
.7
.5
-.1
PC III
-.1
H
-.9
PC I
-.7
.7
-1.7
.1
-.5
-2.5


B ♂♂
PC III
3
4
6
9
12
5
PC II
10
7
2
11
8
.8
5.5
J
1
.2
0.5
H
-.4
PC I
-4.5
-1.0
.6
0
-1.6
-.6

of especial interest because of the high degree of endemism on the islands. However, patterns of variation among populations of *A. dubiaquercus* are difficult to interpret.

Specimens from the Islas Tres Marias are morphometrically inseparable from those from Veracruz except on the basis of color. The male and female from the same locality in Honduras appear to differ as much from one another in several external and cranial characters as either does from specimens from other geographic areas. Mensurally, the bat from Jalisco was the most divergent specimen examined although it is from the nearest mainland locality to the Islas Tres Marias. As much variation is evident among some mainland specimens as appears between those from the islands and the mainland. Thus, the current assignment of one subspecific epithet to populations inhabiting the Islas Tres Marias (*dubiaquercus*) and another to all populations inhabiting the mainland (*meyeri*) is arbitrary.

Mensural variation within *A. dubiaquercus* is not concordant with variation in color. All mainland specimens have dark ears, rhinaria, and flight membranes, whereas exposed membranes in specimens from the Islas Tres Marias are paler. Variation in color of dorsal pelage is similar, with darker specimens occurring on the mainland and somewhat paler specimens on the islands, although the dorsal coloration of the specimen from Jalisco and the one from Ojo de Agua, Veracruz, is similar to that of individuals from the Islas Tres Marias.

Differences in color among island and mainland specimens probably reflect adaptations to local environmental conditions. Individuals from the Islas Tres Marias occupy tropical deciduous forest (Fig. 4A), whereas specimens from the mainland were taken in lowland tropical evergreen forest (Fig. 4C) with the exception of the bat from Jalisco, which was collected in moist pine-oak forest. Presumably, background coloration in deciduous forest (at least during the dry season) is paler than that in more mesic, evergreen forest, and overall coloration of *A. dubiaquercus* probably is responding directly to selective pressures to match these backgrounds.

Relationship of Antrozous *to* Bauerus

Van Gelder (1959) described *Antrozous dubiaquercus* based on five specimens from the Islas Tres Marias, Nayarit, and assigned the

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Fig. 2.—Projections of individual specimens of *Antrozous dubiaquercus* onto the first three components for: A, females; and B, males. Identifying numbers and letters are referred to localities (see Fig. 1). The scale of each component is drawn relative to the percent influence of that component on the total variance (see Table 2).

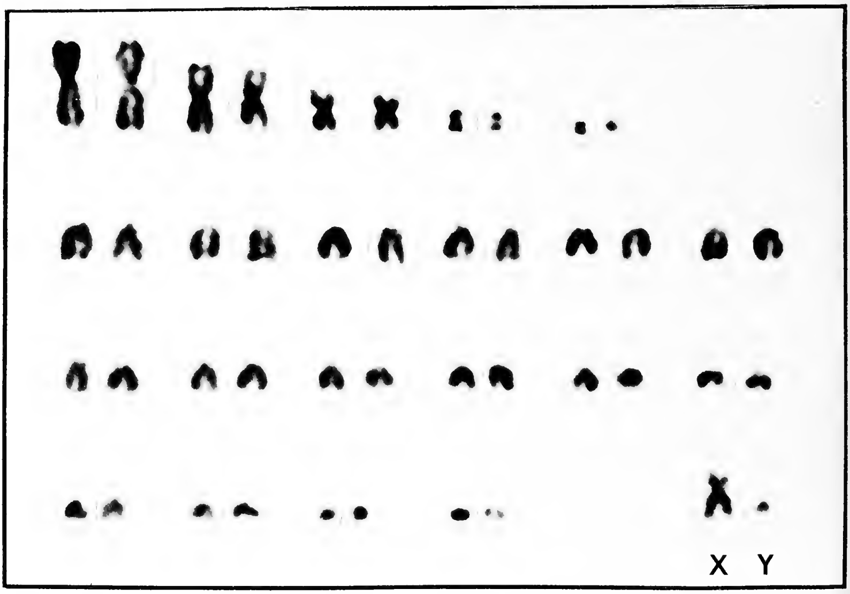

Fig. 3.—Karyotype of a male *Antrozous dubiaquercus* (2n = 44, FN = 52).

species to a new subgenus, *Bauerus*. White (1969) proposed that *Bauerus* be recognized at the generic level based on the presence of an extra lower incisor in *dubiaquercus*. White (1969) included *A. koopmani* within *Antrozous* because it lacks a third lower incisor; however, Martin (1974) and Silva Taboada (1976) noted similarities of this species to *Bauerus*. Pine et al. (1971) described several differences in the morphology of the phallus between *Antrozous* (represented by *A. pallidus*) and *Bauerus* but noted that the presence of a third lower incisor in *Bauerus* was not constant and proposed that the differences separating the higher taxa would best be recognized at the subgeneric level (a third lower incisor is present on at least one ramus of 43 of the 44 additional specimens examined by us and was found in all of the specimens examined by Pine et al., 1971, except the holotype of *A. dubiaquercus*). In the same paper, they regarded the mainland taxon *A.* (*B.*) *meyeri* as a subspecies within *A.* (*B.*) *dubiaquercus*. Martin (1974) noted additional external differences between the phalli of *A.* (*A.*) *pallidus* and *A.* (*B.*) *dubiaquercus* but proposed no taxonomic changes. No phallic data are available for *A. koopmani*.

Antrozous pallidus and *A. dubiaquercus* share several penile characteristics (for example, a dorsally inclined baculum and dorsally ex-

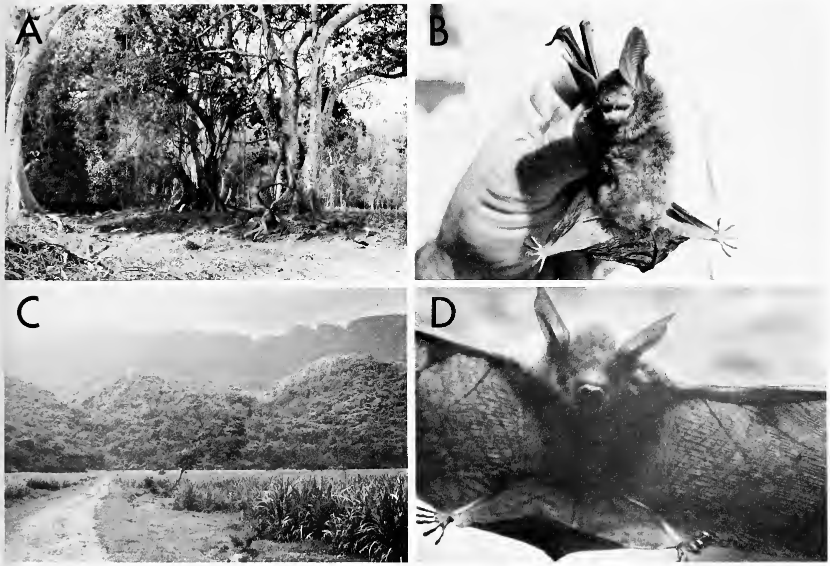

Fig. 4.—A) Tropical deciduous forest on Maria Madre, Islas Tres Marias. B) An *Antrozous dubiaquercus* taken in the habitat shown in A. C) Lowland tropical evergreen forest at Ojo de Agua, Veracruz. D) The *A. dubiaquercus* collected in the habitat shown in C. Photographs A and B by C. B. Robbins; C and D by D. S. Rogers.

posed urethra) not found in other New World vespertilionids, indicating that *Antrozous* is a monophyletic taxon; however, external differences between the male genitalia of the two species are marked. Pine et al. (1971:668) remarked, "although the difference between the penes of *A. dubiaquercus* and *A. pallidus* are rather substantial when one considers that there seems to be little variation in penis structure even between genera in other subfamilies of vespertilionid bats (as far as known), we prefer not to use phallic evidence to determine the rank of *Bauerus* until something is known about the phallus of *Antrozous koopmani*."

Karyotypes of *A. pallidus* and *A. dubiaquercus* also differ. *Antrozous pallidus* possesses a 2n of 46 and FN of 50 (Baker and Patton, 1967; Bickham, 1979) whereas *A. dubiaquercus* has 2n = 44, FN = 52. If the karyotype of *A. dubiaquercus* were derived from a chromosomal complement consisting of more acrocentric elements, such as that of *A. pallidus* (the direction of chromosomal evolution hypothesized by Bickham, 1979, for the karyotypic group containing *A. pallidus*), a minimum of two chromosomal changes could account for the karyotypic differences between the two species. A Robertsonian fusion of two small acrocentric elements and a pericentric inversion or heterochromatic addition in a second small acrocentric chromosome in the karyotype of *A. pallidus* would yield a karyotype similar to that of *A. dubiaquercus*. Chromosomal banding studies might reveal other rearrangement differences between these taxa. Intrageneric karyotypic variation in vespertilionid bats, however, is uncommon (see review by Bickham, 1979).

TAXONOMIC CONCLUSIONS

We prefer to assign subspecific epithets to biological subunits of species, rather than to catalogue geographic variants (see definition of subspecies by Lidicker, 1962). Given the extensive variation among populations of *A. dubiaquercus* and the lack of specimens, it is not possible to identify biologically meaningful subunits; moreover, the present arrangement of subspecies masks the pattern of variation (or lack thereof) among specimens. Accordingly, we regard *A. dubiaquercus* as monotypic.

The chromosomal, cranial (described in detail by Van Gelder, 1959; Pine, 1966, 1967), postcranial (Martin, 1974), and phallic differences between *Antrozous* (*Antrozous*) *pallidus* and *Antrozous* (*Bauerus*) *dubiaquercus* are at least as great as those found among most genera of vespertilionid bats and indicate a long history of genetic isolation. We believe that *Bauerus* is a distinct genus. *Antrozous koopmani* apparently lacks the diagnostic third lower incisor of *Bauerus* (Silva Taboada, 1976) and we tentatively retain this species in *Antrozous*. The following synonomy applies to *Bauerus*.

Bauerus dubiaquercus (Van Gelder)

1959. *Antrozous* (*Bauerus*) *dubiaquercus* Van Gelder, Amer. Mus. Novit., 1973:2, 19 November.
1966. *Baeodon meyeri* Pine, Southwestern Nat., 11:308, 30 June.
1967. *Antrozous* (*Bauerus*) *meyeri,* Pine, Southwestern Nat., 12:485, 31 December.
1969. *Bauerus dubiaquercus,* White, Misc. Publ. Mus. Nat. Hist., Univ. Kansas, 51:277, 11 July.
1971. *Antrozous dubiaquercus meyeri,* Pine et al., J. Mamm., 52:665, 16 December.

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AN ADDITIONAL RECORD OF *MYONYCTERIS RELICTA* BERGMANS, 1980, FROM TANZANIA (MAMMALIA: CHIROPTERA)

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Abstract

A fourth specimen of the East African relict collared fruit bat, *Myonycteris relicta* Bergmans, 1980, is reported. This specimen, from the Nguru Mountains of central Tanzania, supports the contention of a previous connection between East African mountain forests with central African counterparts. External and cranial measurements of the new specimen are compared with other reported *M. relicta* and a sample of *M. torquata*.

In the course of checking the old holdings of Megachiroptera in the Section of Mammals, a unique specimen was found among the *Rousettus* and *Myonycteris* in the collection. Closer examination of this bat revealed it to be a specimen of *Myonycteris relicta* Bergmans, 1980.

Standard external measurements were taken from the specimen label. The remaining measurements were taken in millimeters by means of a dial caliper. The cranial measurements given are based on those published by Bergmans (1980:174).

On 19 September 1960, a single adult adult female *Myonycteris relicta* (CM 57685) was captured at 3000 feet elevation in the Nguru Mountains of Tanzania by John Williams and Arthur C. Twomey. This individual is the fourth reported example of the species and extends

Submitted 4 February 1981.

Table 1.—*Selected external and cranial measurements of* Myonycteris relicta *and* M. torquata *from East and Central Africa.*

	Myonycteris relicta				*Myonycteris torquata*	
Measurements	Tanzania: Nguru Mts., 3000 ft. CM 57685 ♀	Kenya: Shimba Hills RMNH 27909 ♂ (holotype)*	Tanzania: Ambangulu, Usambara Mts. ZMB 54936 ♂*	Tanzania: Ambangulu, Usambara Mts. ZMB 54937 ♀*	Northeastern Zaire and adjacent Uganda ♀♀**	Northeastern Zaire and adjacent Uganda ♂♂**
Total length	120	124	—	—	112, 114	102, 130
Tail length	5	9	—	8.3	6, 12	4, 10
Hindfoot length	17	22	20.5	20	18, 22	15, 18
Ear length	17	19	—	19.9	19, 20	18, 18
Forearm length	65.9	69.3	—	75.1	60.3, 64.4	61.8 (60.3–64.6) 6
Tibia length	26.1	26.7	—	29.1	—	—
Third metacarpel length	46.0	49.5	48.9	53.3	—	—
Third digit, first phalanx length	31.5	32.4	33.8	35.8	—	—
Fourth metacarpel length	43.9	46.4	46.4	50.8	—	—
Fourth digit, first phalanx length	25.7	24.7	—	26.5	—	—
Fifth metacarpel length	44.5	46.0	46.6	51.7	—	—
Fifth digit, first phalanx length	20.8	21.9	—	24.3	—	—
Greatest length of skull	35.9	36.4	36.5	39.2	32.5, 33.3	33.3 (33.2–33.5) 3
Condylobasal length	34.9	35.0	34.8	38.9	31.4, 32.1	31.8 (31.1–32.3) 3
Rostrum length	12.8	13.0	13.4	15.1	11.0, 11.5	11.7 (11.4–11.9) 5
Palatal length	19.2	19.6	19.0	21.1	17.2, 18.1	18.2 (18.0–18.4) 3
Breadth of braincase	14.6	14.7	15.9	14.9	12.6, 12.8	13.6 (13.2–14.1) 4

Table 1.—*Continued.*

	Myonycteris relicta				*Myonycteris torquata*	
Measurements	Tanzania: Nguru Mts., 3000 ft. CM 57685 ♀	Kenya: Shimba Hills RMNH 27909 ♂ (holotype)*	Tanzania: Ambangulu, Usambara Mts. ZMB 54936 ♂*	Tanzania: Ambangulu, Usambara Mts. ZMB 54937 ♀*	Northeastern Zaire and adjacent Uganda ♀♀**	Northeastern Zaire and adjacent Uganda ♂♂**
Interorbital width	7.0	7.1	7.3	8.1	5.5, 5.6	5.7 (5.3–5.9) 5
Postorbital width	8.5	8.9	9.7	8.2	7.3, 7.9	7.6 (7.0–8.1) 3
Zygomatic breadth	21.1	21.4	—	—	19.4	19.8 (19.3–20.7) 4
Mandibular length	27.6	27.9	28.2	30.4	25.2, 25.9	25.6 (25.1–26.0) 5
Width across upper canines	6.6	6.9	7.1	7.8	6.3	6.5 (6.1–6.7) 5
Length of maxillary toothrow	12.9	13.4	13.3	14.9	11.9, 12.2	12.3 (11.7–12.9) 6
Width across upper molars (M2–M2)	—	10.3	10.5	—	—	9.1 (8.0–9.6) 5
Length of mandibular toothrow (cl–m2)***	13.2	13.6	13.4	14.5	13.2, 13.4	13.7 (13.3–13.9) 5

* Measurements from Table 1, Bergmans (1980:174).
** Measurements from Table 5, Bergmans (1976:201); given are mean, range, and sample size.
*** Measurement of *M. torquata* includes m3.

the known range of the species inland in Tanzania to the Nguru Mountains from the other two places of reported occurrence—Mukanda River, Shimba Hills, Kenya, and Ambangulu, Usambara Mountains, Tanzania. Mensural data for the specimen are given in Table 1.

Externally and cranially this new specimen agrees well with the three individuals reported by Bergmans (1980). Noteworthy characteristics include the absence of the lower third molars, the enlarged lower third premolar (p4) and upper third premolar (P4), and the lingual inclination of a line through the upper molars and last premolar. In size, the new specimen is smaller than the three reported by Bergmans (1980). See Table 1 for comparison of selected external and cranial measurements.

Several measurements of the new specimen fall within the range of measurements of a sample of *Myonycteris torquata* from Uganda and Zaire (Table 1). This is the closest sample of *M. torquata* to the known records of *M. relicta* (Bergmans, 1976, 1980). Overlapping measurements include forearm (see also Bergmans, 1976:199, 205), width across upper canines, and length of maxillary toothrow. In spite of this, *M. relicta* is larger than *M. torquata*. The nearest localities of record for *M. torquata* are Bwamba Forest, Uganda, and Salujinga, Zambia (Bergmans, 1976).

The Nguru Mountains are a small mountain chain running southwest to northeast at approximately 6° S, 37°30′ E in Tanzania. Available field notes indicate that John Williams collected birds and some mammals at three places in the Nguru Mountains on 19 September 1960. Specimens were collected in the "Manyangu Forest" from 17 to 19 September, in the "east foothills" on 19 and 20 September, and in the "eastern Nguru Mountains" on 19 September. Unfortunately we are not able to say precisely from which of these three sites, or perhaps another one, the *Myonycteris relicta* came, except that it was taken at 3000 feet elevation.

In his description, Bergmans (1980:180) considered *Myonycteris relicta* a species confined to relict forest remnants in East Africa. Its occurrence there was considered another indication of previous corridors connecting these forests with central and western African forest counterparts. Although the type locality, Mukanda River in the Shimba Hills, Kenya, is in lowland forest, few large blocks of forest remain in East Africa except in the remnant forests of the mountainous regions. Such remnant forest is present in the Nguru Mountains and the occurrence of *M. relicta* there supports Bergmans (1980:180) contention. In addition, this specimen would seem to indicate that the species should be looked for in suitable forests in other mountainous regions of southern Tanzania, namely the Rubeho and Uzungwa mountains and perhaps even the Livingstones, Porotos and Mount Rungwe, and adjacent elevated regions of Zambia and Malawi (Keay, 1959). The remnant forests of the mountains along Lake Tanganyika could also harbor this species, as these serve as the connecting link between the southern forest block of Tanzania and extreme southeastern Kenya and comparable forests in Zaire (Moreau, 1952). The southern forests had been effectively separated from western Kenyan counterparts by an extension of the Somali Arid Zone through central Kenya into northcentral Tanzania (Moreau, 1952:889; Keay, 1959).

This specimen was collected as part of a natural history collection made under the auspices of the 1960 Matthew T. Mellon-Carnegie Museum East African Expedition, sponsored by Matthew T. Mellon and the Matthew T. Mellon Foundation. The aforementioned collectors as well as James R. Mellon are gratefully acknowledged for collecting and preparing mammal specimens.

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SKULL OF THE LOWER PERMIAN DISSOROPHID AMPHIBIAN *PLATYHYSTRIX RUGOSUS*

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Abstract

Description of the skull of the labyrinthodont amphibian *Platyhystrix rugosus*, presented for the first time, is based primarily on a specimen collected by David Baldwin in 1881 in the Lower Permian Cutler Formation near Arroyo del Agua of north-central New Mexico. The specimen is the greater part of a skull and associated partial axial skeleton. Additional skull fragments of *P. rugosus* provide further information on the structure of the skull. The skull of *P. rugosus* exhibits a structural pattern that confirms previous tentative assignments of this genus to the Dissorophidae based solely on vertebral structure. *Astreptorhachis ohioensis* from the Upper Pennsylvanian Conemaugh Group of Ohio, considered closely related to *P. rugosus* on the basis of its vertebral structure, can similarly be assigned to the Dissorophidae. As previously suspected, both species are probably members of a distinct and widely divergent assemblage of armored dissorophids that separated from the central stock during the Middle or Late Pennsylvanian. The occurrence of armored vertebrae within the dissorophids is otherwise unknown until the Early Permian, but its early appearance in this lineage is consistent with the advanced state of the skull of *P. rugosus*.

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INTRODUCTION

Platyhystrix rugosus is one of the more frequently encountered Lower Permian rhachitomous amphibians. Its anatomy and phylogenetic relationships have been until now poorly known, however, because only the dorsal portion of the axial skeleton has been adequately described (Langston, 1953; Lewis and Vaughn, 1965). With the exception of the distinctive neural spines, the dorsal vertebrae have the typical rhachitomous pattern. The spines are greatly elongated, laterally compressed, and distally expanded in the sagittal plane; except for a short proximal portion, the spines exhibit a nodular sculpturing or ornamentation that is presumably dermal in origin (Vaughn, 1971). Dermal sculpturing of the same type but heavier has also been reported on the outer surface of the ribs (Langston, 1953). A series of *Platyhystrix* neural spines illustrated by Lewis and Vaughn (1965) from the Lower Permian Cutler Formation of southwestern Colorado shows clearly that in lateral view the spines formed a greatly expanded sail with a strongly convex dorsal edge. This structure is somewhat analogous to the sail of some pelycosaurian reptiles. To date, only a few cranial fragments from the Lower Permian Cutler Formation of north-central New Mexico have been confidently assigned to *Platyhystrix*; they also exhibit a sculpturing similar to that seen on the neural spines and ribs (Langston, 1953).

The unusual neural spines of *Platyhystrix* have been found in nearly all Lower Permian (Wolfcampian) collecting areas of the Four Corners region of the United States; these include southeastern Utah, southwestern Colorado, and widely scattered areas of New Mexico (Olson and Vaughn, 1970). Carroll (1964) has described several dissorophid spines from two localities in the Lower Permian of Texas that he assigned to *Aspidosaurus* without specific designation. The armor on these neural spines varies in structure from the short, roof-shaped pieces capping the swollen tops of the spines, as in *Aspidosaurus chiton*, to that approaching the armor seen in *Platyhystrix*. Vaughn (1971) noted, however, that the armor of these spines, in which the ornamentation tends to form anastomosing ridges separated by large pits, differs from that of *Platyhystrix*, in which large tubercle-like protuberances tend to be separate; he considered the Texas spines as probably not *Aspidosaurus* but representing an unnamed genus. Lewis and Vaughn (1965) suspected that the same sort of confusion led Langston (1953:405) to state that "Somewhat differently sculptured spines from Texas mentioned by several authors under various names probably belong to other species of *Platyhystrix*." There is at present no evidence to indicate that more than one species of *Platyhystrix* existed or that its distribution extended beyond the Four Corners region. All occurrences of *Platyhystrix* can be considered Lower Permian with one possible exception—El Cobre Canyon in Rio Arriba County of north-central New Mexico. The Cutler Formation beds in this rather limited area have been judged both Early Permain (Vaughn, 1963) and Late Pennsylvanian (Fracasso, 1980). Both assignments merit serious consideration and this controversy can only be satisfactorily resolved through better collections and detailed stratigraphic studies.

Langston (1953) has summarized concisely the taxonomic history of *Platyhystrix* and its confusion with other, non-dissorophid genera. On the basis of the vertebral materials available to him, he concluded that the genus probably represents an unnamed family perhaps allied to the eryopoids. In a phylogenetic chart of the Dissorophidae, Carrol (1964) showed *Platyhystrix* as an offshoot of the *Aspidosaurus* assemblage; this was done presumably on the basis of their similar vertebrae. He further suggested that the *Aspidosaurus-Platyhystrix* assemblage separated from the remainder of the dissorophids late in the Pennsylvanian or early in the Permian. A somewhat more conservative view was taken by Lewis and Vaughn (1965), who considered *Platyhystrix* to be either closely related to or a member of the Dissorophidae. This was based partly on the observation that within the wide structural variety of neural spines possessed by *Aspidosaurus* are some that approach those of *Platyhystrix*. DeMar (1968) also noted the similarities between the neural spines of *Platyhystrix* and those of some species of *Aspidosaurus,* particularly *A. chiton,* but included *Platyhystrix* in the Dissorophidae as an independent armored lineage of unknown derivation. He also extended the fossil record of *Platyhystrix* into the Late Pennsylvanian on the basis of a report by Lewis and Vaughn (1965) of a *Platyhystrix*-like specimen of that age. This specimen, consisting of neural arches and spines from the Upper Pennsylvanian Conemaugh Group of Ohio, was described by Vaughn (1971) as a new genus and species, *Astreptorhachis ohioensis*. Vaughn pointed out that these two taxa are closely related and probably represent an early armored dissorophid lineage, but cautioned that future discoveries may prove them to belong to a family other than the Dissorophidae.

All of the *Platyhystrix* specimens described here were collected from the Lower Permian Cutler Formation near Arroyo del Agua, Rio Arriba County, of north-central New Mexico. Langston (1953) listed five small *Platyhystrix* skull and jaw fragments that were among field collections made by parties from the University of California, Berkeley, in 1934 and 1935. His assignment was based on their extremely papillose sculpturing which matches that seen on ribs belonging to this genus. Three cranial or mandibular fragments, and five probably associated neural spines and a rib were collected from the Quarry Butte locality and catalogued as UCMP 39090. One of the skull fragments was illustrated (Fig. 22e; mistakenly referred to UCMP 39092 in the legend) and described by Langston but not identified; it may be an angular. The most revealing UCMP 39090 fragment contains the left postorbital and most of the squamosal, and preserves most of their contributions to the posterior orbital rim and otic notch. The third fragment appears to be from the orbital rim and may be part of the right postorbital. The remaining two fragments, UCMP 39092, were found isolated and their precise locality is unknown. One, illustrated (Fig. 22f) and described by Langston as possibly belonging to the articular region of the lower jaw, is probably a left surangular. The second fragment, neither described nor illustrated, is a right tabular.

The most significant cranial specimen of *Platyhystrix* was discovered by David Baldwin in 1881. He collected the greater part of a large skull, AMNH 11545, that was apparently closely associated with a large portion of an axial skeleton of *Platyhystrix,* AMNH 11544. Neither specimen has been described. Although the skull is not in direct articulation with the postcranial skeleton, there is good reason to believe that these belonged to one individual. This is supported not only by the presence of a fragmentary *Platyhystrix* neural spine on the ventral surface of the skull, but also by the fact that one of the spine fragments assigned to AMNH 11544 can be fitted to this spine. AMNH 11545 and AMNH 11544 are also of appropriate sizes to be part of a single individual. The only specific locality data accompanying this material states, "east side of Rito Puerco." It is very likely that "Rito Puerco" is a synonym for Rio Puerco, a small river that flows northeast through the classic Cutler Formation collecting beds of the Arroyo del Agua area. It is probable that the specimens were collected in the vicinity of the well known quarries about ½ mi southeast of the village of Arroyo del Agua (Langston, 1953).

The skull materials show a structural pattern similar to that of dissorophid amphibians, confirming previous tentative assignments based on vertebrae that *Platyhystrix,* and very probably *Astreptorhachis,* belong in the Dissorophidae.

Abbreviations AMNH and UCMP are used to refer to collections of the American Museum Natural History and the Museum of Paleontology, University of California, Berkeley, respectively.

Key to abbreviations used in the figures:

bo = basioccipital
cp = cultriform process
ect = ectopterygoid
ex = exoccipital
f = frontal
fo = fenestra ovalis
pal = palatine
pf = postfrontal
pm = premaxilla
po = postorbital
pop = paroccipital process of opisthotic
pp = postparietal

j = jugal
l = lacrimal
m = maxilla
n = nasal
ns = neural spine
oc = occipital condyle
op = opisthotic
p = parietal
pa = parasphenoid
prf = prefrontal
pt = pterygoid
qj = quadratojugal
sph = sphenethmoid
sq = squamosal
st = supratemporal
t = tabular
v = vomer
IX–X, XII = cranial nerve foramina

SYSTEMATIC PALEONTOLOGY

Class Amphibia
Order Temnospondyli
Suborder Rhachitomi
Superfamily Dissorophoidea Bolt, 1969
Family Dissorophidae Boulenger, 1902

Platyhystrix Williston, 1911

Type species.—Platyhystrix rugosus (Case, 1910).

Revised diagnosis.—Large dissorophid temnospondyl that differs from all other members of family in the following features: presence of nodular or papillose dermal sculpturing along lateral borders of skull table and adjoining portions of cheek between orbit and otic notch, on all but a small proximal portion of neural spines and on proximal portions of lateral surfaces of dorsal ribs; neural spines of dorsal vertebrae greatly elongated, flattened from side to side and greatly expanded anteroposteriorly toward their distal ends to form an extensive dorsal sail. The following combination of characters distinguishes the skull from those of other dissorophids: nasal long and narrow with length nearly three times width and equal to over one third the midline length of skull; large parietal extends anteriorly beyond level of posterior margin of orbit; length of postfrontal greater than twice its width and equal to length of supratemporal; dorsal exposure of postorbital nearly equal to length of supratemporal; cheek steeply inclined and meets skull table at nearly right angle; squamosal restricted to cheek; otic notch not closed posteriorly; cultriform process of parasphenoid very narrow.

Platyhystrix rugosus (Case, 1910)

Holotype.—AMNH 4785, a few neural spines of dorsal vertebrae from Cope collection.

Referred specimens.—AMNH 11544, partial axial skeleton, and AMNH 11545, partial skull, almost certainly belonging to a single individual; UCMP 39090 and UCMP 39092, fragments of skull, dorsal vertebrae and ribs.

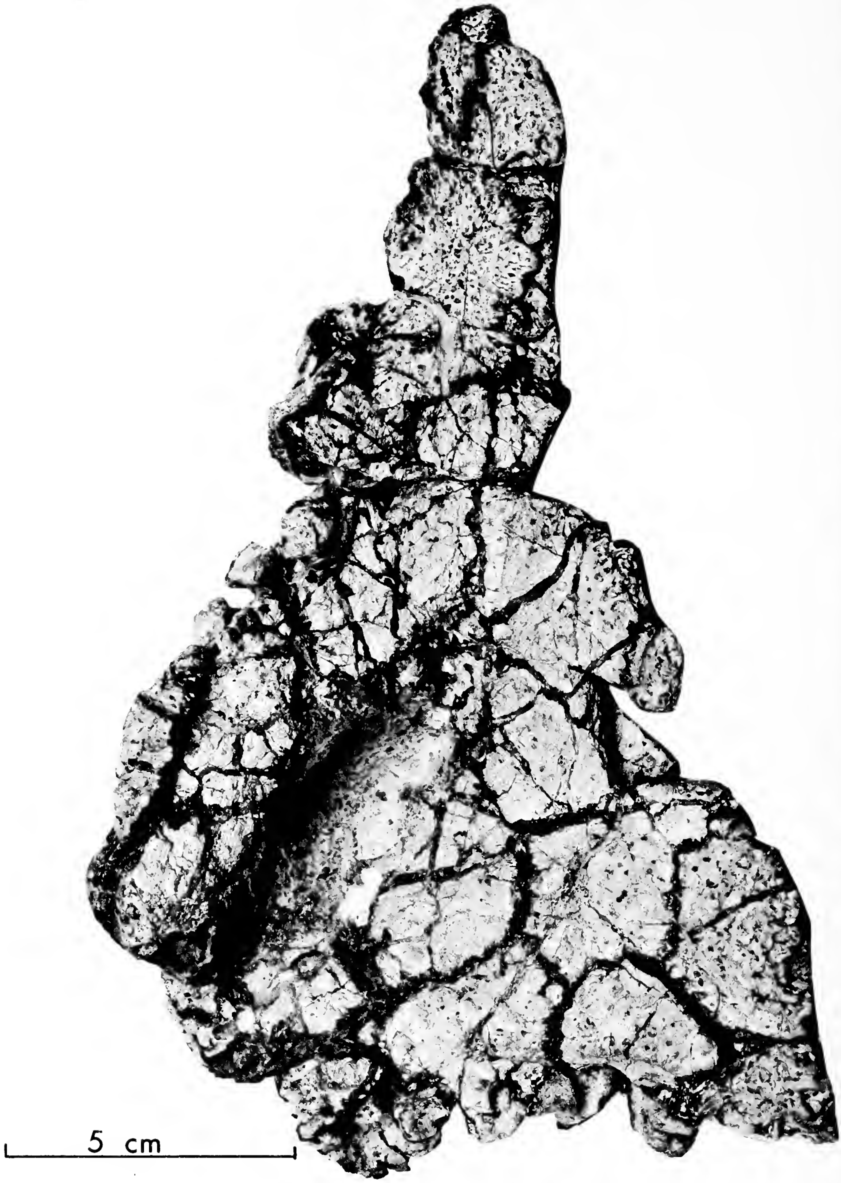

Fig. 1.—*Platyhystrix rugosus*, photograph of skull AMNH 11545 in dorsal view.

Fig. 2.—*Platyhystrix rugosus* AMNH 11545 as seen in Fig. 1 except that spine fragment (ns) of AMNH 11544 has been joined to spine fragment on ventral surface of skull.

Horizon and locality.—All specimens from Lower Permian Cutler Formation near Arroyo del Agua, Rio Arriba County, north-central New Mexico (Langston 1953, Figs. 1, 2).

Diagnosis.—Only known species of *Platyhystrix.*

Description

The description of the skull of *Platyhystrix* is based almost entirely on AMNH 11545 (Figs. 1, 2, 4, 6–8). The skull has suffered considerable crushing and many elements are absent or only partly preserved. Of the dermal skull roof, only the top of the snout, the dorsal table, and the cheeks are sufficiently preserved to allow detailed description. The maxilla, lacrimal, jugal, quadratojugal, quadrate, and prefrontal are represented by small fragments. The palate is represented by portions of the left side. The braincase, visible in ventral and posterior aspects, exhibits some breakage and distortion. Although most of the braincase and part of the skull table have been displaced to the right relative to the rest of the skull, their original relationships can be restored (Fig. 8b) without difficulty. There are no elements of the mandible preserved in AMNH 11545.

A restoration of the skull roof in dorsal view, based on AMNH 11545, is given in Fig. 3. In dorsal aspect the skull appears long and narrow for a dissorophid. The occipital margin is moderately concave. The cheeks, from at least the level of the orbits posteriorly, are nearly vertical. Pertinent skull measurements are as follows: total length along midline, 190+ mm; preorbital length (approx.), 75 mm; postorbital length along midline, 64 mm; width of skull roof across tabulars, 99 mm; length of orbit (approx.), 48 mm; minimum interorbital width (approx.), 60 mm. The ratio between total length and postorbital length is consistent with those measured for other dissorophid species by DeMar (1968). Dermal sculpturing varies greatly on the skull surface, exhibiting its greatest development along the dorsal half of the orbital rim, edges of the skull table, and adjoining areas of the cheek. In these areas it consists mainly of large ridges which in places support numerous massive, tubercular or nodular-like protuberances. The nodular protuberances are most strongly developed on the lateral surfaces of the postorbital and squamosal, and along the lateral margins of the skull table exposures of the supratemporal and tabular. Because of weathering, this type of sculpturing is less distinct on the skull AMNH 11545 than is on the skull and jaw fragments described by Langston (1953), of which the postorbital-squamosal fragment UCMP 39090 is shown in Fig. 5. On other regions of the skull of AMNH 11545, such as the central area of the skull table, the sculpturing is less nodular and consists of a reticulate pattern of ridges surrounding small pits. The sculpturing on the nasals of AMNH 11545 is finer than expected for a dissorophid skull of such large size. Sculpturing preserved only on small areas of the cheeks is developed to the same extent as seen on corresponding regions of other large dissorophids.

The skull roofing bones of *Platyhystrix* (Figs. 1–3) exhibit a sutural pattern similar to that of other dissorophid genera. Both premaxillae are preserved. The left premaxilla is nearly complete, missing only a small portion of its posterodorsal process and the end of its posterior, marginal ramus. The right premaxilla is represented only by the posterodorsal process; its medial and posterior edges are smoothly finished, indicating that these margins are complete. The premaxillae appear to have had a narrow midline contact at the anterior end of the snout. They formed the anterior half of the ventrolateral and the anterior portion of the dorsomedial margins of the external nares. From its dorsomedial contribution to the narial border the premaxilla tapers slightly as it extends posteriorly to form the broadly forked posterodorsal process. The preserved marginal dentition of the left premaxilla consists of seven teeth, represented mainly by their bases, interspersed with spaces for six more within a length of about 25 mm. Maximum

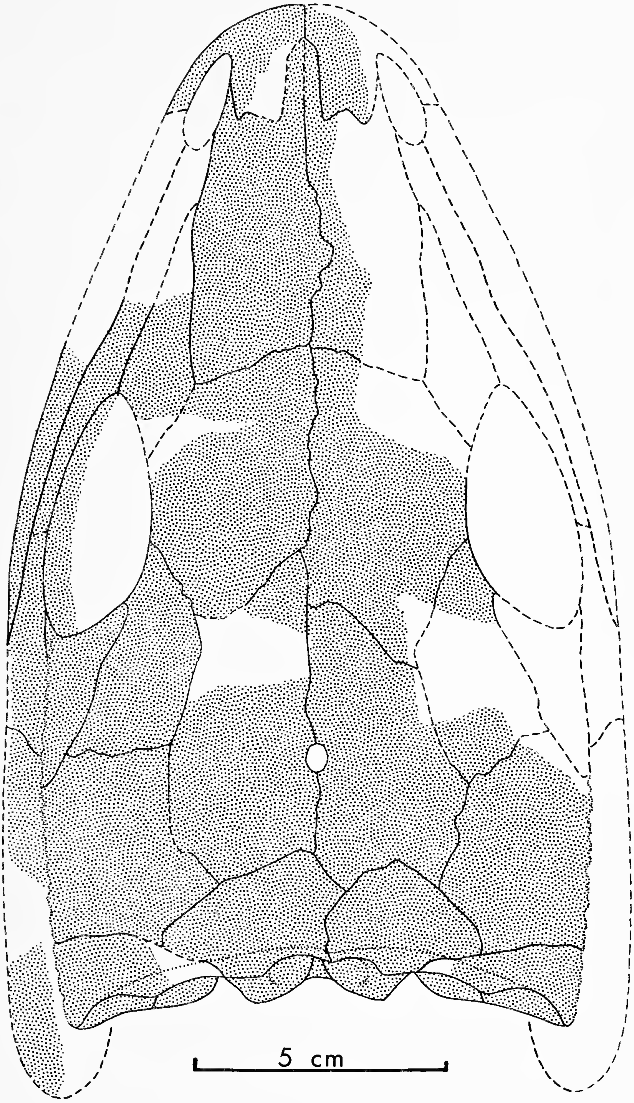

Fig. 3.—Diagrammatic restoration of skull roof of *Platyhystrix rugosus* in dorsal view. Preserved areas represented by shading.

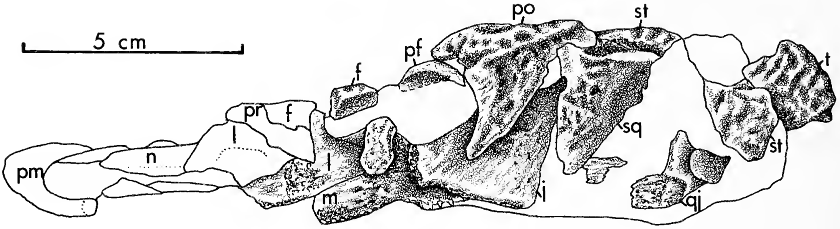

Fig. 4.—*Platyhystrix rugosus,* skull AMNH 11545 in left lateral view.

diameter of the teeth is about 1.5 mm and the length is about 3 to 4 mm. Preservation of the snout is too poor to determine the presence or absence of a median rostral fontanel or an internasal bone seen in some dissorophids (Carroll, 1964). In the absence of any positive evidence, this area of the skull has been restored without either of these features (Fig. 3). There is also some telescoping of the premaxillae onto the dorsal surfaces of the nasals. Therefore, the actual midline skull length of AMNH 11545 exceeded the preserved length of 19 cm.

Portions of the maxilla, lacrimal and jugal can be seen on the left side of AMNH 11545 (Fig. 4). A small part of the maxilla, 4 cm long, is preserved beneath the orbit; its surface is poorly preserved, but appears to have been moderately sculptured. It extends dorsally from the ventral skull margin no more than 10 mm to its suture with the lacrimal. The maxilla bears about 18 teeth, all but three incomplete, in a length of 4 cm. The complete teeth appear to be simple, pointed pegs with a basal width of about 1.3 mm and a length of about 3 mm. The preserved portion of the lacrimal indicates that it was a large element that may have extended far anteriorly to reach the naris as in other dissorophids. The jugal formed the posteroventral margin of the orbit and occupied a large, inverted V-shaped space between the postorbital and squamosal. Although the jugal must have approached closely the ventral margin of the skull, it is unlikely that it overlapped the maxilla to reach the jaw margin as in some dissorophids (Carroll, 1964; DeMar, 1968). As a result of poor preservation it is not known if the palatine was exposed on the skull roof along the ventral margin of the orbit as noted in a number of dissorophids (DeMar, 1968; Bolt, 1974*c*). A large portion of the left quadratojugal is exposed in medial view (Figs. 6, 7). Its borders are incomplete except where it is sutured to a small fragment of the quadrate (not shown in figures).

Both nasals (Figs. 1–3) are present but only the left is complete. It is a long, narrow element; it is nearly three times as long as wide and represents approximately 35% of the midline length of the skull. The frontals are incomplete, missing the anterolateral corners and portions of the orbital margins. In midline length the frontals are slightly shorter than the parietals and significantly shorter than the nasals. The frontal contributes extensively to the dorsomedial orbital margin. Although the dorsal surfaces of the parietals are weathered and crushed, part of the left and most of the right are preserved. The maximum length of the parietal is twice its maximum width. Anteriorly, the parietals extend well beyond the level of the posterior margins of the orbits. The area where the pineal foramen is usually located has been severely damaged and no part of its border is discernable.

Both the moderate-sized tabulars and large postparietals are wedge-shaped in dorsal view; the tabular-postparietal contact is between their narrow ends. Both bones have well developed, posteroventrally directed occipital flanges, but only the flange of the postparietal contacts of the braincase, suturing to the dorsal process of the exoccipital; a medial occipital flange of the tabular joins the paroccipital process of the opisthotic

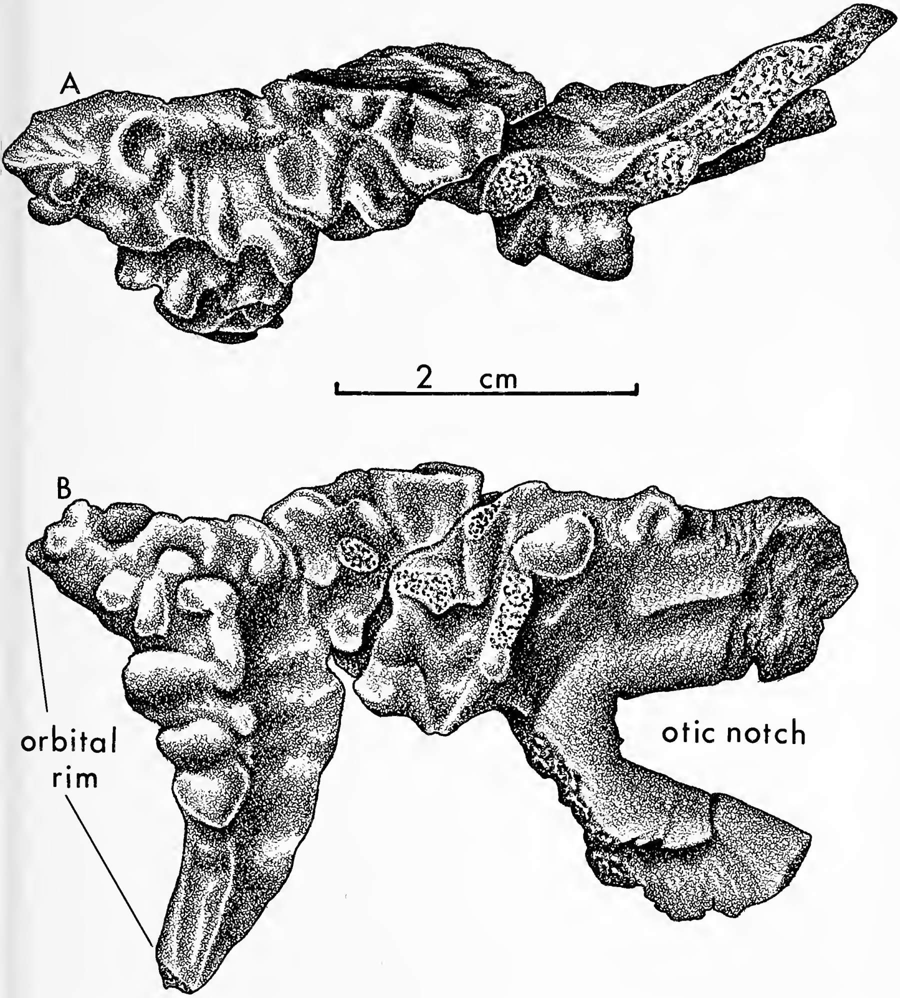

Fig. 5.—*Platyhystrix rugosus,* left postorbital-squamosal UCMP 39090 in (A), dorsal, and (B), lateral views.

(see below). The large supratemporal has a broad contact with the postfrontal and postorbital. The squamosal does not contribute to the skull table, but is restricted to the lateral surface of the skull; this is also indicated in UCMP 39090 (Fig. 5). The postfrontal and postorbital are large, long elements. The postfrontal is restricted to the skull table and it is more than twice as long as wide; it contributes to the posterodorsal margin of the orbit. The postorbital has a long, narrow exposure on the skull table.

From their dorsal exposures along the lateral edge of the skull table the postorbital,

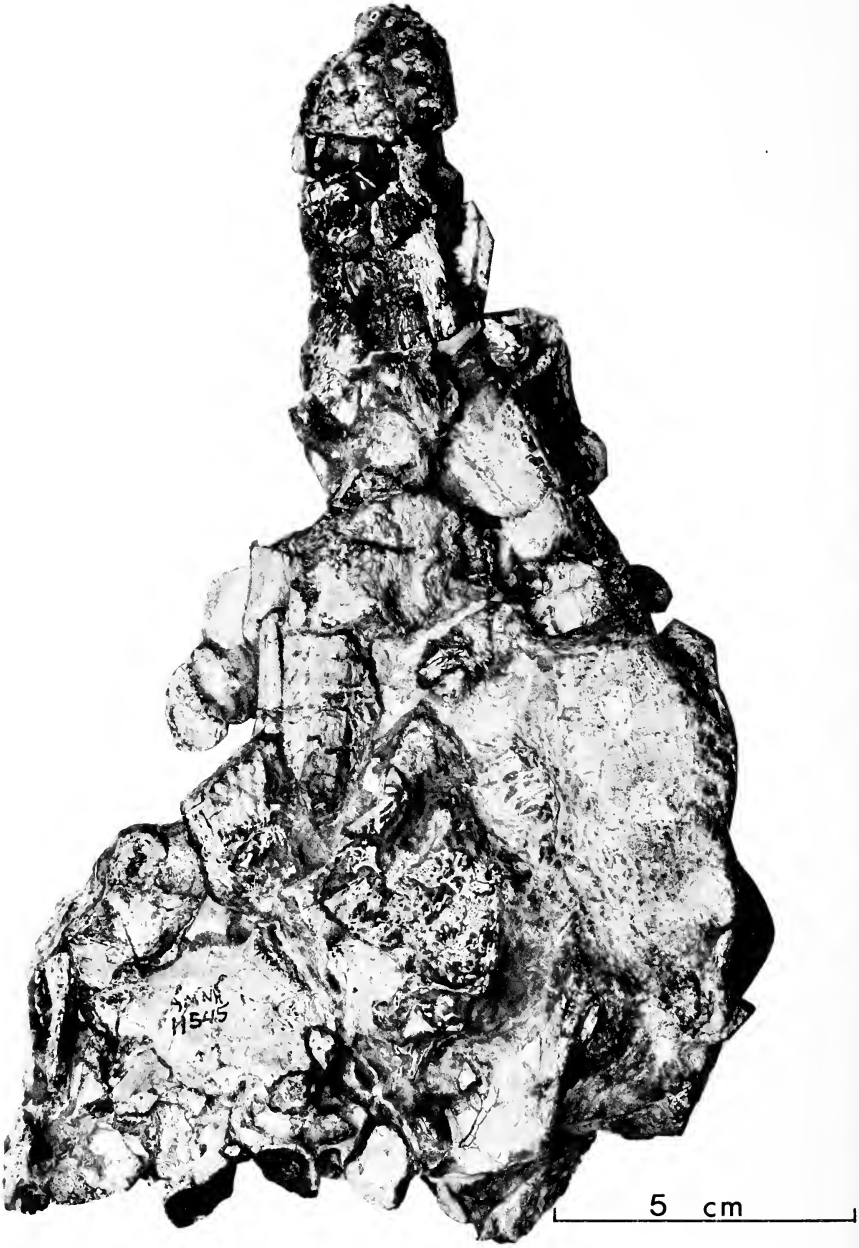

Fig. 6.—*Platyhystrix rugosus*, photograph of skull AMNH 11545 in ventral view.

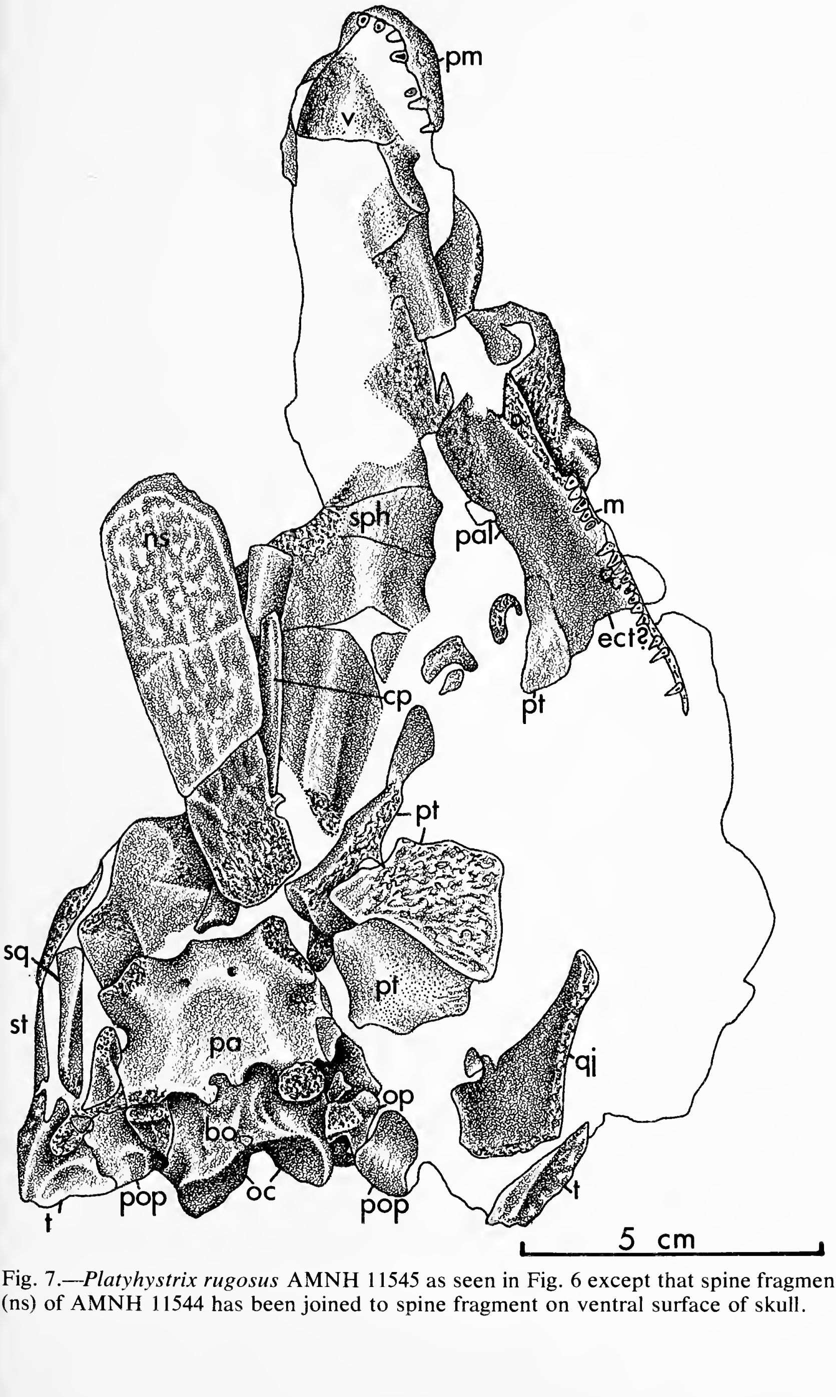

Fig. 7.—*Platyhystrix rugosus* AMNH 11545 as seen in Fig. 6 except that spine fragment (ns) of AMNH 11544 has been joined to spine fragment on ventral surface of skull.

supratemporal and tabular extend ventrally in a vertical plane onto the cheek of the skull roof (Fig. 4). The laterally exposed component of the postorbital is large and triangular; its great anteroventral extent indicates that the skull was deep in this region. Together the dorsal and lateral components of the postorbital form a deep, angular, posterior margin of the orbit. The postorbitals in AMNH 11545 and UCMP 39090 are identical in both their dorsally and laterally exposed portions, but only in the latter (Fig. 5) is the sculpturing completely preserved. Judging from UCMP 39090, the squamosal formed the anterior corner and most of the ventral margin of a very deep otic notch. It is strongly sculptured except for a smooth area that borders the notch. The specimens are too incomplete to determine whether a smooth, thin crescent-shaped flange projected ventrally into the otic notch from near the supratemporal-squamosal contact as previously described for dissorophids (Carroll, 1964; DeMar, 1968; Bolt, 1974*b*). The right squamosal in AMNH 11545 is represented only by a long, narrow fragment of the posterodorsal margin of the otic notch that has been displaced dorsally to lie medial to the laterally exposed component of the supratemporal (Figs. 6, 7); it is sufficiently well preserved, however, to suggest that the squamosal extended posteriorly to contact the tabular and exclude the supratemporal from the margin of the otic notch as it does in other dissorophids (Bolt, 1974*b*). Most of the lateral surface of the supratemporal is sculptured; however, it becomes extremely thin as it forms a smooth, narrow area along its posteroventral margin. Of the tabular, supratemporal and squamosal contributions to the otic notches, only those of the tabulars are essentially completely preserved. The subrectangular lateral surface of the tabular is sculptured except for a very small area at its anteroventral corner. Anteriorly the tabular has a wide contact with the supratemporal. A smooth occipital flange extends medially from the posterolateral edge of the tabular to contact the paroccipital process of the opisthotic (Fig. 8). This flange of the tabular also projects a short distance below the level of the lateral exposure of the bone. There is no indication that the tabular developed a ventrally directed process that joined a dorsally directed process of the quadrate to close the otic notch posteriorly as in the dissorophids *Dissorophus, Cacops,* and *Longiscitula* (DeMar, 1966*a*, 1968; Bolt, 1977*a*).

Only portions of the left side of the palate are sufficiently well preserved to allow comment (Figs. 6, 7). The preserved surfaces are covered by fine denticles. Enough of the vomer remains to indicate that it was long and formed the anterior and much of the medial border of the long (approximately 4.5 cm) internal naris. Vomerine tusks are not visible. The palatine is nearly complete, but its posterior suture with the ectopterygoid cannot be discerned. Anteriorly it forms the posterior and part of the medial borders of the internal naris, and medially the lateral margin of the very large interpterygoid vacuity. What appear to be the bases of two palatine tusks are located just posterior to the internal naris. The extent of the ectopterygoid is difficult to define. A large tusk is partially preserved near the ectopterygoid-maxillary suture. The pterygoid is represented by at least six poorly preserved fragments. What appears to be the palatal portion of the basipterygoid articulation is located slightly anterolateral to the basipterygoid process of the braincase.

The braincase of *Platyhystrix* is in general like that of other rhachitomes (Swain, 1941; Boy, 1971). The well developed parasphenoid (Figs. 6, 7) is exposed in ventral view; its main body is probably fused with the basisphenoid. The narrow, rod-like cultriform process (4.5 cm long) is preserved though broken at several levels with some displacements. Most of the sphenethmoid is exposed in ventral view. It is V-shaped in cross-section with a rounded midline keel which rested on the dorsal surface of the cultriform process. The main body of the parasphenoid is a large, smooth, subrectangular plate that underlies most of the posterior portion of the braincase. The surfaces of the anterolateral corners are slightly convex and cover the thick basisphenoid core of the large basipterygoid processes. The basipterygoid processes are large with flat unfinished surfaces facing anterolaterally. This area is insufficiently preserved to establish whether

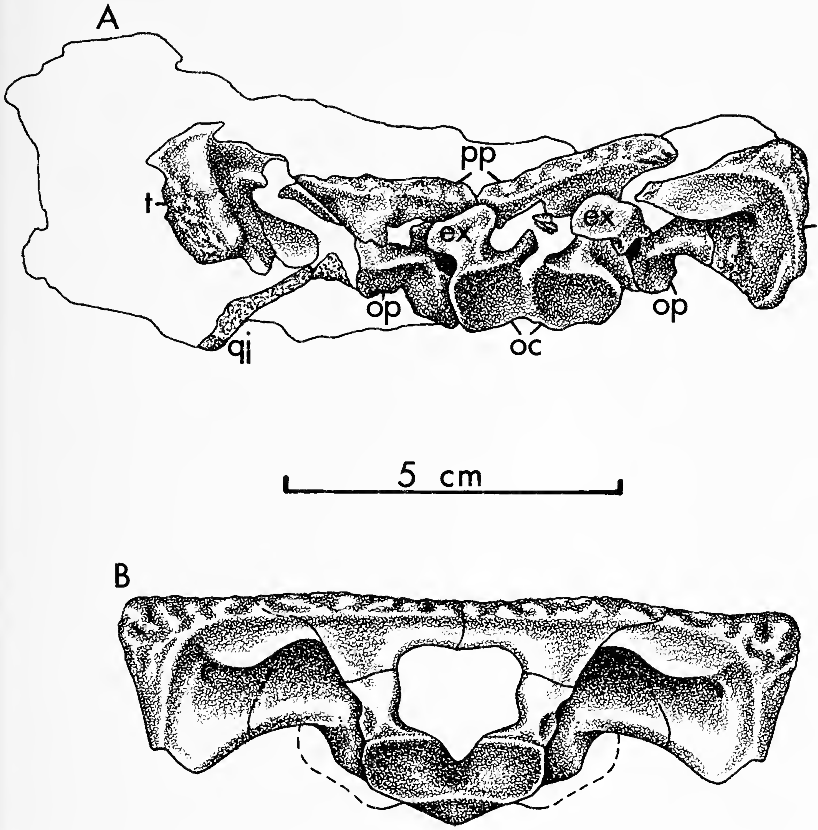

Fig. 8.—*Platyhystrix rugosus,* occiput of skull AMNH 11545. A) as preserved; B) restored.

the joint between the palate and braincase was movable. Posterior to the basipterygoid processes the lateral margins of the parasphenoid curve dorsally to end as thin, free edges. The posterolateral corners are thickened and ridged slightly to form the cristae ventrolaterales; attached to the left crista is a small, poorly ossified fragment whose identity is uncertain. Medial to the cristae the posterior margin of the parasphenoid is strongly concave on either side of a short, bifurcate stem. The foramina for the internal carotids are clearly visible near the midline between the basipterygoid processes. The basioccipital and exoccipitals are fused and extend well beyond the posterior margin of the parasphenoid. Although the sutures separating the basioccipital and exoccipitals cannot be defined, it is assumed that the basioccipital forms the narrow, irregular rugose area on the ventral midline.

In posterior view (Fig. 8) the exoccipitals form the lateral portions of the distinctly double occipital condyle; presumably the basioccipital only contributes a narrow ventral wedge between them. The condyle is horizontally oval in outline and the articular surface

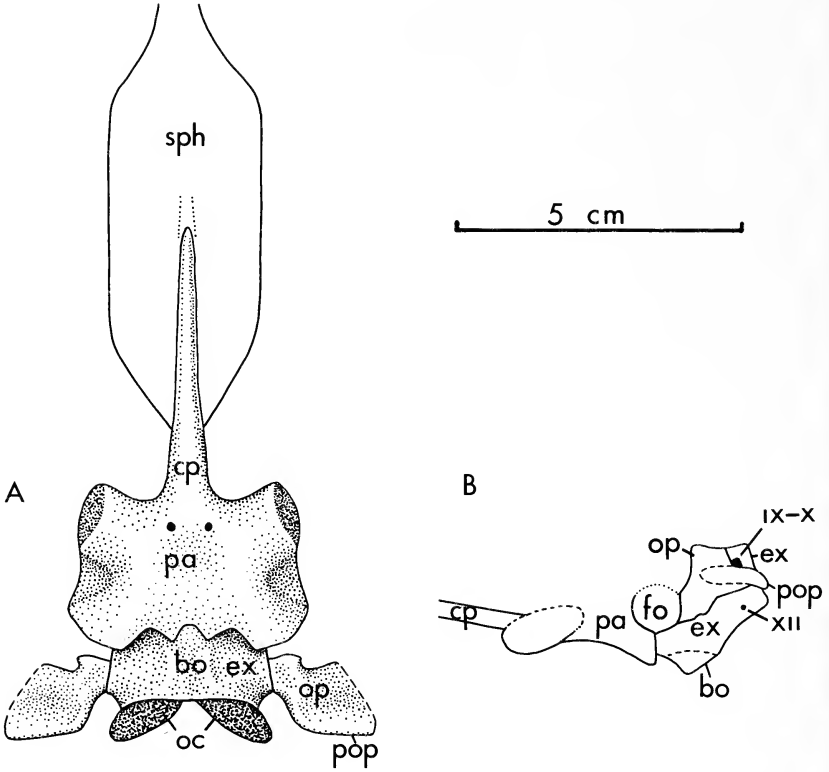

Fig. 9.—*Platyhystrix rugosus,* restored braincase of skull AMNH 11545. A) ventral view; B) diagrammatic outline sketch in left lateral view.

is strongly concave with posteriorly projecting dorsolateral margins. The exoccipitals are separated along the midline of the braincase floor by a narrow channel that was presumably occupied by an unossified portion of the basioccipital. Above the condyles the exoccipitals extend dorsally as stout, slightly waisted processes on either side of the foramen magnum; they do not meet dorsally and there is no trace of an ossified supraoccipital. The large dorsal sutural surfaces of the exoccipitals attached not only to the occipital flanges of the postparietals, but may have also extended a short distance forward beneath the skull table. Small branches of cranial nerve XII (hypoglossal) exit on the lateral surface of the exoccipital just anterior to the condyle rim (Fig. 9). A short distance anterodorsally the exoccipital forms the posterior edge of the large vagus foramen for cranial nerves IX–X. The leading edge of the exoccipital slopes anteroventrally below the vagus foramen. Only the opisthotic portion of the otic region is adequately exposed and preserved for description. This bone forms a stout vertical pillar that extends from near the base of the anterior edge of the exoccipital to the ventral surface of the postparietal near its occipital margin. The opisthotic forms the anterior margin of the vagus foramen and the posterodorsal margin of the large fenestra ovalis.

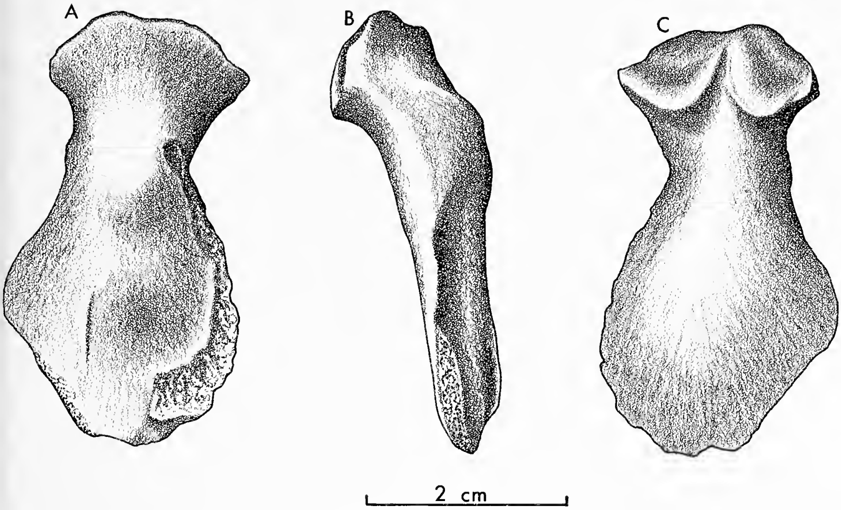

Fig. 10.—*Platyhystrix rugosus,* left sacral rib of AMNH 11544 in (A) lateral, (B) anterior, and (C) medial views.

The left fenestra ovalis is visible; it is bounded posteroventrally by the exoccipital and ventrally by the parasphenoid. The anterior and dorsal borders of the fenestra ovalis were probably formed by the prootic, but this area of the braincase is insufficiently preserved to be certain. At the level of the vagus foramen the paroccipital process of the opisthotic extends laterally and expands abruptly into a nearly flat, anteroposteriorly expanded plate. Distally the paroccipital process slopes steeply posteroventrally and its posterodorsal surface is continuous with that of the medial occipital flange of the tabular; the posterior edge of the paroccipital process extends a short distance posteriorly beyond the posteroventral occipital flanges of the postparietal and tabular. The posttemporal fenestra is bounded by the posteroventral and medial occipital flanges of the tabular and the paroccipital process.

Identifiable elements of the partial axial skeleton AMNH 11544 include the greater parts of five dorsal neural spines, numerous small fragments of other neural spines, two complete intercentra and what may be portions of two additional intercentra, three proximal ends of ribs, numerous fragments of probably unarmored rib shafts, a small section of an armored rib shaft, and a pair of essentially complete sacral ribs. It is estimated that a minimum of seven or eight dorsal neural spines are represented. Vaughn (1971) calculated that fifteen or fewer spines made up almost all of the sail of *Platyhystrix.* In size, structure, variation in shape, and ornamentation the spines of AMNH 11544 conform exactly with those of the *Platyhystrix* specimen described by Langston (1953) and Lewis and Vaughn (1965). In overall size the sail of AMNH 11544 was undoubtedly very close to that indicated by the series of 11 dorsal spines described by Lewis and Vaughn (1965). Except for their slightly smaller size, the two complete intercentra agree with that identified by Langston (1953) as a posterior dorsal. The heads of the three ribs are expanded and triangular in outline with the capitular corner extending a few millimeters beyond the rest of the articular surface to produce a slightly concave proximal margin. The three heads measure 14, 17, and 19 mm in greatest width and narrow to 5, 8, and 11 mm in width in distances of 10, 15, and 18 mm, respectively. In lateral view there is no obvious separation of the rib heads into capitulum and tuberculum. In proximal view, however, there tends to be a slight anteroposterior constriction of the articular surface to produce a sort of dumbell-shaped outline with the tubercular portion being somewhat thicker. There are no signs of a lateral sculptured covering on the proximal rib ends or on the numerous fragments believed to be rib shafts, but there is a small section of rib shaft that is armored. Langston (1953) has described *Platyhystrix* ribs as having a heavily papillose sculptured covering on the proximal two thirds of their lateral surfaces. It is assumed that either some of the ribs of *Platyhystrix* lacked this covering, or that its extent on individual ribs was variable, or both. None of the rib fragments possess an uncinate process. The pair of sacral ribs (Fig. 10) are of typical labyrinthodont structure. The head is stoutly constructed and its articular surface is partially divided into two unequal, subcircular portions; the larger surface probably represents the tuberculum. Distal to the head there is a narrowing of the rib to form a short neck that is circular in cross-section, followed by an anteroposterior expansion into a broad, ventrally directed, leaf-shaped structure.

Comparisons

The superfamily Dissorophoidea was proposed by Bolt (1969) to unite the families Dissorophidae, Trematopsidae, and Doleserpetontidae. This grouping was later expanded by Boy (1972) to include two branchiosaur families, the Branchiosauridae and Micromelerpetontidae. Boy envisioned the latter two families as representing secondarily aquatic, at least partially neotenic, divergent lineages of an unknown amphibian stock that rapidly adapted to a terrestrial or riparian habit and differentiated into the other dissorophoid families. The monotypic family Doleserpetontidae Bolt (1969) was erected for the sole reception of the Lower Permian *Doleserpeton annectens*. In a more recent discussion of this species, however, Bolt (1977*b*) concluded that *D. annectens* is closely related to the Lower Permian dissorophid *Tersomius* and, though specifically distinct from either of the two recognized species of *Tersomius,* it may not be generically distinct. A close relationship between the Dissorophidae and Trematopsidae was first proposed by Olson (1941); Boy's (1972) analysis of the Dissorophoidea also supports this conclusion. This theory of relationship has been especially reinforced by the descriptions of two dissorophids, the Late Pennsylvanian *Actiobates* (Eaton, 1973) and the Early Permian *Longiscitula* (DeMar, 1966*a*), and a trematopsid, the Early Permian *Ecolsonia* (Vaughn, 1969). Each apparently possesses a combination of cranial features considered characteristic of both families. In noting the close relationship between dissorophids and trematopsids, Eaton (1973) recommended that only one family, Dissorophidae, be recognized to include members of both groups. In light of these observations, it is important to demonstrate that the known skull materials of *Platyhystrix* clearly indicate inclusion of this genus in the Dissorophidae rather than in the closely related Trematopsidae.

The sculpturing of the skull roof of *Platyhystrix* is similar in its greatly varied development to that of most moderate to large sized dissorophids. As in other dissorophids, the greatest development is seen along the dorsal margin of the orbit and the lateral and posterior margins of the skull table. In trematopsids the sculpturing consists of the typical labyrinthodont pattern of closely spaced pits separated by anastomosing ridges and is uniformly developed throughout the dermal skull roof; there is no development of protuberances or ridges on the skull table. In contrast to the condition in *Platyhystrix* and other dissorophids, the premaxillae of the trematopsids are generally more massive and form a far more bluntly rounded snout (see figures by Olson 1941; Carroll, 1964; DeMar, 1968). In *Platyhystrix* the parietals are longer than the frontals. In other dissorophids the frontals typically either exceed slightly or are approximately equal to the parietals in length, whereas in trematopsids the frontals are as much as one and one-half times longer than the parietals (Olson, 1941; Vaughn, 1969*b*). The greater length of the frontals in trematopsids is usually expressed by their greater extension beyond the level of the anterior orbital margins. Although the anterior extent of the orbits in *Platyhystrix* can only be estimated, it seems obvious that, as is typical in dissorophids, the frontals did not extend noticeably beyond this level. Probably related to this difference is the generally greater relative preorbital skull length of the trematopsids compared to that of the dissorophids. Measurements made from published illustrations (Olson, 1941; Carroll, 1964; DeMar, 1968; Eaton, 1973) indicate that in the trematopsids the preorbital length ranges from about 44% to 57% (average about 49%) of the skull length (measured along the midline), whereas in the dissorophids the range is about 30% to 45% (average about 39%). The same measurement for *Platyhystrix* is about 38%.

Bolt (1974*b*, 1977*a*) has shown that the otic notch regions of trematopsids and dissorophids are similar in most respects, but differences in at least two features can be used here to demonstrate that *Platyhystrix* is a dissorophid. In *Platyhystrix* and other dissorophids the sculpturing of the dorsal skull surface continues onto the cheek above the otic notch, extending over much of the supratemporal and all but a very small area on the anteroventral margin of the tabular. The smooth, narrow border that surrounds most of the otic notch, therefore, pinches out just as it enters the tabular. In the trematopsids, on the other hand, the entire surface of the cheek dorsal to the otic notch is smooth. In addition, the sculptured skull table of trematopsids extends a short distance out from the smooth lateral skull surface dorsal to the otic notch to form a ventrally smooth shelf that Bolt (1974*b*) refers to as the supratympanic shelf. The supratympanic shelf is poorly developed or absent in dissorophids.

Marginal dentition also offers a way of distinguishing between the two families. The marginal teeth of trematopsids differ from those of dissorophids in being relatively much larger, often recurved and far less numerous (see figures by Olson, 1941; Carroll, 1964). In his review of the trematopsids Olson (1941) stated that their combined number of maxillary and premaxillary teeth varies considerably, ranging from about 18 to 40 on each side of the skull. The dentitions of the trematopsids *Trematopsis seltini* and *Trematops stonei,* described later by Olson (1956, 1970), also appear to conform to those of other members of the family. Premaxillary-maxillary tooth counts are available for six dissorophid genera (Carroll, 1964; DeMar, 1968) and they range from 45 to 70 or more teeth. Judging from the small preserved portions of the marginal dentition of AMNH 11545, *Platyhystrix* may have had as many as 65 simple, peg-like teeth on either side of the upper jaw. Obviously, these teeth were considerably smaller than those of any trematopsid skull of comparable size. It should also be noted that there are no known cranial features of *Platyhystrix* that are inconsistent with the inclusion of this genus in the Dissorophidae.

As far as the specimens at hand reveal, the skull of *Platyhystrix rugosus* possesses only two derived features that distinguish it from those of all other dissorophids. The most obvious is the presence of the heavy nodular or papillose dermal sculpturing. The skull of *Platyhystrix* also appears distinct because of its large size. Of course, size is of limited use taxonomically; nevertheless, the large size of the skull AMNH 11545, over 19 cm in midline length, is a conspicuous and striking feature that is apparently not unusual for the species. The postorbital-squamosal skull fragment UCMP 39090 suggests a skull size approximately equal to that of AMNH 11545 and the tabular UCMP 39092 is even larger than that of AMNH 11545. Vaughn (1969*a*) has described a badly weathered dissorophid skull from the Lower Permian Laborcita Formation of New Mexico which he suspected may belong to *Platyhystrix*; he has documented the presence of this genus in that formation with the discovery of a *Platyhystrix* neural spine. The one feature that supports this identification, as noted by Vaughn, is the large size of the skull, measuring 115 mm in width between the maxillary rims at the level of the centers of the orbits. This suggests a skull even larger than AMNH 11545. It should also be mentioned that the above skull sizes are appropriate for the *Platyhystrix* vertebrae described by Langston (1953) and Lewis and Vaughn (1965). The largest previously reported skulls of dissorophid genera are of *Dissorophus, Cacops,* and *Longiscitula,* which have maximum midline lengths of 13.7, 12.5 and 12.0 cm respectively; in other dissorophid genera in which this measurement is directly obtainable the range is from 5.0 to just over 9.0 cm (DeMar, 1966*a*, 1968; Bolt, 1974*a*). Some of the dissorophids known only from postcranial materials, however, may have approached *Platyhystrix* in skull size. Comparing relative sizes of postcranial elements, Bolt (1974*a*) stated that *Alegeinosaurus* may have been approximately the size of *Cacops,* whereas *Aspidosaurus crucifer, A. glascocki,* and *A. apicolis* may have been considerably larger. Olson's (1972) restoration of the dissorophid *Fayella* suggests that the skull may have reached about 17 cm in length.

Apart from size and dermal sculpturing, the skull of *Platyhystrix* differs from those of other dissorophids only on the combined basis of several features. The differences are, however, of sufficient magnitude and number as to make individual comparisons impractical. Instead, an expanded diagnosis that includes both cranial and axial characters is given in the Systematic Paleontology section. Further, many of the differences between the skull of *Platyhystrix* and those of other dissorophids are brought out in the following section.

DISCUSSION

The Dissorophidae are one of the largest Paleozoic amphibian families. Of the 16 or more genera that have been included in this family, only 12 have sufficiently well known skulls to permit comparisons: the Pennsylvanian *Amphibamus* and *Actiobates*; the Permian *Tersomius, Brevidorsum, Broiliellus, Conjunctio, Aspidosaurus, Longiscitula, Dissorophus, Cacops* and *Platyhystrix*; the Lower Triassic *Micropholis* (Watson, 1913; Broili and Schroder, 1937; Gregory, 1950; Carroll, 1964; DeMar, 1966*a*, 1968; Eaton, 1973). Of these genera, a dissorophid assignment of only three has been or can be questioned. Boy (1972) has doubted the otherwise widely accepted view that the unarmored *Amphibamus* is the most primitive member of the Dissorophidae (Gregory, 1950; Carroll, 1964; Bolt, 1979). He regarded *Amphibamus* as the sole member of a separate family, Amphibamidae, having an apomorphic sister-group relationship to the Doleserpetontidae, Dissorophidae, and Trematopsidae. However, almost all of the shared derived characters Boy recognized in *Amphibamus* to support this relationship (relatively short postorbital region, loss of axial ribs and parasphenoidal teeth, perforated stapes) could just as easily be argued to represent paedomorphic, ontogenetic (Bolt, 1979), primitive or convergent conditions. It could also be argued that on the basis of Eaton's (1973) brief description of *Actiobates* there are equally strong morphological grounds for its assignation to the Trematopsidae. Although *Micropholis* has been considered a dissorophid (Romer, 1966; Bolt, 1977), its systematic position within the Dissorophoidea remains problematical. On the basis of rather long lists of comparisons, Boy (1972) presented ample reasons for placing *Micropholis* in its own family, Micropholidae, and viewing it as probably representing a distinct and widely divergent lineage from those comprising the remainder of the large complex of dissorophoids. Although *Micropholis* may be a dissorophoid, judging from Boy's comments it seems unlikely that it is a dissorophid. Finally, it has been pointed out to us (Baird, personal communication) that, because Carroll (1964) has synonymized *Pelion* with *Amphibamus,* the family name Peliontidae Cope (1875), rather than Dissorophidae Boulenger (1902), should be applied to the grouping being considered here in accordance with the law of priority. Although Peliontidae is the earliest, valid applicable family name, we have chosen to use the far more familiar name Dissorophidae to avoid confusion.

Aside from a few possibly important exceptions, dissorophid cranial anatomy can be characterized as morphologically conservative but distinctive, and as providing few clues for recognizing intrafamilial relationships. On the other hand, vertebral structure, or its so-called "armor," is quite variable and, therefore has been relied on heavily in phylogenetic studies of the dissorophids (Carroll, 1964; DeMar, 1966*a,* 1968), even though dermal armor is absent or unknown in a few early forms. The tentative phylogeny presented by DeMar (1968), though based mainly on dermal armor, incorporates some cranial and axial skeleton characters, as well as data based on adaptational and paleoecological hypotheses developed by him. Yet, he concluded (DeMar, 1968:1236) that, "Despite the large number of genera and species known for this family, the margin for uncertainty, in evaluating their phylogenetic relationships, is large." Although Carroll (1964) and DeMar (1968) reached different conclusions regarding dissorophid phylogeny, they were in essential agreement in the recognition of primitive and advanced members. Using this aspect of their studies as a framework, a number of features can be cited to indicate that the skull of *Platyhystrix* represents a structural grade of organization between that of the more primitive dissorophids restricted almost entirely to the Pennsylvanian and the earliest Permian (Wolfcampian) and that of the more advanced forms of the later Early Permian (Leonardian). The former group includes *Amphibamus, Tersomius, Actiobates, Brevidorsum, Conjunctio, Dissorophus angustus,* and *Broiliellus,* whereas the latter group includes *Dissorophus multicinctus, Cacops,* and *Longiscitula.* This division, however, is not without some controversial systematic assignments. On the basis of cranial anatomy, placement of *Aspidosaurus* in either of these two groups is difficult, if not impossible. The type species, *A. chiton* (Broili, 1904), although represented by much of the skull and portions of the vertebral column, was not available in recent morphological and taxonomic studies of the dissorophids. The only other species of *Aspidosaurus* known by adequate skull and postcranial materials is *A. novomexicanus.* Langston (1953), however, reassigned the type and two referred specimens to the genus *Broiliellus*. More recently Carroll (1964) recognized the original generic assignment of the type as valid and made the two specimens referred to *Broiliellus* by Langston the basis of a new genus and species, *Conjunctio multidens*. Although *Aspidosaurus* is undoubtedly a valid genus, it probably does not include *A. novomexicanus* (DeMar, 1966*b*). It should also be pointed out that both DeMar (1968) and Bolt (1974*a*) have questioned Carroll's (1964) erection of *D. angustus*, the former claiming that it is not *Dissorophus* and the latter suspecting that it may represent a growth stage of *D. multicinctus*.

DeMar (1968) noted that the dissorophids show a trend toward increasing depth of the otic notch by backward growth of the lateral margin of the skull table, particularly the tabular. The relatively short otic notch of *Amphibamus, Actiobates, Tersomius,* and *Conjunctio* distinguishes them from other dissorophids. The advanced condition of a posteriorly closed otic notch has been reported only in *D. multicinctus, Cacops,* and *Longiscitula*. Dermal sculpturing is weakly developed only in *Amphibamus* and *Tersomius,* but in *Platyhystrix* it exhibits a development unequaled in any other genus. In its possession of a long, narrow nasal bone *Platyhystrix* can be grouped with *D. multicinctus* and *Longiscitula* in which the length ranges from two and a half to three times the width; in *Amphibamus, Actiobates, Tersomius, Conjunctio,* and *Broiliellus,* on the other hand, the length ranges from slightly greater than to about twice the width. There is also a tendency among the dissorophids toward backward expansion of the postorbital and postfrontal. For example, in *Platyhystrix* and the more advanced later Early Permian forms the portion of the postfrontal posterior to the orbit ranges in length from slightly greater than to nearly twice its width, whereas in the more primitive Pennsylvanian and earliest Permian forms its length ranges from about one half to slightly less than its width. Unfortunately, configurations of the nasal and postfrontal bones are not available for *Cacops* (Case, 1911). The above comparisons indicate that the skull of *Platyhystrix* is structurally advanced over those of essentially contemporaneous (Wolfcampian) dissorophids.

In his study of the Dissorophidae, Carroll (1964) envisioned the vertebral armor as having evolved only once and not until the Early Permian. DeMar (1966*b*, 1968), on the other hand, has presented a strong case for the development of armor independently in several different lines of dissorophids during the Late Pennsylvanian or Early Permian. Bolt (1974*a*), however, cautions that many of the differences in armor used by both authors to distinguish genera and species, and to construct phylogenies may actually reflect nothing more than different growth stages. Despite these difficulties, it can still be said that the armor of *Platyhystrix* is sufficiently distinct to preclude its close phylogenetic relationship with any of the Permian dissorophids excepting possibly of certain *Aspidosaurus* species (Carroll, 1964; DeMar, 1968). Important here is Vaughn's (1971) description of *Astreptorhachis ohioensis* from the Late Pennsylvanian Conemaugh Group of Ohio, which is based on neural arches and spines having a very *Platyhystrix*-like structure. The apparent relative shortness of the neural spines and the unusual fusion of adjacent neural arches and distal portions of the spines are key features that distinguish *A. ohioensis* from *P. rugosus*. As pointed out by Vaughn, the fusion between adjacent vertebrae is a feature not expected in a Pennsylvanian relative of the Permian *P. rugosus,* yet the similarities in their neural spines make the recognition of a close phylogenetic relationship inescapable, though obviously not a direct ancestor-descendant link. Vaughn (1971) assigned *A. ohioensis* to the Dissorophidae with some reservation because of the uncertain familial status of *P. rugosus* at that time. The evidence presented here that *P. rugosus* possessed a dissorophid skull corroborates this assignment. It can also be concluded, as Vaughn (1971) did, that both species are members of a divergent armored offshoot that separated in the Middle or Late Pennsylvanian from the main evolutionary line or lines that gave rise to the other Early Permian dissorophids. *A. ohioensis* is the only known Pennsylvanian armored dissorophid. The early occurrence of highly specialized armor in the *Platyhystrix*-like dissorophids is consistent with the relatively advanced state of the skull of *P. rugosus*.

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APPENDICULAR MYOLOGY, PHYLOGENY, AND CLASSIFICATION OF THE AVIAN ORDER CORACIIFORMES (INCLUDING TROGONIFORMES)

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Abstract

This investigation of phylogenetic relationships in the avian order Coraciiformes addresses the questions of whether the order is monophyletic, whether the individual families are monophyletic, and what the pattern of phylogenetic relationships is among the families. The musculature of the forelimb and hindlimb in 37 species was dissected and variations were used in a cladistic analysis. Monophyly of the order is poorly corroborated but remains the preferred hypothesis based on current knowledge. The classification is based on the phylogeny and all proposed taxa are monophyletic. The order is divided into two suborders. The suborder Coracii contains the families Coraciidae, Brachypteraciidae, and Leptosomidae. The suborder Alcedines is divided into the infraorders Bucerotomorphae and Alcedinomorphae. The Bucerotomorphae contains only the family Bucerotidae, whose division into subfamilies Bucorvinae and Bucerotinae is supported by the results of this study. The infraorder Alcedinomorphae is divided into two subinfraorders. The Upupides include the families Phoeniculidae and Upupidae, whose close relationship is supported by an especially large number of synapomorphies. The subinfraorder Alcedinides includes the superfamilies Momotoidea, containing the Todidae and Momotidae, and Alcedinoidea, including the Meropidae and

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Alcedinidae. The division of the Alcedinidae into subfamilies and tribes offers some confirmation from limb musculature for previous hypotheses of intrafamilial relationships. The present study supports inclusion of the Trogonidae in the Coraciiformes, specifically within the subinfraorder Alcedinides, thus allying the trogons most closely with the assemblage of todies, motmots, bee-eaters, and kingfishers. Uncertainties in the data, however, preclude a more accurate placement of this family relative to the others, so it is listed as *incertae sedis* within the Alcedinides.

INTRODUCTION

This is a study of the phylogenetic relationships in the avain order Coraciiformes based on a cladistic analysis of variations in the muscles of the forelimb and hindlimb. The order as generally recognized (for example, Wetmore, 1960) includes the families Alcedinidae (kingfishers), Todidae (todies), Momotidae (motmots), Meropidae (bee-eaters), Coraciidae (rollers), Brachypteraciidae (ground-rollers), Leptosomidae (formerly Leptosomatidae) (cuckoo-rollers), Upupidae (hoopoes), Phoeniculidae (wood-hoopoes), and Bucerotidae (hornbills). The major questions addressed are these: (1) Is the order Coraciiformes monophyletic? (2) Are the individual families monophyletic? (3) What is the pattern of phylogenetic relationships among the families?

The heterogeneous order Coraciiformes is not easily characterized. Most coraciiforms exhibit syndactyly, a tendency for toes II, III, and IV to be connected basally for part of their lengths, although the details vary in different families. A hallux (digit I) is always present. The palate is desmognathous, with basipterygoid processes rudimentary or absent. The birds included in the order show similarities in formula muscles, pterylosis, and in the frequent possession of brilliant plumages. They are cavity nesters and most species lay from three to six white eggs. The young are nidicolous and naked except in the hoopoes and wood-hoopoes. Most feed on small vertebrates or insects, and the distribution of the order is predominantly in the eastern hemisphere. Part of the problem of defining the group is that there are exceptions to many of the characters that have been used in the past.

The relationships of the Coraciiformes to other birds are obscure, although they are usually regarded as being close to the Passeriformes and Piciformes. A relationship with the trogons (Trogonidae) has been suggested based on overall similarity and derived stapedial morphology (Feduccia, 1975*a*). Nevertheless, the trogons have generally been placed in an order of their own (Trogoniformes), mostly because of their unique heterodactyl foot structure. The trogons are included in the present study. A thorough review of the taxonomic history of the Coraciiformes and Trogoniformes is provided by Sibley and Ahlquist (1972), so we will merely note at appropriate places a few recent studies of immediate relevance to our work.

MATERIALS AND METHODS

Anatomy

The forelimb and hindlimb muscles of 37 species representing 34 genera in 10 families were dissected with the aid of a stereomicroscope and an iodine muscle stain (Bock and Shear, 1972). For most species only one specimen was dissected. *Coracias benghalensis* was the reference species for which a detailed description of each muscle was written, and against which the homologues in the other species were compared. Among the structural variations in muscles examined were the location and nature of the origin and insertion, the shape of the belly, the fiber architecture of the muscle and the relationship of fibers to tendons, the size of the muscle relative to adjacent structures, and any additional features of note. A large series of drawings of the musculature was made with the aid of a drawing tube attached to the microscope. The present paper is concerned only with a phylogenetic analysis of the forms studied using myological variation as a source of data. The anatomical descriptions and drawings are found in Maurer (1977). Myological nomenclature generally follows the Nomina Anatomica Avium (Baumel et al., 1979).

The following species were dissected (nomenclature from Morony et al., 1975): Alcedinidae, Cerylinae—*Ceryle alcyon, Chloroceryle americana*; Alcedininae—*Alcedo cristata, Ispidina picta, Ceyx argentatus*; Daceloninae—*Pelargopsis capensis, Dacelo guadichaud, Clytoceyx rex, Halcyon smyrnensis, Tanysiptera galatea*; Todidae—*Todus mexicanus, T. subulatus*; Momotidae—*Electron platyrhynchum, Eumomota superciliosa, Baryphthengus ruficapillus, Momotus momota*; Meropidae—*Merops hirundineus, M. pusillus, M. albicollis, M. apiaster*; Leptosomidae—*Leptosomus discolor*; Coraciidae—*Coracias garrulus, C. caudata, C. benghalensis, Eurystomus orientalis*; Upupidae—*Upupa epops*; Phoeniculidae—*Phoeniculus bollei, Rhinopomastus cyanomelas*; Bucerotidae—*Tockus erythrorhynchus, Penelopides panini, Aceros undulatus, Anthracoceros malabaricus, Ceratogymna elata, Bucorvus abyssinicus*; Trogonidae—*Pharomachrus* sp., *Trogon citreolus, Harpactes erythrocephalus.* No specimens of the Brachypteraciidae were available for dissection.

Phylogeny

After the variation in each muscle was recorded, a phylogenetic character analysis was carried out to determine primitive-derived sequences. Kluge (1971), Ross (1974), Hecht and Edwards (1977), and Gaffney (1979) are among the many workers who have discussed these procedures. The basic technique used was outgroup comparison. A character state that occurred both among some members of a presumed monophyletic group and also in outside taxa was considered to be primitive within the clade in question. A variant from this condition that occurred only within the group studied was considered derived within that group. For purposes of comparison with the groups studied herein, we reviewed the conditions in muscles among birds generally, and especially in groups such as the Piciformes and Passeriformes, which are commonly considered to be closely related to the Coraciiformes. These comparative data were taken from George and Berger (1966) and from various investigations underway in our laboratory (for example Borecky, 1977; Bentz, 1979; Raikow, 1978; Swierczewski and Raikow, 1981). The data were used to construct a cladogram by clustering taxa into groups through the possession of shared derived character states (synapomorphies) in the usual manner of cladistic analysis.

Classification

A classification of the Coraciiformes was prepared based on the pattern of phylogenetic relationships hypothesized in the cladogram. It is of the cladistic type in that the hierarchical structure of the phylogeny is transformed into the hierarchical structure of the classification. Classification has long been a highly subjective procedure lacking in a consistent methodology. We prefer a classification that is internally consistent, and have therefore followed several principles in constructing our classification. There are various approaches to cladistic classification (see Eldredge and Cracraft, 1980, for discussion); ours is based on the following rules:

1) Only clades are classified.—Clades are the products of evolutionary history, while nonmonophyletic groups are simply artifacts of phenetic clustering, adaptational hypotheses, or tradition. Nonmonophyletic groupings may occasionally be useful ("nonpasserines," "birds of prey," "finches") but we see no reason to recognize them as formal taxa.

2) Sister groups are classified at the same category level.—This provides a consistent and pleasing symmetry to the classification by allowing the immediate recognition of sister taxa.

3) Traditional family taxa are maintained.—We comment briefly on subfamily divisions in the Bucerotidae and Alcedinidae, but in general have not attempted to work out the relationships between the genera within families.

4) Nomenclature is conservative.—The names of groups and their category levels are kept as close as possible to previous classifications so as to maximize continuity between classifications.

RESULTS

Our hypothesis of phylogenetic relationships is shown in Fig. 1. Superimposed on this diagram are the taxa that constitute our classification; from this one may see how we derived the classification from the phylogeny. The classification is given in Table 1. Each taxon is hypothesized to be a clade, hence each is an individual hypothesis of monophyly. For each taxon the synapomorphies corroborating the hypothesis are shown alongside the taxon in the classification. In this way the data supporting each component of the total hypothesis are available for examination. The data are given in Table 2. Each character is numbered; these are the numbers referred to in Table 1. The primitive and derived character states are given for each character; the cladogram was of course constructed using the derived states only. For each character, in addition, Table 2 gives the taxa or taxon in which the derived state occurs. Derived states that occur in more than one taxon are hypothesized to have evolved independently in the different groups. In constructing the cladogram we attempted to adhere to the principle of parsimony in minimizing the number of convergent events. With this format our entire argument is set forth unambiguously for maximum ease of understanding and criticism. We regard this as one of the major advantages of cladistic methodology over other approaches to systematic analysis.

The cladogram was generated entirely on the basis of 57 limb muscle characters. We will also discuss some characters used by previous workers, but will not attempt to examine all of the ideas about coraciiform relationships that have been proposed in the past. The following discussion is keyed to the arrangement shown in Fig. 1.

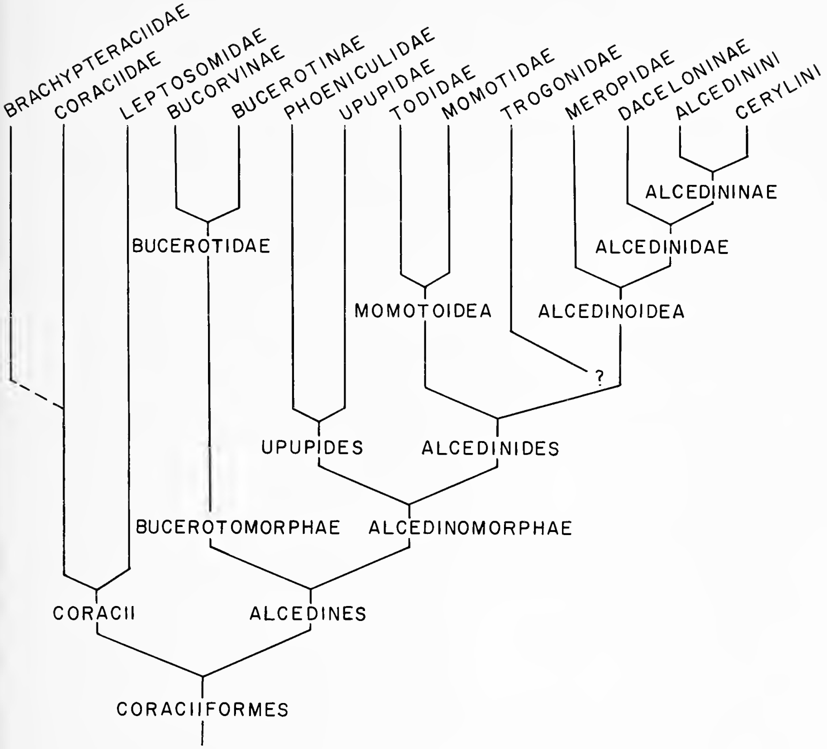

Fig. 1.—A phylogeny of the avian order Coraciiformes. The family Brachypteraciidae was not studied owing to the unavailability of specimens, and is tentatively included here based on previous studies. Otherwise the phylogeny is isomorphic with a cladogram constructed entirely on the basis of a cladistic analysis of 57 limb muscle characters. A proposed higher-level classification is indicated. See Tables 1 and 2 for the data, and the text for discussion.

Coraciiformes

The whole order is clustered by the loss of two muscles, Mm. ambiens and iliofemoralis externus (characters 45, 46, Tables 1 and 2), and by the extensive fusion of the deep plantar tendons (character 53). The latter condition is further modified in some groups. These derived states are among the traditional characters used in defining the order. We did not discover any new limb muscle characters clustering the whole order, and these traditional characters, although sound, are not unique to the Coraciiformes. In addition to the myological characters there are others in osteology, behavior, etc. that have traditionally been used to justify the assemblage (Sibley and Ahlquist, 1972:219).

Table 1.—*A classification of the Coraciiformes with the synapomorphies corroborating each monophyletic taxon.*

Classification	Limb muscle synapomorphies[1]
Order Coraciiformes	45, 46, 53
Suborder Coracii	15, 30
Family Coraciidae	41
Family Brachypteraciidae	(not investigated)
Family Leptosomidae	3, 11, 24
Suborder Alcedines	24, 31, 43
Infraorder Bucerotomorphae	2, 6, 8, 10, 12, 15, 18, 19, 27, 32, 35, 37, 38, 40, 42, 44
Family Bucorvidae	Same as Bucerotomorphae
Subfamily Bucorvinae	34
Subfamily Bucerotinae	5, 23, 26
Infraorder Alcedinomorphae	36, 47
Subinfraorder Upupides	4, 6, 7, 9, 13, 14, 16, 17, 21, 22, 25, 28, 29, 42, 48, 49, 51, 54
Family Phoeniculidae	32
Family Upupidae	37, 55
Subinfraorder Alcedinides	15, 56
Family Trogonidae (*incertae sedis*)	6, 21, 33, 48
Superfamily Momotoidea	25, 48, 49, 50, 51
Family Todidae	20, 37, 39, 41
Family Momotidae	
Superfamily Alcedinoidea	7, 33
Family Meropidae	1, 39, 42, 44, 49, 50
Family Alcedinidae	20, 41, 57
Subfamily Daceloninae	49
Subfamily Alcedininae	48, 51
Tribe Alcedinini	
Tribe Cerylini	49, 52

[1] See Table 2.

These may also be subject to reservations based on occurrence in other groups or exceptions within the Coraciiformes. Sibley and Ahlquist's (1972) study of egg-white proteins was not enlightening with respect to this question.

On the other hand, there is no significant evidence in support of any alternative arrangement. Sibley and Ahlquist (1972:20, 239) suggested a possible connection between the Alcedinidae and the family Galbulidae of the order Piciformes. The results of another investigation in our laboratory (Swierczewski and Raikow, 1981) have led to a rejection of that hypothesis. The ambiguity of the overall coraciiform situation is nicely summarized by the juxtaposition of two quotations from different sections of Sibley and Ahlquist (1972). They consider it "probable" that "the Coraciiformes of Wetmore are polyphyletic" (p. 241), but "resist the temptation to split the order because no compelling

Table 2.—*Characters used in phylogenetic analysis.*

Character	Primitive state	Derived state	Taxa having derived state
1	Latissimus dorsi pars caudalis present	Absent	Meropidae
2	Latissimus dorsi pars caudalis origin more cranial	More caudal	Bucerotomorphae
3	Latissimus dorsi pars caudalis origin limited to neural spines of dorsal vertebrae	Origin also extends to dorsal iliac crest and spinal crest of synsacrum	Leptosomidae
4	Rhomboideus profundus origin from neural spines only	Partial origin from transverse processes	Upupides
5	Rhomboideus profundus with one belly	Two bellies	Bucerotinae
6	Pectoralis pars propatagialis longus fleshy	Tendinous	Bucerotomorphae, Upupides, Trogonidae
7	Tensor propatagialis with one belly	Two bellies	Upupides, Alcedinoidea
8	Tensor propatagialis pars longa present	Absent	Bucerotomorphae
9	Deltoideus major with tendon to latissimus dorsi pars caudalis absent	Present	Upupides
10	Deltoideus major scapular anchor present	Absent	Bucerotomorphae
11	Deltoideus minor insertion cranial to supracoracoideus tendon	Insertion onto supracoracoideus tendon	Leptosomidae
12	As 11	Insertion distal to supracoracoideus tendon	Bucerotomorphae
13	Biceps brachii with 2 tendons of insertion	Three tendons of insertion	Upupides
14	Scapulotriceps with one head	Two heads	Upupides
15	Scapulotriceps humeral anchor present	Absent	Coracii, Bucerotomorphae, Alcedinides[1]

Table 2.—*Continued.*

Character	Primitive state	Derived state	Taxa having derived state
16	Expansor secundariorum humeral belly present	Absent	Upupides
17	Pronator superficialis insertion semitendinous	Tendinous	Upupides
18	Flexor digitorum profundus with 2 heads	One head	Bucerotomorphae[2]
19	Extensor metacarpi radialis origin by one head	Two heads	Bucerotomorphae
20	Extensor metacarpi ulnaris origin separate from that of ectepicondyloulnaris	Origins fused	Alcedinidae, Todidae
21	Extensor digitorum communis origin from humerus	From humerus and radius	Upupides, Trogonidae
22	Extensor digitorum communis insertion on alular phalanx present	Absent	Upupides
23	Ectepicondyloulnaris origin by one tendon	Two tendons	Bucerotinae
24	Extensor longus digiti majoris pars distalis present	Absent	Alcedines, Leptosomidae
25	Extensor longus alulae radial head present	Absent	Upupides, Momotoidea
26	Extensor longus alulae ulnar head present	Absent	Bucerotinae[3]
27	Interosseus dorsalis bipennate	Unipennate	Bucerotomorphae[4]
28	Interosseus dorsalis present	Absent	Upupides, *Tockus*
29	Interosseus ventralis bipennate	Unipennate	Upupides
30	Iliotibialis lateralis acetabular part fleshy	Aponeurotic	Coracii[5]
31	Iliotibialis lateralis acetabular and postacetabular parts present	Absent	Alcedines, *Eurystomus*

Table 2.—*Continued.*

Character	Primitive state	Derived state	Taxa having derived state
32	Iliotrochantericus caudalis origin from dorsal iliac crest	From spinal crest of synsacrum	Bucerotomorphae, Phoeniculidae
33	Flexor cruris lateralis pars accessoria present	Absent	Trogonidae, Alcedinoidea
34	Flexor cruris lateralis accessory tendon from pars pelvica to femur at insertion of caudofemoralis absent	Present	Bucorvinae
35	Pubo-ischio-femoralis pars medialis undivided	Divided	Bucerotomorphae
36	Pubo-ischio-femoralis bellies separate	Fused	Alcedinomorphae[6], *Eurystomus*
37	Obturatorius lateralis pars dorsalis present	Absent	Bucerotomorphae, Upupidae, Todidae, *Rhinopomastus*
38	Obturatorius medialis oval	Triangular	Bucerotomorphae
39	Gastrocnemius pars medialis (interna) with one head	Two heads	Todidae, Meropidae
40	Gastrocnemius pars medialis (interna) origin from medial surface of tibiotarsus	From caudal surface	Bucerotomorphae
41	Fibularis longus branch to FPD3 tendon present	Absent	Coraciidae, Todidae, Alcedinidae
42	Fibularis longus present	Absent	Bucerotomorphae, Upupides, Meropidae
43	Popliteus present	Absent	Alcedines
44	Plantaris present	Absent	Bucerotomorphae, Meropidae
45	Ambiens present	Absent	Coraciiformes
46	Iliofemoralis externus present	Absent	Coraciiformes
47	Abductor digiti II present	Absent	Alcedinomorphae[1]

Table 2.—*Continued.*

Character	Primitive state	Derived state	Taxa having derived state
48	Adductor digiti II present	Absent	Upupides, Momotoidea, Alcedininae[7], Trogonidae, *Pelargopsis*
49	Extensor brevis digiti III present	Absent	Upupides, Momotoidea, Meropidae, Cerylini, Daceloninae[8], *Corythornis*
50	Extensor brevis digiti IV present	Absent	Momotoidea, Meropidae[9]
51	Abductor digiti IV present	Absent	Upupides, Momotoidea, Alcedininae, *Tanysiptera*
52	Flexor perforatus digiti III—flexor perforatus digiti IV vinculum absent	Present	Cerylini
53	Flexor hallucis longus—flexor digitorum longus tendons not extensively fused	Extensively fused (Gadow's Type V)	Coraciiformes
54	Type V deep plantar tendons present	Flexor hallucis longus alone supplies hallux, with branch to flexor digitorum longus	Upupides
55	Vinculum tendinum flexorum (deep plantar vinculum) present	Absent	Upupidae
56	Flexor hallucis longus supplies hallux	Tendon excluded from hallux	Alcedinides[1]
57	Type V deep plantar tendons	Flexor hallucis longus directly supplies only digits III and IV	Alcedinidae

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[1] Except Trogonidae.
[2] Except *Anthracoceros*.
[3] Except *Tockus*.
[4] Absent in *Tockus*.
[5] Except *Eurystomus*.
[6] Except Todidae.
[7] Except *Alcedo*.
[8] Except *Halcyon*.
[9] Except *Merops hirundineus*.

evidence exists to ally any group of the Coraciiformes more closely to a non-coraciiform than to other members of the Coraciiformes" (p. 230).

In short, there is a fair amount of rather circumstantial evidence in support of coraciiform monophyly and no significant argument against it. We will therefore proceed on the working assumption that the monophyly of the order Coraciiformes is the best hypothesis at the present state of our knowledge.

Coracii

The rollers and cuckoo-rollers, Coraciidae and Leptosomidae, appear to form a relatively primitive group, lacking many derived myological states found in the remaining families. The group is defined cladistically by the scapulotriceps humeral anchor (character 15) and the aponeurotic acetabular part of M. iliotibialis lateralis (character 30). Because the first of these occurs in several groups, it is a weak character. The grouping is supported by a series of skull characters and certain aspects of the postcranial skeleton (Cracraft, 1971).

No specimens of the family Brachypteraciidae were examined in the present study. It is tentatively placed next to the Coraciidae in our diagram on the recommendation of Cracraft (1971). The Coraciidae are set apart from the Leptosomidae by character 41. The Leptosomidae are set apart from the Coraciidae by derived states 3, 11, and 24. Two of these are unique and attest to the distinctiveness of this family. Additionally, the Leptosomidae are defined by osteological traits (Cracraft, 1971) and by other traits that are almost certainly derived within the order—a powder down patch, a semi-zygodactyl foot, and a bronchial syrinx (Sclater, 1865).

Alcedines

The remaining families are clustered by muscular reductions and losses (characters 24, 31, 43). Additionally M. fibularis longus is reduced in all except the Momotidae and Trogonidae, but it is unclear whether this muscle is independently reduced in the various families or whether the condition in the motmots and trogons is an evolutionary reversal.

Bucerotomorphae

The hornbills (Bucerotidae) form a highly distinctive group with sixteen derived states, most of which are unique, in their limb muscles (Tables 1, 2). Two groups may be recognized that correspond to Bannerman's (1933) subfamilies. These are the Bucorvinae, containing only the ground hornbills of the genus *Bucorvus,* and the Bucerotinae, including all other forms. The Bucorvinae are clustered by a specialization of the flexor cruris lateralis (34) and by terrestrial habits, which would appear to be derived within this mostly arboreal order of birds. The Bucerotinae have several derived states separating them from the Bucorvinae (5, 23, 26), and in addition, it appears certain that the remarkable walling-up nesting behavior of the former is also a synapomorphy of the subfamily. Kemp (1979) presented a different view of hornbill phylogeny, in which *Bucorvus* is considered to be a phyletically advanced genus rather than being the sister group of all the other genera as suggested here. We prefer our hypothesis because Kemp's is based largely on behavioral characteristics about which he himself expresses uncertainty, and because his cladogram includes several clades for which he provides no defining characters.

Alcedinomorphae

This cluster is only weakly defined by limb myology. There are two derived states, but each has an exception (Tables 1, 2). The bellies of M. pubo-ischio-femoralis are fused (also in *Eurystomus*) (character 36), and the adductor digiti II is lost (47) except in the Trogonidae.

Upupides

The generally accepted idea of a close relationship between the hoopoes and wood-hoopoes is strongly corroborated by the limb musculature, with 18 synapomorphies (Nos. 4, 6, 7, 9, 13, 14, 16, 17, 21, 22, 25, 28, 29, 42, 48, 49, 51, 54), in addition to which each family is distinguished from the other (Tables 1, 2). Feduccia (1975*b*) hypothesized a similar relationship between the Upupidae and Phoeniculidae on the basis of a derived "anvil" stapes morphology.

Alcedinides

This group, including the Todidae, Momotidae, Meropidae, Alcedinidae, and Trogonidae, corresponds to the "Alcediniform assemblage" that Feduccia (1975*a*) defined on the basis of a derived morphology of the stapes. The first four families are clustered by characters 15 and 56, and by being tunnel nesters and having similar egg-white patterns (Sibley and Ahlquist, 1972), but the trogons do not fit with these characteristics (see below).

Momotoidea

The todies and motmots, Todidae and Momotidae, are shown to be sister groups by five synapomorphies (25, 48, 49, 50, 51; Tables 1, 2). Olson (1976) provided osteological and paleontological evidence that the todies are descended from a momotid-like ancestor. Kepler (1977) linked todies and motmots by morphological, behavioral, and developmental characteristics. The Momotidae are not further distinguished by derived myological characteristics, but that the Todidae are the more highly advanced of the two families is shown by several additional synapomorphies (20, 37, 39, 41; Tables 1, 2).

Alcedinoidea

The bee-eaters and kingfishers, Meropidae and Alcedinidae, are shown to be sister groups by two apomorphic muscular characters (7, 33), the latter also shared with the trogons, discussed below. The two families are each further defined as separate monophyletic groups by the possession of additional synapomorphies (Tables 1, 2). Within the Alcedinidae some separation into groups of genera corresponding to recognized subfamilies is provided by limb muscle characters, which support the general picture that the forest kingfishers (Daceloninae) are more primitive than the fishing kingfishers (Alcedininae). The latter group is sometimes separated into two subfamilies. There is some suggestion of support for this division (here into tribes Alcedinini and Cerylini) from the limb muscles, but the data are not unequivocal. Because this is such a large and diverse family, and because we dissected a relatively few forms, we emphasize the need for more comprehensive studies of the kingfishers. Fry (1980) has recently reviewed the family.

Trogonidae

This family has long been a taxonomic puzzle, its relationships having been much debated (Sibley and Ahlquist, 1972:213–218). It is generally agreed that the trogons are probably close to the Coraciiformes. Their distinctiveness has been emphasized perhaps excessively by the uniquely derived condition of their heterodactyl foot, a perching adaptation in which digits I and II are directed backward in opposition to III and IV. In the most recent attempt to clarify the relationship of trogons, Feduccia (1975*a*) made a cladistic analysis of the stapes (middle ear ossicle) and allied the trogons with the Todidae, Momotidae, Meropidae, and Alcedinidae in an order "Alcediniformes," which corresponds to our subinfraorder Alcedinides.

What does the limb musculature contribute to the hypotheses that the trogons are coraciiform, and more specifically, part of the Alcedinides? The trogons share characters 45 and 46 with the Coraciiformes. They differ, however, in no. 53, having Gadow's type VIII deep plantar tendon arrangement rather than type V. We consider it possible that this autapomorphous condition evolved from the type V arrangement by a partial rearrangement of the distal ends of the tendons of the flexor hallucis longus (FHL) and flexor digitorum longus (FDL). Such rearrangements are common among birds; for example, a more complex one than that suggested here occurred in the evolution of the Piciformes (Swierczewski and Raikow, 1981). Following Gadow, a hypothesis for the evolution of the arrangement of the deep plantar tendons of the trogons from the primitive coraciiform condition is shown in Fig. 2 (see Gadow, 1894:617). Fig. 2A shows the condition (Gadow's type V) found in the Coraciidae, Leptosomidae, and Bucerotidae, that we believe to be primitive in the Coraciiformes (but derived in the class Aves). In this arrangement the two deep flexor tendons fuse and then bifurcate, one branch supplying the hallux, the other subsequently dividing to supply digits II, III, and IV. Fig. 2C shows the condition found in trogons (Gadow's type VIII). FHL supplies digits I and II, and FDL supplies III and IV. A vinculum (v) connects the two. The speculative diagram in Fig. 2B shows how the trogon condition could have evolved from the primitive coraciiform condition. At (a) separation of the coalesced tendons would have occurred, whereas at (b) a division would have arisen. The vinculum would be the remnant of the formerly extensive connection. Presumably this change would have occurred by a modification in embryonic development, possibly involving changes in tendon fiber orientation associated with modified tensional forces resulting from the shifted position of the second digit. Such a modification would give the unique trogon arrangement in which the tendon of the FHL supplies digits I and II, while the tendon of the FDL supplies digits III and IV. This symmetrical distribution of tendons is obviously a functional correlate of the heterodactyl foot, providing a balanced distribution of muscle force to the two opposing pairs of toes. The toe arrangement and tendon arrangement are thus parts of a single derived functional specialization, autapomorphic for the Trogonidae, and need not be considered a refutation of the hypothesis that the trogons are coraciiform.

The Alcedines are defined by characters 21, 34, and 43, with which the trogons are in agreement. The Alcedinomorphae are defined by character 36, with which the trogons agree, and 47, with which they do not. Character 47 is the loss of the abductor digiti II, a small intrinsic foot muscle that is retained by trogons. This argues against Feduccia's and our hypothesis. However, the loss of small toe muscles is a frequent occurrence in birds, and it is possible that this muscle was lost independently in several groups, but we have no way to decide this.

The Alcedinides, corresponding to Feduccia's Alcediniformes, are clustered by characters 15 and 56, with which the trogons do not conform. Character 56 is perhaps not important; a feature of the deep plantar tendons, its modification in trogons could be part of the change associated with heterodactyly.

There is finally the irksome question of why heterodactyly should arise in a group situated in the midst of an assemblage of syndactyl

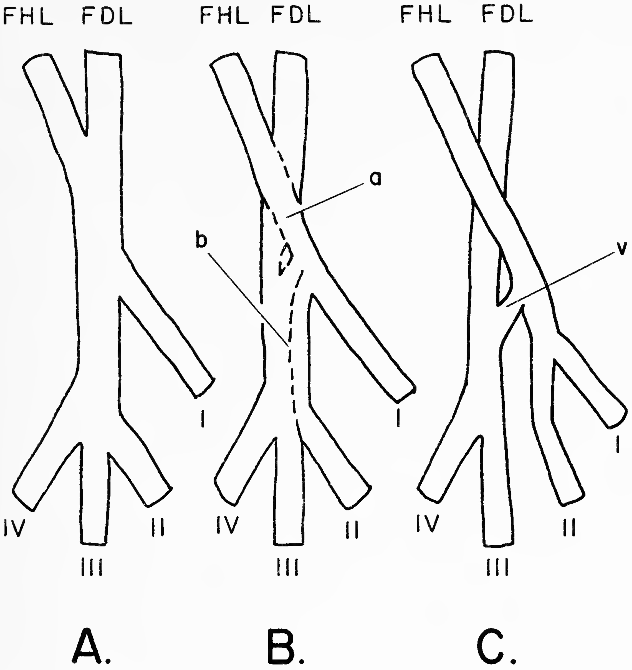

Fig. 2.—A hypothesis for the evolution of the unique arrangement of the deep plantar tendons in trogons. In A is shown the arrangement believed to be primitive within the Coraciiformes, whereas in C is shown the arrangement found in trogons. B shows a speculative diagram indicating changes that could have occurred in A to give C. See text for discussion. Abbreviations: FHL, tendon of M. flexor hallucis longus; FDL, tendon of M. flexor digitorum longus; a, area of separation of coalesced tendons; b, line along which tendon splits apart; v., vinculum; I, II, III, IV, numbers of digits.

forms, as the two conditions are regarded as alternative perching specializations. Bock and Miller (1959) consider syndactyly to be a perching adaptation in which the binding together of the forward toes holds them at right angles to the branch, providing a maximally efficient grip. They consider heterodactyly an alternative solution to the problem of evolving an effective perching foot. It therefore seems more likely that the heterodactyl foot evolved from an anisodactyl condition than from a syndactyl condition. Extreme syndactyly may also be functionally significant in digging, and the possibility exists that syndactyly arose independently in the various coraciiform groups.

On the basis of the above discussion of limb muscle characteristics, we feel that the family Trogonidae is reasonably included in the order Coraciiformes, and in the subinfraorder Alcedinides. The peculiarities of its hindlimb muscles may well be associated with the evolution of the heterodactyl foot, but because they are apomorphic we cannot determine the sister taxon of the Trogonidae using myological characters, and therefore in our classification we have listed it as *incertae sedis* within the Alcedinides. The placement of the Trogonidae in the cladogram (Fig. 1) is suggested by character 33, which links the Meropidae, Alcedinidae, and Trogonidae, but because of the other problematical characters this placement is highly tentative.

DISCUSSION

Some characters suggest alternative clustering arrangements, but we have chosen the hypothesis that minimizes the number of independent origins of derived states, and which seems to us to be the most consistent with the data analyzed in the context of our general understanding of the overall problem. The degree of confidence that each individual hypothesis of monophyly generates will depend in part on the number and kind of characters supporting it. These points are discussed more fully elsewhere (Swierczewski and Raikow, 1981).

The hypothesis of coraciiform monophyly is not strongly corroborated by present information. Although there are several derived states clustering the group, these also occur in other birds and could as well have been derived at a higher level within the class Aves as at the level postulated herein. The ambiens (45) is also, for instance, absent in the Piciformes and Passeriformes. The iliofemoralis externus (46) is similarly absent in the Piciformes and in most Passeriformes, and its presence in a few members of the latter group is believed to be a secondary reoccurrence (Raikow et al., 1979). Thus these characters could well define a cluster consisting of these three orders, whose close affinity is generally admitted. However, both the Piciformes and Passeriformes are well-defined clades (Swierczewski and Raikow, 1981; Raikow, in preparation), so that this hypothesis would still leave two possibilities—the Coraciiformes could constitute a nonmonophyletic group within the larger clade (like the "reptiles" within the clade Amniota), or it could be monophyletic as defined by character 53, extensive fusion of the deep plantar tendons. Speculations along these lines could be extended at great length but to no useful purpose. On the basis of present understanding we feel it best to proceed with a hypothesis of coraciiform monophyly, with the recognition that future studies providing *new data* might well necessitate the abandonment of that position.

CONCLUSION

The phylogeny developed in this study entirely on the basis of data from one system, the limb muscles, correlates well with previous workers' conclusions based on other data. Feduccia's hypothesis of the monophyly of the Alcediniformes (our Alcedinides) is supported, as is his contention that the Trogonidae are part of that assemblage. The exact position of the Trogonidae remains uncertain, however. The idea that the traditional families of the Coraciiformes are each monophyletic is upheld in most cases by derived conditions in their limb myology. Monophyly of the hornbills and of the hoopoe/wood-hoopoe assemblages are especially well corroborated. In contrast, the monophyly of the Coraciiformes as a whole, and of some clades within it, are much less strongly supported. Our study appears to be the most thorough that has been made of this group, and we consider that our phylogeny and the classification derived from it are the most solidly documented studies to date of this most troublesome group of birds, but future studies will no doubt lead to further clarification of the problem.

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SYSTEMATIC REVIEW OF THE TEXAS POCKET GOPHER, *GEOMYS PERSONATUS* (MAMMALIA: RODENTIA)

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Abstract

The Texas pocket gopher (*Geomys personatus*), which occupies a range in southern Texas and extreme northeastern Tamaulipas, was examined for morphological variation. Univariate and multivariate analyses were used to determine age, secondary sexual, individual, and geographic variation. Significant differences were found among the three age classes and between the sexes for 12 of 13 cranial measurements. Males displayed higher individual variation than females. Distributions of the six previously recognized subspecies (*fallax, fuscus, maritimus, megapotamus, personatus,* and *streckeri*) were examined. An additional subspecies is recognized and described. Of the seven subspecies of *G. personatus, fuscus* and *streckeri* form a group distinct from other subspecies.

Introduction

The Texas pocket gopher, *Geomys personatus,* which is restricted to South Texas and the coastal beaches of Tamaulipas, was described by True (1889) from specimens taken on Padre Island, Texas. Subsequently, Merriam (1895) described *G. p. fallax* and Goldman (1915) described *G. p. tropicalis.* Davis (1940) published the first major re-

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vision of the species and described four additional subspecies—*fuscus, maritimus, megapotamus,* and *streckeri* (changed from *minor* by Davis, 1943). Alvarez (1963) subsequently recognized *tropicalis* as a distinct species and this has been confirmed by later studies (Davis et al., 1971; Selander et al., 1975). Therefore, the recognized subspecies of *G. personatus* at the beginning of the current study included *fallax, fuscus, maritimus, megapotamus, personatus,* and *streckeri* (Hall, 1981).

Since the work of Davis (1940), several authors have commented on the need to reexamine the systematics and taxonomy of the species. Kennerly (1954) compared morphometrics and habitats of five subspecies, using eight samples and 342 specimens. He concluded local differentiation exists among populations with a cline of smaller-sized individuals with increased distance from the coast. Davis et al. (1971) reported karyotypic data from 18 localities throughout the range of *G. personatus.* For five subspecies examined, the diploid number ranged from 68 to 72, and the fundamental number from 70 to 76. Parasite data indicate speciation has occurred in the lice found on *G. personatus* (Price and Emerson, 1971; Price and Hellenthall, 1975; Timm and Price, 1979). *Geomydoecus texanus* has been reported from all subspecies except *G. p. fuscus* and *G. p. streckeri,* which are hosts to *Geomydoecus dalgleishi* and *Geomydoecus truncatus,* respectively.

This study is based on an analysis of greater numbers of specimens than were available to Davis (1940) and Kennerly (1954). Furthermore, additional populations, reported as range extensions for Karnes Co. in Texas (Kennerly, 1958*a*) and coastal Tamaulipas (Selander et al., 1962) were not included in previous analyses of geographic variation. Study of the 1051 available specimens, many of which were obtained by the authors, affords for the first time a detailed description of nongeographic and geographic variation in this species using univariate and multivariate statistical techniques. This is the fourth in a series of papers describing morphological variation in members of the genus *Geomys* (Williams and Genoways, 1977, 1978, 1980).

METHODS

Three external and 13 cranial measurements were taken from specimens examined. External measurements (total length, length of tail, length of hind foot) used were those initially recorded by the collector. Cranial measurements were recorded as described by Williams and Genoways (1977) and were taken by means of dial calipers, accurate to one-tenth of a millimeter. Males and females were separated and then assigned to one of three age groups as described by Williams and Genoways (1977).

For analysis of geographic variation, adult specimens were grouped into 16 samples as follows (Fig. 1): *sample 1*—Kinney and Val Verde cos.; *sample 2*—Dimmit and Zavala cos.; *sample 3*—La Salle Co.; *sample 4*—western Webb and western Zapata cos.; *sample 5*—Brooks, Duval, Jim Hogg, and eastern Webb cos.; *sample 6*—mainland of northern Kenedy and southern Kleberg cos.; *sample 7*—Cameron, Hidalgo, southern

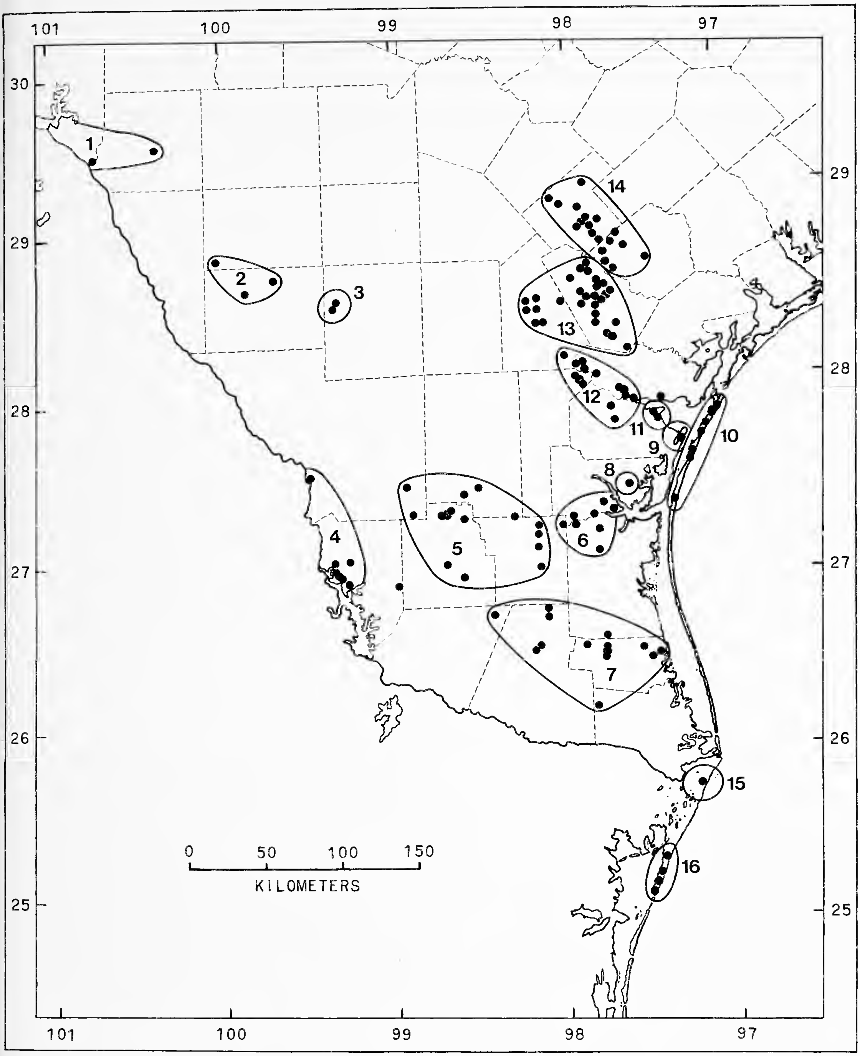

Fig. 1.—Approximate geographic areas included in the 16 samples of *Geomys personatus*. Dots represent collecting localities of specimens examined in this study. See text for localities included in each sample.

Kenedy, and Willacy cos.; *sample 8*—north of Baffin Bay in Kleberg Co.; *sample 9*—mainland of Nueces Co., east of Corpus Christi; *sample 10*—barrier islands (Mustang Island and Padre Island) of Kleberg and Nueces cos.; *sample 11*—immediate vicinity of Corpus Christi, Nueces Co.; *sample 12*—Jim Wells, southeastern Live Oak, western

Nueces, and San Patricio cos.; *sample 13*—Bee and Live Oak (northern two-thirds) cos.; *sample 14*—Goliad and Karnes cos.; *sample 15*—coastal beach of Tamaulipas, approximately 34 km of ESE Matamoros; *sample 16*—coastal beach of Tamaulipas, approxmately 88 km S Matamoros. Acronyms used in lists of specimens examined are given in the acknowledgments. The acronym for Carnegie Museum of Natural History used in text is CM.

Univariate analyses were performed using the program UNIVAR. This program generates 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 Gabrial (1964) was used to determine maximally nonsignificant subsets.

Cluster and principal components analyses were performed using the MINT program. Matrices of Q-mode correlation (among OTU's) and phenetic and distance coefficients were computed. Cluster analyses were conducted using UPGMA (unweighted pair-group method using arithmetic averages) on the correlation and distance matrices and a phenogram was generated for each. Phenograms were compared with their respective matrices, and a coefficient of cophenetic correlation was computed. The first three principal components were extracted and projections of the OTU's onto them were prepared.

Stepwise discriminant analysis and canonical analysis (BMDP7M, Dixon and Brown, 1977) are techniques that 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, placing them with the group to which they are nearest on the discriminant functions.

Discriminant function analyses were performed using the BMD-04M subroutine of the Biomedical Computer Programs (Dixon, 1971). This program used variance-covariance mathematics to differentially weigh characters relative to their within-group and between-group variation. Two reference samples were used for discriminant analyses in this paper—one of *Geomys bursarius* and the second of *G. personatus*. These reference samples were used to generate discriminant multipliers for each character, and these were multiplied by the value of their respective characters; all such values were summed for each individual to yield its discriminant score. Discriminant scores were obtained for individuals of questioned identity using the multipliers generated by the reference samples, in order to properly identify the questioned individuals.

Specimens from Texas (30) used as a reference sample for *Geomys attwateri* (see Tucker and Schmidly, 1981, for use of *G. attwateri*) were as follows: ARANSAS CO., Aransas Refuge, 1 (TCWC); 10 mi SE Austwell, 2 (TCWC); Rockport, 3 (TNHC); 2 mi SW Rockport, 1 (TNHC); 8 mi SW Rockport, 2 (TCWC); ATASCOSA CO., 2 mi NW Campbellton, 2 (TCWC); 7 mi E Lytle, 5 (TNHC); 7 mi SE Lytle, 3 (TNHC); McCoy, 1 (TNHC); FRIO CO., 1 mi N Moore, 3 (TCWC); GOLIAD CO., 1½ mi SSE Berclaire, 1 (TNHC); 2 mi SSE Berclaire, 1 (TNHC); GONZALES CO., 1.5 mi S Leesville, 1 (TNHC); 5 mi SE Luling, 1 (TNHC); 11 mi S Luling, 1 (TNHC); GUADALUPE CO., 11 mi S Seguin, 1 (TNHC); VICTORIA CO., 6 mi S Victoria, 1 (TCWC).

Specimens (30, also in list of specimens examined for *G. p. fallax*) used as a reference sample for *Geomys personatus fallax* were from the following Texas localities: JIM WELLS CO., Sandia, 3; 1.8 mi S, 2.3 mi E Sandia, 1; LIVE OAK CO., 8 mi NW George West, 1; 5 mi NW George West, 1; 4 mi N George West, 2; 3 mi N George West, 3; 5 mi S Three Rivers, 1; NUECES CO., Calallen, 4; 1 mi E Calallen, 1; 17 mi W Corpus Christi, 5; SAN PATRICIO CO., 5 mi SE Edroy, 4; 3 mi SW Mathis, 2; ¼ mi SE Odem, 1; County unknown, 10 mi from mouth of Nueces River, 1.

RESULTS

Nongeographic Variation

The sample of *Geomys personatus* from Mustang Island, Nueces Co., Texas, was subjected to univariate analyses to determine the type and extent of nongeographic variation (age, secondary sexual, and individual) in the species.

Variation with age.—In males, all measurements studied, except interorbital constriction, were found to vary significantly with age; in females all measurements varied significantly with age (Table 1). In external measurements, adults and subadults of each sex formed a group that differed significantly from juveniles. In all cranial measurements (except interorbital constriction) all three age classes of males and females formed nonsignificant subsets. The interorbital constriction of females had a subset formed by juveniles and subadults that was significantly different from adults (there were no significant differences among age groups of males). In all measurements for both sexes, adults had the largest means, followed by subadults, and then by juveniles. Clearly the three age classes that we recognized are morphologically distinct. Only adult individuals are used in subsequent analyses.

Secondary sexual variation.—The same adult males and females used in analysis of variation with age were used to test for secondary sexual variation (Table 1). Males averaged significantly larger than females in all measurements except interorbital constriction, for which the mean was only slightly larger. In all analyses of geographic variation, males and females were treated separately.

Individual variation.—Coefficients of variation ranged from 3.5 to 9.5 for adult males and 2.7 to 7.5 for adult females, for the 16 external and cranial measurements tested (Table 1). The mean coefficient of variation for these measurements was 5.0 and 4.1 for males and females, respectively. In both sexes the coefficient of variation was usually higher for external measurements than for cranial measurements. The only exception was interorbital constriction of males, which had the highest value (9.5); the lowest value for males was in squamosal breadth (3.5). For cranial measurements of females, the diastema had the highest value (5.0) and condylobasal length had the lowest (2.7). Males had larger coefficients of variation than females for all measurements except length of tail and squamosal breadth.

Geographic Variation

Univariate analyses.—Eleven samples of males and 12 of females had a sufficient number (three or more) of specimens to allow their use in univariate analyses. Results of the analyses of variance and SS-STP for these samples are shown in Table 2.

Table 1.—*Variation with age in external and cranial measurements of* Geomys personatus *from the barrier beach of Kleberg and Nueces counties, Texas. 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 as listed in this table were used to test for secondary sexual variation. Measurement names marked with an asterisk indicate those with significant (0.05) secondary sexual variation.*

Sex and age class	N	Mean (range) ± 2 SE	CV	SS-STP		
		*Total length**				
Males						
Adults	24	314.7 (264.0–360.0) ± 7.80	6.1	I		
Subadults	25	306.6 (260.0–332.0) ± 6.27	5.1	I		
Juveniles	7	257.6 (232.0–271.0) ± 10.06	5.2		I	
Females						
Adults	18	284.9 (263.0–312.0) ± 7.00	5.2	I		
Subadults	34	276.6 (247.0–312.0) ± 5.04	5.3	I		
Juveniles	9	238.2 (215.0–265.0) ± 11.53	7.3		I	
		*Length of tail**				
Males						
Adults	24	105.0 (91.0–123.0) ± 3.17	7.4	I		
Subadults	25	104.1 (78.0–121.0) ± 4.61	11.1	I		
Juveniles	7	87.4 (77.0–94.0) ± 4.40	6.7		I	
Females						
Adults	18	94.6 (80.0–106.0) ± 3.36	7.5	I		
Subadults	34	92.9 (71.0–112.0) ± 3.20	10.0	I		
Juveniles	9	80.3 (66.0–90.0) ± 5.12	9.6		I	
		*Length of hind foot**				
Males						
Adults	24	39.3 (33.0–43.0) ± 1.10	6.9	I		
Subadults	25	38.9 (33.0–42.0) ± 1.03	6.6	I		
Juveniles	7	36.2 (34.0–37.0) ± 0.88	3.2		I	
Females						
Adults	18	36.8 (32.0–39.0) ± 1.01	5.8	I		
Subadults	34	36.2 (32.0–40.0) ± 0.72	5.8	I		
Juveniles	9	33.1 (30.0–37.0) ± 1.73	7.8		I	
		*Greatest length of skull**				
Males						
Adults	23	58.2 (54.1–62.5) ± 0.94	3.9	I		
Subadults	25	55.3 (50.6–60.2) ± 0.93	4.2		I	
Juveniles	6	45.6 (43.8–47.8) ± 1.22	3.3			I
Females						
Adult	14	53.3 (51.2–55.3) ± 0.84	2.9	I		
Subadult	33	50.7 (47.5–55.5) ± 0.64	3.6		I	
Juveniles	9	43.4 (37.9–47.2) ± 2.30	8.0			I
		*Condylobasal length**				
Males						
Adults	26	57.2 (53.0–60.8) ± 0.82	3.7	I		

Table 1.—*Continued.*

Sex and age class	N	Mean (range) ± 2 SE	CV	SS-STP		
Subadults	27	54.4 (46.4–59.8) ± 1.06	5.1		I	
Juveniles	6	44.3 (42.2–46.3) ± 1.18	3.3			I
Females						
Adults	19	52.0 (50.1–54.5) ± 0.65	2.7	I		
Subadults	36	49.5 (46.4–54.4) ± 0.57	3.5		I	
Juveniles	9	42.5 (37.5–46.5) ± 2.25	7.9			I
		_Basal length_*				
Males						
Adults	26	53.9 (50.2–57.4) ± 0.78	3.7	I		
Subadults	27	50.5 (43.4–56.0) ± 1.01	5.2		I	
Juveniles	6	40.7 (38.9–42.8) ± 1.23	3.7			I
Females						
Adults	19	48.6 (46.7–51.5) ± 0.65	2.9	I		
Subadults	36	46.0 (42.8–50.1) ± 0.56	3.7		I	
Juveniles	9	38.9 (33.7–42.9) ± 2.34	9.0			I
		_Palatal length_*				
Males						
Adults	26	37.8 (34.9–40.2) ± 0.57	3.8	I		
Subadults	27	35.1 (30.0–39.3) ± 0.75	5.6		I	
Juveniles	7	27.3 (24.0–29.0) ± 1.34	6.5			I
Females						
Adults	19	33.6 (32.2–35.9) ± 0.52	3.4	I		
Subadults	38	31.7 (29.0–35.3) ± 0.47	4.5		I	
Juveniles	9	26.5 (22.6–29.7) ± 1.75	9.9			I
		_Palatofrontal depth_*				
Males						
Adults	26	20.3 (19.0–22.2) ± 0.30	3.8	I		
Subadults	27	19.0 (16.9–21.1) ± 0.34	4.7		I	
Juveniles	7	15.6 (14.5–16.7) ± 0.57	4.9			I
Females						
Adults	19	18.6 (17.8–19.7) ± 0.26	3.0	I		
Subadults	38	17.5 (16.0–19.5) ± 0.26	4.5		I	
Juveniles	9	15.2 (13.2–16.9) ± 0.99	9.7			I
		_Length of nasals_*				
Males						
Adults	23	20.7 (18.7–22.5) ± 0.42	4.9	I		
Subadults	26	19.0 (17.1–22.6) ± 0.44	5.9		I	
Juveniles	7	14.7 (12.7–16.0) ± 0.85	7.7			I
Females						
Adults	14	18.2 (17.3–19.5) ± 0.43	4.4	I		
Subadults	37	17.1 (15.5–18.9) ± 0.34	6.1		I	
Juveniles	9	14.0 (10.9–16.2) ± 1.24	13.1			I
		_Diastema_*				
Males						
Adults	26	21.0 (19.1–22.8) ± 0.43	5.2	I		

Table 1.—*Continued.*

Sex and age class	N	Mean (range) ± 2 SE	CV	SS-STP		
Subadults	27	18.9 (15.1–22.1) ± 0.58	7.9		I	
Juveniles	7	14.1 (11.7–15.7) ± 1.02	9.5			I
Females						
Adults	19	18.1 (16.6–19.8) ± 0.41	5.0	I		
Subadults	38	16.8 (14.6–19.4) ± 0.34	6.2		I	
Juveniles	9	13.2 (10.4–15.0) ± 1.25	14.2			I
		*Zygomatic breadth**				
Males						
Adults	26	35.8 (32.9–38.0) ± 0.63	4.5	I		
Subadults	27	32.9 (28.2–36.5) ± 0.79	6.2		I	
Juveniles	7	25.3 (23.6–26.7) ± 0.91	4.8			I
Females						
Adults	18	31.4 (29.8–32.7) ± 0.45	3.0	I		
Subadults	36	29.6 (26.9–32.9) ± 0.47	4.8		I	
Juveniles	9	24.9 (20.4–28.5) ± 1.95	11.7			I
		*Mastoid breadth**				
Males						
Adults	26	32.7 (29.9–35.9) ± 0.51	4.0	I		
Subadults	27	30.5 (27.1–34.0) ± 0.61	5.2		I	
Juveniles	6	25.0 (23.3–26.3) ± 0.83	4.1			I
Females						
Adults	19	29.4 (27.4–31.1) ± 0.53	3.9	I		
Subadults	38	27.9 (25.6–31.3) ± 0.41	4.5		I	
Juveniles	9	24.1 (20.7–26.5) ± 1.41	8.8			I
		*Squamosal breadth**				
Males						
Adults	26	23.9 (22.4–26.0) ± 0.33	3.5	I		
Subadults	27	22.6 (20.3–24.7) ± 0.39	4.5		I	
Juveniles	6	19.7 (18.8–20.2) ± 0.40	2.5			I
Females						
Adults	19	22.4 (21.0–23.6) ± 0.40	3.9	I		
Subadults	38	21.2 (19.4–23.2) ± 0.27	3.8		I	
Juveniles	9	19.4 (18.0–20.6) ± 0.68	5.3			I
		*Rostral breadth**				
Males						
Adults	25	12.8 (11.4–13.9) ± 0.24	4.6	I		
Subadults	27	12.1 (9.3–13.3) ± 0.29	6.3		I	
Juveniles	7	9.7 (8.7–10.9) ± 0.62	8.5			I
Females						
Adults	19	11.6 (10.6–12.2) ± 0.22	4.1	I		
Subadults	38	10.9 (10.2–11.8) ± 0.14	4.0		I	
Juveniles	9	9.8 (8.2–11.0) ± 0.57	8.7			I

Table 1.—*Continued.*

Sex and age class	N	Mean (range) ± 2 SE	CV	SS-STP		
Interorbital constriction						
Males						
Adults	25	7.4 (6.1–9.6) ± 0.28	9.5	ns		
Subadults	27	7.1 (6.3–8.1) ± 0.15	5.5			
Juveniles	7	6.8 (6.1–7.3) ± 0.33	6.3			
Females						
Adults	19	7.2 (6.6–7.7) ± 0.13	3.8	I		
Subadults	38	7.0 (6.3–8.0) ± 0.11	4.8		I	
Juveniles	9	6.9 (6.5–7.3) ± 0.17	3.7		I	
*Breadth across maxillaries**						
Males						
Adults	26	9.9 (9.1–10.7) ± 0.15	3.8	I		
Subadults	27	9.4 (7.6–10.1) ± 0.19	5.3		I	
Juveniles	7	8.3 (7.9–8.7) ± 0.19	3.1			I
Females						
Adults	19	9.5 (8.9–10.1) ± 0.15	3.4	I		
Subadults	38	9.1 (8.4–9.8) ± 0.10	3.5		I	
Juveniles	9	8.5 (7.8–9.1) ± 0.29	5.1			I

In all measurements of males, sample 10 had the largest mean. For 12 measurements, samples 8 and 9 had the second and third largest means. In the remaining measurements the means of these samples ranked third and fourth (two measurements), third and fifth, and second and fifth. For eight measurements, the fourth to seventh positions were taken by samples 5, 6, 7, and 16; in seven measurements, three of four of these positions were taken by these samples. The eighth, ninth, and tenth positions of ranked means were typically taken by samples 4, 12, and 13. For 11 measurements, each position was taken by the three samples; for the remaining five measurements, two of the three positions were taken by these samples. Sample 2 had the smallest means and ranked eleventh for all measurements.

A similar pattern of ranking was observed in females. Sample 10 ranked the largest in all measurements, except for two external measurements where the mean of this sample ranked second largest. Samples 8 and 9 fell into the second and third positions for 13 measurements. In the remaining measurements, these two samples ranked first and fourth, first and fifth, and second and fourth. For 11 measurements, means of samples 5, 6, 7, and 16 fell into the fourth to seventh ranked positions; for three measurements, three of the four positions were filled by these samples. Samples 4, 12, 13, and 14 filled the eighth to eleventh positions in 13 measurements; two measurements had three

Table 2.—*Geographic variation in external and cranial measurements of* Geomys personatus. *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. Samples with fewer than three individuals are omitted from this table.*

Sex and locality number	N	Mean (range) ± 2 SE	CV	Results of SS-STP					
		Total length							
Males									
10	35	315.3 (264.0–360.0) ± 5.83	5.5	I					
8	5	303.8 (294.0–322.0) ± 9.77	3.6	I	I				
9	4	299.3 (282.0–310.0) ± 13.50	4.5	I	I	I			
6	3	295.7 (289.0–307.0) ± 11.39	3.3	I	I	I	I		
7	8	291.0 (272.0–303.0) ± 8.99	4.4		I	I	I		
5	21	288.7 (269.0–310.0) ± 5.25	4.2		I	I	I		
16	10	279.8 (264.0–306.0) ± 8.78	5.0		I	I	I	I	
4	11	275.0 (248.0–314.0) ± 10.81	6.5			I	I	I	I
13	11	271.5 (242.0–304.0) ± 9.62	5.9				I	I	I
12	15	268.3 (247.0–290.0) ± 5.38	3.9					I	I
2	10	249.9 (226.0–280.0) ± 9.52	6.0						I
Females									
10	29	286.9 (263.0–312.0) ± 4.88	4.6	I					
8	3	285.0 (280.0–293.0) ± 8.08	2.5	I	I				
9	9	265.7 (242.0–284.0) ± 9.31	5.6		I	I			
16	15	259.9 (234.0–278.0) ± 6.72	5.0		I	I	I		
5	17	257.9 (240.0–274.0) ± 4.89	3.9		I	I	I		
7	14	257.1 (238.0–280.0) ± 5.83	4.3		I	I	I	I	
6	5	254.0 (223.0–278.0) ± 20.97	9.2		I	I	I	I	
14	8	253.6 (237.0–274.0) ± 7.62	4.3		I	I	I	I	
4	13	252.9 (229.0–269.0) ± 6.83	4.9			I	I	I	
13	9	241.3 (228.0–252.0) ± 5.66	3.5				I	I	I
12	12	239.7 (220.0–270.0) ± 7.61	5.5					I	I
2	15	225.7 (216.0–234.0) ± 3.06	2.6						I
		Length of tail							
Males									
10	35	105.0 (86.0–125.0) ± 2.89	8.1	I					
8	5	101.8 (93.0–110.0) ± 6.05	6.6	I	I				
9	4	96.5 (92.0–100.0) ± 3.42	3.5	I	I	I			
16	10	91.8 (65.0–106.0) ± 7.37	12.7	I	I	I	I		
6	3	90.0 (81.0–97.0) ± 9.45	9.1		I	I	I		
7	8	89.5 (80.0–108.0) ± 7.48	11.8		I	I	I		
4	11	88.4 (62.0–105.0) ± 6.38	11.9		I	I	I		
5	21	87.5 (69.0–103.0) ± 3.81	10.0		I	I	I		
12	15	83.9 (65.0–97.0) ± 4.17	9.6		I	I	I		
13	11	81.4 (59.0–94.0) ± 6.26	12.8			I	I		
2	10	79.1 (64.0–96.0) ± 5.55	11.1				I		
Females									
8	3	95.7 (94.0–97.0) ± 1.76	1.6	I					
10	29	95.7 (80.0–110.0) ± 2.49	7.0	I					

Table 2.—*Continued.*

Sex and locality number	N	Mean (range) ± 2 SE	CV	Results of SS-STP				
16	14	86.9 (76.0–96.0) ± 3.17	6.8	I	I			
9	9	83.8 (74.0–99.0) ± 6.49	11.6		I	I		
7	14	83.6 (70.0–93.0) ± 3.67	8.2		I	I		
4	13	80.0 (68.0–89.0) ± 4.04	9.1		I	I	I	
14	8	79.1 (74.0–87.0) ± 3.01	5.4		I	I	I	
13	9	76.7 (66.0–89.0) ± 4.65	9.1		I	I	I	
5	17	76.1 (59.0–88.0) ± 4.01	10.9			I	I	
12	12	75.8 (60.0–81.0) ± 3.59	8.2			I	I	
6	5	75.2 (63.0–87.0) ± 9.52	14.1			I	I	
2	15	70.1 (62.0–80.0) ± 2.60	7.2				I	
		Length of hind foot						
Males								
10	35	39.5 (33.0–43.0) ± 0.84	6.3	I				
9	4	38.5 (36.0–41.0) ± 2.38	6.2	I	I			
8	5	37.9 (36.2–40.5) ± 1.48	4.4	I	I			
5	21	36.5 (32.8–40.0) ± 0.78	4.9		I	I		
16	10	36.4 (35.0–39.0) ± 0.80	3.5		I	I		
7	8	36.3 (34.0–38.0) ± 0.95	3.7		I	I		
6	3	36.0 (35.0–37.0) ± 1.15	2.8		I	I	I	
4	11	35.5 (31.4–38.0) ± 1.12	5.2		I	I	I	
13	10	33.4 (30.0–36.0) ± 1.05	5.0			I	I	I
12	15	33.0 (28.0–35.0) ± 0.89	5.3				I	I
2	10	30.8 (27.0–34.4) ± 1.61	8.3					I
Females								
8	3	36.9 (35.7–38.6) ± 1.73	4.1	I				
10	29	36.7 (32.0–39.0) ± 0.70	5.1	I				
7	14	33.9 (32.0–35.4) ± 0.57	3.2		I			
5	17	33.5 (31.0–35.0) ± 0.64	3.9		I			
9	9	33.2 (30.0–36.0) ± 1.45	6.5		I	I		
4	13	33.1 (31.0–35.0) ± 0.86	4.7		I	I		
16	15	33.0 (29.0–36.0) ± 0.96	5.6		I	I		
6	5	32.8 (30.0–38.0) ± 2.96	10.1		I	I	I	
14	8	32.1 (31.0–32.8) ± 0.43	1.9		I	I	I	
12	12	30.5 (26.0–35.0) ± 1.40	8.0			I	I	I
13	9	30.0 (27.5–32.6) ± 1.18	5.9				I	I
2	15	27.7 (24.0–30.0) ± 1.08	7.6					I
		Greatest length of skull						
Males								
10	32	57.9 (54.1–62.5) ± 0.72	3.5	I				
9	4	55.3 (53.2–58.4) ± 2.25	4.1	I	I			
8	5	54.7 (52.0–56.6) ± 1.69	3.5	I	I	I		
6	4	52.9 (51.3–53.9) ± 1.16	2.2		I	I	I	
7	8	52.9 (50.7–54.8) ± 1.05	2.8		I	I	I	
5	21	51.7 (48.7–56.1) ± 0.80	3.5		I	I	I	I
16	10	51.6 (48.4–54.2) ± 1.21	3.7			I	I	I
13	15	50.7 (46.8–55.7) ± 1.13	4.3				I	I

Table 2.—*Continued.*

Sex and locality number	N	Mean (range) ± 2 SE	CV	Results of SS-STP							
4	11	49.9 (47.1–55.4) ± 1.57	5.2				I	I			
12	15	49.8 (47.5–52.5) ± 0.64	2.5					I			
2	9	45.1 (42.5–48.4) ± 1.46	4.8						I		
Females											
10	24	52.9 (50.2–55.3) ± 0.59	2.7	I							
8	3	51.2 (49.2–52.7) ± 2.08	3.5	I	I						
9	11	49.5 (46.4–52.3) ± 1.16	3.9		I	I					
6	8	48.5 (46.1–51.8) ± 1.27	3.7		I	I	I				
7	10	46.9 (44.5–48.8) ± 0.99	3.3			I	I	I			
16	13	46.9 (45.7–48.5) ± 0.54	2.1				I	I			
5	18	46.3 (44.3–48.1) ± 0.69	3.1				I	I	I		
14	8	45.0 (43.6–46.5) ± 0.79	2.5					I	I	I	
4	13	44.1 (41.9–46.4) ± 0.71	2.9						I	I	
12	12	43.9 (41.2–46.2) ± 0.89	3.5							I	
13	11	43.3 (41.0–45.8) ± 0.87	3.3							I	
2	13	40.0 (37.8–42.3) ± 0.79	3.6								I
		Condylobasal length									
Males											
10	37	56.8 (53.0–60.8) ± 0.66	3.5	I							
9	4	53.8 (52.1–56.4) ± 1.91	3.5	I	I						
8	5	53.4 (51.2–55.4) ± 1.72	3.6		I	I					
6	4	51.6 (50.0–52.6) ± 1.13	2.2		I	I	I				
7	8	51.5 (49.4–53.2) ± 1.15	3.2		I	I	I				
5	23	50.7 (48.0–55.1) ± 0.80	3.8		I	I	I	I			
16	10	50.3 (47.0–52.4) ± 1.02	3.2		I	I	I	I			
13	16	49.7 (45.3–55.1) ± 1.15	4.6			I	I	I			
12	15	48.9 (46.0–51.5) ± 0.70	2.8				I	I			
4	11	48.4 (46.1–54.2) ± 1.51	5.2					I			
2	10	43.7 (39.5–48.2) ± 1.66	6.0						I		
Females											
10	30	51.7 (49.0–54.5) ± 0.50	2.7	I							
8	3	49.7 (47.8–51.2) ± 2.02	3.5	I	I						
9	11	48.4 (45.6–50.8) ± 1.02	3.5		I						
6	8	47.3 (45.1–50.5) ± 1.18	3.5		I	I					
16	17	45.5 (43.7–47.4) ± 0.49	2.2			I	I				
7	15	45.4 (43.2–47.9) ± 0.72	3.1			I	I				
5	18	45.3 (43.3–46.9) ± 0.58	2.7			I	I	I			
14	8	44.2 (42.9–45.7) ± 0.75	2.4				I	I	I		
12	13	43.2 (40.3–45.5) ± 0.85	3.5					I	I		
4	13	42.9 (40.5–45.0) ± 0.73	3.1						I		
13	13	42.7 (39.7–45.0) ± 0.87	3.7						I		
2	16	39.2 (36.8–41.4) ± 0.65	3.3							I	
		Basal length									
Males											
10	37	53.6 (50.2–57.4) ± 0.62	3.5	I							
9	4	51.1 (49.6–53.5) ± 1.83	3.6	I	I						

Table 2.—*Continued.*

Sex and locality number	N	Mean (range) ± 2 SE	CV	Results of SS-STP							
8	5	50.6 (48.4–52.7) ± 1.76	3.9	I	I	I					
7	8	48.8 (46.0–50.7) ± 1.25	3.6		I	I	I				
6	4	48.8 (47.2–49.7) ± 1.12	2.3		I	I	I	I			
5	23	47.9 (44.6–52.3) ± 0.82	4.1		I	I	I	I			
16	10	47.7 (44.7–50.0) ± 1.01	3.3		I	I	I	I			
13	16	46.8 (42.5–51.8) ± 1.10	4.7			I	I	I			
12	15	46.6 (43.2–49.9) ± 0.82	3.4				I	I			
4	11	45.6 (43.0–51.5) ± 1.58	5.7					I			
2	10	41.4 (37.1–45.7) ± 1.63	6.2						I		
Females											
10	30	48.2 (41.9–51.5) ± 0.65	3.7	I							
8	3	46.8 (45.2–48.3) ± 1.80	3.3	I	I						
9	10	45.5 (42.6–48.1) ± 1.07	3.7		I	I					
6	8	44.6 (42.4–47.6) ± 1.13	3.6		I	I	I				
16	17	42.9 (41.6–44.7) ± 0.45	2.2			I	I				
5	18	42.7 (40.6–44.6) ± 0.61	3.0				I	I			
7	15	42.7 (40.4–45.5) ± 0.71	3.2				I	I			
14	10	41.7 (40.3–43.1) ± 0.67	2.5				I	I	I		
12	12	40.6 (37.7–43.0) ± 0.95	4.0					I	I		
13	14	40.1 (37.6–42.7) ± 0.78	3.7						I		
4	13	40.1 (37.5–41.8) ± 0.73	3.3						I		
2	16	36.9 (34.8–38.7) ± 0.64	3.5							I	
		Palatal length									
Males											
10	37	37.6 (34.9–40.2) ± 0.47	3.8	I							
9	4	36.1 (34.9–37.8) ± 1.36	3.8	I	I						
8	5	35.5 (34.0–37.3) ± 1.36	4.3	I	I	I					
6	4	34.1 (33.6–35.1) ± 0.69	2.0		I	I	I				
7	8	33.8 (31.7–35.1) ± 0.86	3.6		I	I	I				
5	23	33.4 (31.0–36.4) ± 0.65	4.6		I	I	I				
13	16	32.6 (28.7–36.7) ± 0.96	5.9			I	I				
16	10	32.6 (30.2–34.4) ± 0.76	3.7			I	I				
12	15	32.2 (29.1–34.4) ± 0.66	3.9				I				
4	11	32.0 (30.5–35.7) ± 1.00	5.2				I				
2	10	28.6 (25.6–32.2) ± 1.26	7.0					I			
Females											
10	30	33.5 (32.2–35.9) ± 0.37	3.0	I							
8	3	32.2 (31.1–33.0) ± 1.16	3.1	I	I						
9	11	31.6 (29.9–33.6) ± 0.73	3.9		I						
6	8	30.9 (29.1–32.9) ± 0.83	3.8		I	I					
5	19	29.5 (28.1–32.9) ± 0.54	4.0			I	I				
7	15	29.5 (27.7–31.7) ± 0.53	3.5			I	I	I			
16	17	29.1 (27.0–30.6) ± 0.45	3.2			I	I	I	I		
14	10	28.7 (27.1–29.8) ± 0.57	3.1				I	I	I	I	
12	13	27.9 (25.6–29.7) ± 0.66	4.3					I	I	I	
4	13	27.6 (25.6–28.8) ± 0.54	3.5						I	I	
13	14	27.4 (25.8–29.4) ± 0.63	4.3							I	
2	16	25.1 (23.4–26.7) ± 0.46	3.7								I

Table 2.—*Continued.*

Sex and locality number	N	Mean (range) ± 2 SE	CV	Results of SS-STP							
		Palatofrontal depth									
Males											
10	37	20.2 (18.5–22.2) ± 0.24	3.6	I							
9	4	19.9 (18.7–20.8) ± 1.01	5.1	I	I						
8	5	19.4 (18.8–20.7) ± 0.70	4.0	I	I						
7	8	19.2 (17.8–20.6) ± 0.73	5.4	I	I	I					
6	4	18.9 (17.6–19.6) ± 0.89	4.7		I	I	I				
5	23	18.5 (17.1–20.0) ± 0.29	3.7		I	I	I				
16	10	18.4 (17.0–19.3) ± 0.50	4.3		I	I	I				
13	16	17.9 (16.6–19.7) ± 0.36	4.0			I	I				
12	15	17.8 (17.1–18.5) ± 0.19	2.1				I				
4	11	17.7 (16.6–20.3) ± 0.60	5.7				I				
2	10	15.9 (14.5–17.4) ± 0.59	5.9					I			
Females											
10	31	18.5 (17.6–19.7) ± 0.19	2.9	I							
8	3	18.4 (17.6–19.1) ± 0.87	4.1	I	I						
9	11	17.9 (17.1–18.9) ± 0.35	3.2	I	I	I					
6	8	17.5 (16.7–18.1) ± 0.33	2.7		I	I	I				
5	19	17.2 (16.4–19.1) ± 0.29	3.6		I	I	I				
7	15	17.1 (15.7–18.3) ± 0.33	3.7			I	I	I			
16	17	17.0 (16.1–18.0) ± 0.23	2.8				I	I	I		
14	10	16.5 (15.6–17.3) ± 0.30	2.9				I	I	I	I	
4	13	16.4 (15.4–17.2) ± 0.36	3.9					I	I	I	
12	13	16.2 (15.4–17.2) ± 0.24	2.6						I	I	
13	15	15.7 (15.1–16.9) ± 0.25	3.1							I	
2	16	14.6 (14.1–15.4) ± 0.22	3.0								I
		Length of nasals									
Males											
10	32	20.9 (18.7–22.5) ± 0.35	4.8	I							
9	4	20.2 (19.1–21.9) ± 1.34	6.6	I	I						
8	5	19.7 (18.2–21.4) ± 1.14	6.4	I	I	I					
7	8	19.0 (17.9–20.4) ± 0.59	4.4		I	I	I				
5	21	18.8 (17.0–20.2) ± 0.39	4.8		I	I	I				
6	4	18.6 (17.6–20.3) ± 1.16	6.3		I	I	I				
13	14	18.3 (16.3–20.3) ± 0.67	6.9		I	I	I				
12	15	17.9 (16.7–19.1) ± 0.39	4.2			I	I				
16	10	17.8 (16.7–18.9) ± 0.42	3.7				I				
4	11	17.8 (15.9–19.4) ± 0.68	6.4				I	I			
2	9	15.9 (14.7–18.0) ± 0.65	6.1					I			
Females											
10	24	18.4 (17.3–19.5) ± 0.29	3.9	I							
9	11	17.7 (16.5–19.1) ± 0.56	5.2	I	I						
8	3	17.4 (17.1–17.7) ± 0.35	1.7	I	I	I					
6	8	16.7 (15.6–18.4) ± 0.71	6.0		I	I					
7	10	16.3 (14.5–17.9) ± 0.59	5.7		I	I	I				
5	19	16.3 (15.1–18.8) ± 0.44	5.9			I	I				

Table 2.—*Continued.*

Sex and locality number	N	Mean (range) ± 2 SE	CV	Results of SS-STP						
16	13	15.7 (14.5–16.5) ± 0.45	5.2			I	I	I		
14	8	15.7 (14.9–16.8) ± 0.47	4.2			I	I	I		
12	12	15.1 (13.8–16.2) ± 0.41	4.7				I	I		
4	13	14.9 (14.2–16.3) ± 0.38	4.6					I		
13	11	14.7 (13.9–15.7) ± 0.37	4.2					I	I	
2	13	13.3 (12.0–14.6) ± 0.44	6.0						I	
		Diastema								
Males										
10	37	20.8 (18.7–22.8) ± 0.36	5.3	I						
9	4	19.7 (19.2–20.4) ± 0.55	2.8	I	I					
8	5	19.7 (19.0–20.7) ± 0.58	3.3	I	I	I				
6	4	19.1 (18.5–19.6) ± 0.53	2.8	I	I	I				
7	8	18.7 (17.2–19.8) ± 0.71	5.4		I	I				
5	23	18.7 (17.4–21.5) ± 0.46	5.9		I	I				
13	16	18.4 (15.7–21.6) ± 0.65	7.1		I	I				
12	15	18.2 (16.4–19.6) ± 0.48	5.1		I	I				
16	10	18.1 (16.4–19.3) ± 0.57	5.0		I	I				
4	11	17.6 (16.5–20.6) ± 0.83	7.8			I	I			
2	10	15.7 (13.8–17.9) ± 0.79	8.0				I			
Females										
10	31	18.0 (16.3–19.8) ± 0.31	4.8	I						
8	3	17.4 (17.1–17.9) ± 0.48	2.4	I	I					
9	11	17.2 (16.3–18.9) ± 0.50	4.8	I	I	I				
6	8	16.6 (15.1–18.3) ± 0.70	5.9		I	I	I			
5	19	16.0 (14.7–17.8) ± 0.33	4.5			I	I	I		
16	17	15.6 (14.3–16.9) ± 0.35	4.6				I	I	I	
7	15	15.6 (14.5–17.0) ± 0.44	5.5				I	I	I	
14	10	15.4 (14.5–17.0) ± 0.53	5.4				I	I	I	
12	13	15.2 (13.8–16.4) ± 0.47	5.5				I	I	I	
13	15	14.9 (13.6–16.8) ± 0.45	5.9					I	I	
4	13	14.6 (13.5–15.2) ± 0.26	3.2						I	I
2	16	13.3 (12.4–14.4) ± 0.32	4.8							I
		Zygomatic breadth								
Males										
10	37	35.5 (32.3–38.0) ± 0.54	4.6	I						
9	4	33.7 (32.0–35.2) ± 1.61	4.8	I	I					
8	5	33.4 (30.8–36.0) ± 1.79	6.0	I	I	I				
6	4	33.1 (30.5–34.6) ± 1.87	5.7	I	I	I	I			
7	8	32.4 (30.1–35.2) ± 1.30	5.7		I	I	I			
16	10	32.2 (29.9–34.1) ± 0.93	4.6		I	I	I			
5	23	31.7 (28.7–35.5) ± 0.73	5.5		I	I	I			
13	15	31.5 (29.5–33.8) ± 0.64	3.9		I	I	I			
12	15	30.9 (28.2–32.4) ± 0.55	3.5			I	I			
4	10	30.3 (28.3–33.9) ± 0.97	5.1				I			
2	10	27.0 (24.5–30.2) ± 1.19	7.0					I		

Table 2.—*Continued.*

Sex and locality number	N	Mean (range) ± 2 SE	CV	Results of SS-STP						
Females										
10	30	31.4 (29.5–33.6) ± 0.35	3.0	I						
8	3	30.6 (29.7–31.7) ± 1.16	3.3	I						
9	11	30.1 (28.4–32.8) ± 0.72	4.0	I	I					
16	16	28.4 (27.2–29.9) ± 0.37	2.6		I	I				
6	8	28.2 (26.4–30.7) ± 0.94	4.7			I				
7	15	27.9 (26.3–29.5) ± 0.45	3.1			I	I			
5	18	27.9 (26.7–28.9) ± 0.32	2.4			I	I			
14	9	27.1 (26.2–28.2) ± 0.39	2.2			I	I	I		
12	13	26.7 (24.8–28.5) ± 0.62	4.2				I	I		
4	13	26.4 (24.0–28.5) ± 0.70	4.8					I		
13	13	25.9 (24.1–27.5) ± 0.56	3.9					I		
2	15	23.9 (23.0–24.5) ± 0.22	1.7						I	
		Mastoid breadth								
Males										
10	37	32.6 (29.4–35.9) ± 0.44	4.1	I						
6	4	31.5 (29.9–32.4) ± 1.11	3.5	I	I					
8	5	31.2 (29.8–32.1) ± 0.78	2.8	I	I	I				
9	4	31.1 (28.5–32.7) ± 1.79	5.8	I	I	I	I			
7	8	30.5 (28.1–32.7) ± 1.05	4.9		I	I	I	I		
5	23	29.7 (26.9–32.9) ± 0.58	4.7		I	I	I	I		
16	10	29.5 (28.4–31.3) ± 0.64	3.4		I	I	I	I		
13	16	29.1 (27.5–32.0) ± 0.51	3.5			I	I	I		
4	11	28.6 (26.8–31.0) ± 0.78	4.5				I	I		
12	15	28.6 (27.2–30.6) ± 0.50	3.4					I		
2	10	25.2 (23.0–28.1) ± 0.96	6.0						I	
Females										
10	31	29.4 (27.4–31.3) ± 0.39	3.7	I						
8	3	28.9 (27.6–29.9) ± 1.36	4.1	I	I					
9	11	28.2 (27.3–30.5) ± 0.52	3.1	I	I					
6	8	27.8 (25.9–29.2) ± 0.70	3.6		I	I				
7	15	26.8 (25.4–28.2) ± 0.48	3.4		I	I	I			
5	18	26.5 (25.5–30.0) ± 0.49	3.9			I	I	I		
16	17	26.3 (25.0–28.0) ± 0.43	3.3			I	I	I		
14	10	26.2 (25.5–27.4) ± 0.44	2.7			I	I	I	I	
12	13	25.4 (23.7–27.0) ± 0.44	3.1				I	I	I	
4	13	25.2 (22.5–27.3) ± 0.77	5.5					I	I	
13	15	24.9 (23.3–26.3) ± 0.53	4.1						I	
2	16	22.8 (21.5–24.1) ± 0.44	3.9							I
		Squamosal breadth								
Males										
10	37	23.8 (22.3–26.0) ± 0.26	3.3	I						
6	4	23.3 (22.1–25.1) ± 1.28	5.5	I	I					
9	4	23.1 (21.4–24.1) ± 1.16	5.0	I	I					

Table 2.—*Continued.*

Sex and locality number	N	Mean (range) ± 2 SE	CV	Results of SS-STP					
7	8	23.0 (21.6–24.6) ± 0.84	5.2	I	I	I			
8	5	22.8 (22.3–23.4) ± 0.40	2.0	I	I	I	I		
5	23	22.4 (20.5–24.4) ± 0.44	4.7		I	I	I		
16	10	22.3 (21.2–23.5) ± 0.44	3.1		I	I	I		
13	16	22.0 (20.4–24.2) ± 0.45	4.1		I	I	I		
12	15	21.6 (20.1–24.0) ± 0.52	4.6			I	I		
4	11	21.4 (20.6–23.0) ± 0.47	3.7				I		
2	10	19.3 (17.7–21.2) ± 0.70	5.7					I	
Females									
10	31	22.4 (21.0–23.6) ± 0.29	3.6	I					
8	3	21.7 (20.9–22.2) ± 0.79	3.1	I	I				
6	8	21.5 (20.5–22.0) ± 0.35	2.3	I	I				
9	11	21.4 (20.4–23.2) ± 0.51	3.9		I				
7	15	21.1 (19.7–22.1) ± 0.41	3.8		I	I			
16	17	21.0 (20.0–22.4) ± 0.34	3.3		I	I			
5	19	20.8 (19.6–23.4) ± 0.40	4.2		I	I	I		
14	10	20.3 (19.6–21.2) ± 0.33	2.6		I	I	I	I	
12	13	20.0 (19.3–20.9) ± 0.26	2.4			I	I	I	
4	13	19.9 (18.2–21.7) ± 0.63	5.7				I	I	
13	15	19.4 (17.8–20.6) ± 0.44	4.3					I	I
2	16	18.2 (17.4–19.0) ± 0.24	2.7						I
		Rostral breadth							
Males									
10	36	12.8 (11.0–14.3) ± 0.23	5.4	I					
8	5	12.1 (11.5–12.6) ± 0.37	3.4	I	I				
9	4	12.1 (11.7–12.7) ± 0.43	3.6	I	I	I			
6	4	12.1 (11.4–12.7) ± 0.53	4.4	I	I	I			
7	8	11.5 (10.8–12.3) ± 0.42	5.1		I	I	I		
16	10	11.4 (10.9–11.9) ± 0.25	3.4		I	I	I		
5	23	11.2 (10.1–12.5) ± 0.23	4.9			I	I	I	
13	16	10.7 (10.1–11.4) ± 0.17	3.2				I	I	I
4	11	10.6 (9.8–11.5) ± 0.34	5.4					I	I
12	15	10.4 (10.0–10.9) ± 0.13	2.4						I
2	10	9.9 (9.3–10.6) ± 0.27	4.2						I
Females									
10	31	11.6 (10.6–12.4) ± 0.17	4.0	I					
8	3	11.5 (10.9–12.2) ± 0.75	5.6	I					
9	11	11.0 (10.4–12.0) ± 0.26	3.9	I	I				
16	17	10.4 (10.1–11.0) ± 0.13	2.6		I	I			
6	8	10.3 (9.9–10.6) ± 0.19	2.6		I	I			
7	15	10.1 (9.5–11.0) ± 0.27	5.1			I	I		
5	19	10.0 (9.5–10.9) ± 0.18	3.9			I	I	I	
14	10	9.8 (9.3–10.2) ± 0.17	2.8			I	I	I	I
4	13	9.5 (8.8–10.1) ± 0.21	3.9				I	I	I

Table 2.—*Continued.*

Sex and locality number	N	Mean (range) ± 2 SE	CV	Results of SS-STP						
13	15	9.5 (8.7–10.6) ± 0.24	4.9					I	I	I
12	13	9.4 (8.7–10.2) ± 0.23	4.4						I	I
2	16	8.9 (8.2–9.3) ± 0.17	3.7							I
		Interorbital constriction								
Males										
10	35	7.1 (6.1–7.9) ± 0.16	6.8	I						
7	8	7.1 (6.7–7.8) ± 0.26	5.2	I						
8	5	7.0 (6.4–7.7) ± 0.48	7.6	I	I					
9	4	6.9 (6.7–7.1) ± 0.17	2.5	I	I	I				
4	11	6.9 (6.0–7.5) ± 0.26	6.4	I	I	I				
5	23	6.8 (6.1–7.3) ± 0.13	4.7	I	I	I				
16	10	6.7 (6.3–7.2) ± 0.18	4.3	I	I	I	I			
12	14	6.4 (5.9–6.7) ± 0.17	5.0		I	I	I			
6	4	6.3 (6.2–6.6) ± 0.17	2.7			I	I			
13	16	6.3 (5.8–6.7) ± 0.12	3.8				I			
2	10	6.3 (5.8–6.9) ± 0.20	5.1				I			
Females										
10	31	7.1 (6.5–7.7) ± 0.11	4.3	I						
9	11	6.9 (6.3–7.2) ± 0.18	4.4	I	I					
8	3	6.8 (6.4–7.3) ± 0.55	7.0	I	I					
4	13	6.7 (5.9–7.4) ± 0.24	6.5	I	I					
16	17	6.7 (6.2–7.3) ± 0.14	4.5		I					
5	18	6.7 (5.8–7.1) ± 0.16	5.0		I	I				
7	15	6.6 (6.1–7.2) ± 0.17	5.1		I	I				
14	10	6.6 (6.2–7.0) ± 0.17	4.0		I	I				
6	8	6.6 (5.9–7.1) ± 0.26	5.7		I	I	I			
12	13	6.4 (6.1–6.7) ± 0.11	3.2		I	I	I			
13	15	6.3 (6.0–6.7) ± 0.13	3.9			I	I			
2	16	6.1 (5.8–6.3) ± 0.09	2.8				I			
		Breadth across maxillaries								
Males										
10	37	9.9 (9.1–10.7) ± 0.15	4.5	I						
9	4	9.8 (9.1–10.8) ± 0.72	7.4	I	I					
7	8	9.6 (9.0–10.1) ± 0.23	3.3	I	I					
6	4	9.6 (9.0–10.2) ± 0.49	5.1	I	I	I				
8	5	9.5 (9.3–9.8) ± 0.20	2.4	I	I	I				
16	10	9.3 (8.8–9.6) ± 0.16	2.7		I	I				
5	23	9.3 (8.9–10.0) ± 0.12	3.2		I	I				
4	11	8.9 (8.5–9.3) ± 0.18	3.4			I	I			
13	16	8.8 (8.4–9.3) ± 0.12	2.7				I	I		
12	15	8.6 (8.1–9.3) ± 0.16	3.5				I	I		
2	10	8.2 (7.8–8.9) ± 0.25	4.8					I		
Females										
10	31	9.6 (8.9–10.4) ± 0.12	3.3	I						
8	3	9.6 (9.4–9.8) ± 0.24	2.2	I	I					

Table 2.—*Continued.*

Sex and locality number	N	Mean (range) ± 2 SE	CV	Results of SS-STP						
9	11	9.2 (8.6–9.6) ± 0.20	3.7	I	I	I				
6	8	9.2 (8.7–9.9) ± 0.26	3.9		I	I	I			
5	19	8.9 (8.2–9.8) ± 0.16	4.0		I	I	I	I		
7	15	8.9 (8.2–9.6) ± 0.17	3.8		I	I	I	I		
16	17	8.8 (8.5–9.2) ± 0.10	2.3			I	I	I		
14	10	8.6 (8.4–9.2) ± 0.17	3.2				I	I	I	
4	13	8.5 (7.9–9.2) ± 0.22	4.5					I	I	
12	13	8.3 (7.9–8.9) ± 0.17	3.7						I	
13	15	8.3 (7.7–8.7) ± 0.15	3.6						I	I
2	16	7.9 (7.4–8.3) ± 0.11	2.9							I

of four ranked positions filled by these samples. Sample 2 had the smallest means and ranked twelfth for all measurements.

All external and cranial measurements of males and females exhibited significant geographic variation. Among measurements for males, three had four subsets (length of tail, diastema, and interorbital constriction), seven had five subsets (length of hind foot, palatal length, palatofrontal depth, length of nasals, zygomatic breadth, squamosal breadth, and breadth across maxillaries), and six had six subsets (total length, greatest length of skull, condylobasal length, basal length, mastoid breadth, and rostral breadth). For females, the number of nonsignificant subsets included four for two measurements (length of tail and interorbital constriction), five for one measurement (length of hind foot), six for four measurements (total length, length of nasals, zygomatic breadth, and squamosal breadth), seven for six measurements (condylobasal length, basal length, diastema, mastoid breadth, rostral breadth, and breadth across maxillaries), and eight for three measurements (greatest length of skull, palatal length, and palatofrontal depth). The number of samples contained in a nonsignificant subset ranged from one in both sexes to eight in males and nine in females. The amount of overlap between nonsignificant subsets ranged between broad to no overlap between adjacent subsets. In the SS-STP analyses for most characters, sample 2 formed a nonoverlapping, nonsignificant subset. For males and females over half of the cranial measurements (greatest length of skull, condylobasal length, basal length, palatal length, palatofrontal depth, zygomatic breadth, and mastoid breadth; also squamosal breadth in males) had a subset formed by this sample. Only one other measurement had a subset that did not overlap with other subsets (length of hind foot of females of samples 8 and 10).

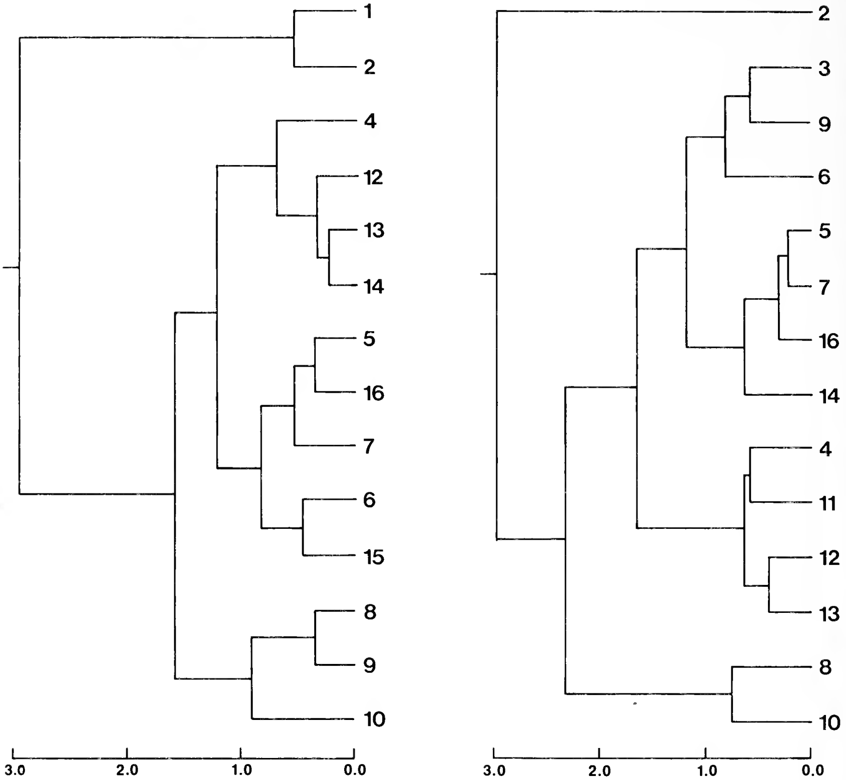

Fig. 2.—Phenograms of *Geomys personatus* (males left, females right) computed from distance matrices and clustered by unweighted pair-group method using arithmetic averages (UPGMA). Samples are identified in text and Fig. 1. The cophenetic correlation coefficient for the phenogram for males is 0.847 and for the females 0.734.

Other SS-STP analyses were generally characterized by broad overlapping subsets. However, some trends of sample grouping were evident. For females, samples 8 and 10 formed a subset in six measurements; in seven other measurements a subset was formed by samples 8, 9, and 10. For males, five measurements had a subset formed by samples 8, 9, and 10; in five other measurements these samples were included with sample 6 (four times) or 16 (one). In the smaller-sized pocket gophers, a subset formed by samples 2, 4, 12, and 13 was found in two male measurements; a subset of samples 2, 12, and 13 was found in two male and three female measurements; a subset of samples 2 and 4 was found in two male and one female measurement; and a subset of samples 2 and 3 was found in three female measurements. No other trends were noted.

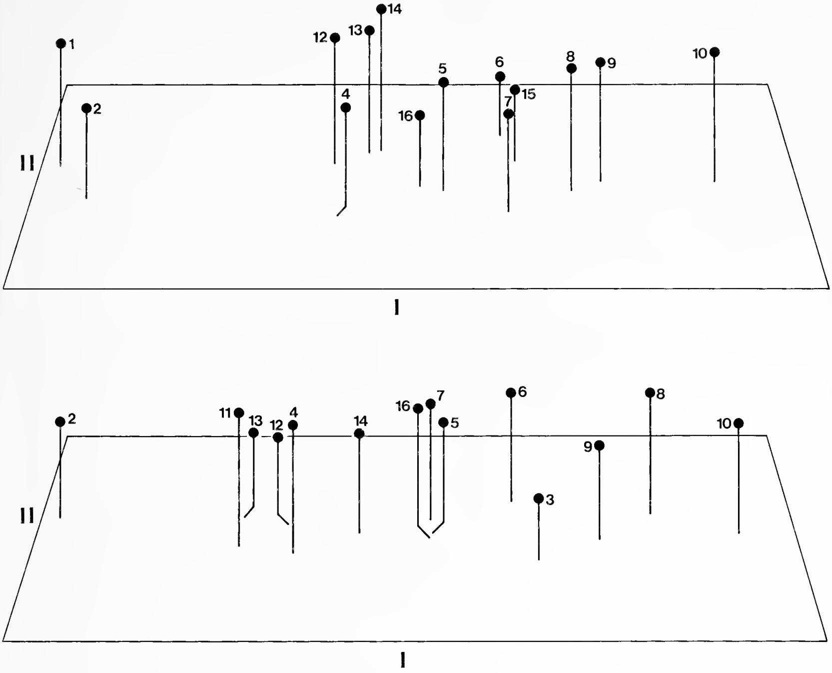

Fig. 3.—Three-dimensional projections of *Geomys personatus* (males above; females below) onto the first three principal components based upon matrices of correlation among 13 cranial measurements. Components I and II are indicated in the figure, and component III is represented by height. See Fig. 1 and text for key to samples.

Multivariate analysis.—Fourteen samples for males and females were used in multivariate analyses of geographic variation in *Geomys personatus*. No adult specimens were available from samples 3 and 11 in males and 1 and 15 in females.

Distance phenograms, generated for males and females with the MINT program, are illustrated in Fig. 2. The cophenetic correlation values for males and females were 84.7% and 73.4%, respectively.

In males, samples 1 (Kinney and Val Verde counties) and 2 (Dimmit and Zavala counties) are widely separated from all other samples. Although the other samples form a distinct group when compared with samples 1 and 2, clustering within that group agrees with geographic relationships. Samples 10 (barrier islands of Kleberg and Nueces counties), 9, and 8 (mainland of Kleberg and eastern Nueces counties) formed one cluster, which subdivides into the island (10) and mainland (9 and 8) samples. The other samples formed two clusters, one of which contained samples 5, 6, 7, 15, and 16. These are from the south-

Table 3.—*Factor matrix from correlation among 13 cranial characters of* Geomys personatus *studied.*

Character	Males Component I	Males Component II	Males Component III	Females Component I	Females Component II	Females Component III
Greatest length of skull	0.998	−0.015	0.032	0.993	−0.080	0.020
Condylobasal length	0.995	−0.055	0.061	0.992	−0.088	−0.020
Basal length	0.995	−0.047	0.060	0.993	−0.099	−0.002
Palatal length	0.993	−0.034	0.088	0.994	−0.074	−0.061
Palatofrontal depth	0.992	−0.010	0.026	0.984	−0.000	0.136
Length of nasals	0.953	0.006	0.272	0.977	0.023	−0.174
Diastema	0.976	−0.148	0.102	0.977	0.018	−0.191
Zygomatic breadth	0.975	−0.145	−0.062	0.977	0.146	−0.079
Squamosal breadth	0.979	−0.091	−0.030	0.993	−0.060	−0.055
Mastoid breadth	0.951	−0.061	−0.153	0.971	−0.063	0.134
Rostral breadth	0.943	0.015	−0.206	0.959	0.044	0.071
Interorbital constriction	0.760	0.644	0.041	0.911	0.389	0.086
Breadth across maxillaries	0.955	0.088	−0.237	0.976	−0.122	0.144

ern part of Texas (southeastern Webb, southern Duval, southern Kleberg, Jim Hogg, Brooks, Kenedy, Starr, Hidalgo, Willacy, and Cameron counties) and along the coast of Tamaulipas. The last cluster is divided into two subclusters. One contains samples 12, 13, and 14, all of which are located in the vicinity of the Nueces River (Karnes, Bee, Goliad, Live Oak, Jim Wells, San Patricio, and northern Nueces counties), whereas the other contained sample 4, which is from along the Rio Grande River (western Webb and Zapata counties) and is geographically isolated from samples 12, 13, and 14.

In females, the relationships between samples was similar to those observed in males with a few exceptions. Sample 2 (Dimmit and Zavala counties) was widely separated from all other samples. The other samples formed four distinct clusters. Samples 10 (barrier islands of Texas) and 8 (vicinity of Baffin Bay, Texas) formed a loose cluster. The next cluster contained samples 11, 12, 13 (all located in the vicinity of the Nueces River), and 4 (located along the Rio Grande River in western Webb and Zapata counties). Another cluster contained samples 5 and 7 (central southernmost part of Texas), 16 (coast of Tamaulipas), and 14 (Goliad and Karnes counties). The last cluster contained samples 3 (La Salle Co.), 6 (mainland of Kenedy and Kleberg counties), and 9 (mainland of Nueces Co.).

The first three principal components extracted from the matrix of correlation among characters are shown for males and females in Fig. 3. The amounts of phenetic variation explained by the first three principal components for males were 92.3%, 3.7%, and 1.8%, respectively;

for females, 95.4%, 1.7%, and 1.2%. Results of factor analyses, showing the influence of each character for the first three components are given in Table 3.

All characters of both sexes are heavily weighted in component I, thus indicating that the major differences among samples are in size rather than in shape (Table 3). In component II of both sexes, interorbital constriction is the only character having a noticeably higher weighting. This trend is carried over into component III for males; no characters had high weightings for females in component III.

In the three-dimensional projections for males and females (Fig. 3), all samples are aligned almost in a straight line along component I, with little change in position along components II and III. The samples from Dimmit and Zavala counties (also males from Kinney and Val Verde counties—no females are available) are situated to the left in the plots, and are the most distinct of all samples examined. The remainder of the samples form an elongated cluster along component I. Unless the geographic and taxonomic aspects are considered, the location and amount of separation of individual samples is somewhat complicated, particularly when both sexes are considered. Generally four groups are evident for both sexes that comply with the taxonomic arrangement of Davis (1940). The largest-sized individuals, represented by sample 10 (from Mustang and Padre islands), form one group on the right side of the plots. The next group, represented by samples 8 and 9, is situated geographically between Baffin Bay and Corpus Christi Bay. This group is plotted to the left of sample 10. The next group consists of a series of loosely clustered samples (3, 5, 6, 7, 15, and 16), which primarily occur in the southernmost part of Texas and on the coast of Tamaulipas. The fourth group, including samples 4, 11, 12, 13, and 14, has the smallest-sized individuals of the four groups that plotted together. Samples 11, 12, 13, and 14 are from the vicinity of the Nueces River; sample 4, which contains the same-sized individuals, is restricted to the lower Rio Grande River and is geographically isolated from samples 11, 12, 13, and 14.

Canonical analysis provides a mechanism for graphically representing phenetic relationships among samples with the characters weighted by variance-covariance analysis. In Table 4, characters used in these analyses for males and females are listed from the most useful to the least useful in discriminating groups. For males, Variate I accounts for 65.6% of the total dispersion, and Variate II accounts for 10.6%. The diastema is the only character with a high positive (greater than 1.0) canonical coefficient for Variate I. No character in Variate I had a negative value greater than 1.0. In Variate II, a positive value greater than 1.0 was exhibited by breadth across maxillaries, and a negative value greater than 1.0 was exhibited by rostral breadth. For females,

Table 4.—*Variables used in discriminant function analysis of* Geomys personatus. *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.*

	Males			Females		
Step	Character	F-value	U-statistic	Character	F-value	U-statistic
1	Greatest length of skull	36.47	0.2020	Greatest length of skull	68.77	0.1227
2	Rostral breadth	4.66	0.1338	Rostral breadth	4.02	0.0863
3	Squamosal breadth	3.67	0.0953	Palatofrontal depth	3.73	0.0619
4	Interorbital constriction	2.89	0.0921	Condylobasal length	3.46	0.0452
5	Palatal length	2.43	0.0567	Zygomatic breadth	2.36	0.0360
6	Condylobasal length	2.36	0.0447	Diastema	2.19	0.0291
7	Breadth across maxillaries	2.19	0.0358	Breadth across maxillaries	2.13	0.0237
8	Zygomatic breadth	1.67	0.0300	Basal length	1.88	0.0196
9	Basal length	1.52	0.0255	Length of nasals	1.95	0.0161
10	Length of nasals	1.62	0.0214	Squamosal breadth	1.75	0.0135
11	Mastoid breadth	1.17	0.0188	Mastoid breadth	2.51	0.0105
12	Diastema	0.91	0.0170	Interorbital constriction	1.22	0.0092
13	Palatofrontal depth	0.87	0.0154	Palatal length	1.12	0.0082

Variate I accounts for 75.2% and Variate II accounts for 8.2% of the total dispersion. In Variate I, interorbital constriction and squamosal breadth exhibited a high positive (greater than 1.0) canonical coefficient; there were no characters with negative values greater than 1.0. In Variate II, palatal length and palatofrontal depth had positive values greater than 1.0 and breadth across maxillaries had negative values greater than 1.0.

Plots of the first two canonical variates for males and females is characterised by a series of overlapping samples with samples on the left being separated from those on the right (Fig. 4). For both sexes, sample 10 occurs on the left side of the plot. Samples 8 and 9 overlap with each other, sample 10, and then become part of a conglomeration of overlapping samples in the center of the plot. At the right side of the plot, sample 2 appears more separated than other samples (except sample 10), but still maintains a definite overlap. The only possibility of a nonoverlapping sample occurs with sample 1 in the plot for males. In this case, the sample is on the right side and in close proximity to sample 2.

Taxonomic Conclusions

Prior to this study, six subspecies of *Geomys personatus* were recognized (Davis, 1940, 1943; Hall, 1981). Our analyses indicate a great amount of variation among populations of this species, which generally agrees with previous subspecific designations. However, our study reveals an additional population of *G. personatus* that deserves subspecific recognition. Also, we found *G. p. fuscus* and *G. p. streckeri* to form a closely related subspecific grouping that is distinct from the other subspecies of *G. personatus*. Finally, we noted that members of the species occurring in Tamaulipas belong to *G. p. megapotamus*, instead of *G. p. personatus* as was indicated by Hall (1981) and by Selander et al. (1962). Thus, we recognize *G. personatus* to contain seven subspecies. These include the currently recognized taxa (*fallax*, *fuscus*, *maritimus*, *megapotamus*, *personatus*, and *streckeri*), plus one new subspecies that is described below (Fig. 5).

SYSTEMATIC ACCOUNTS

Geomys personatus davisi, new subspecies

Holotype.—Adult female, skin and skull, no. 48689 Carnegie Museum of Natural History; from 3 mi N, 2.8 mi W Zapata, Zapata Co., Texas; collected on 16 November 1976 by Stephen L. Williams; original no. 2081; karyotype no. TK 6857.

Distribution.—Currently known from the Rio Grande Valley of Texas, in western Webb and Zapata counties.

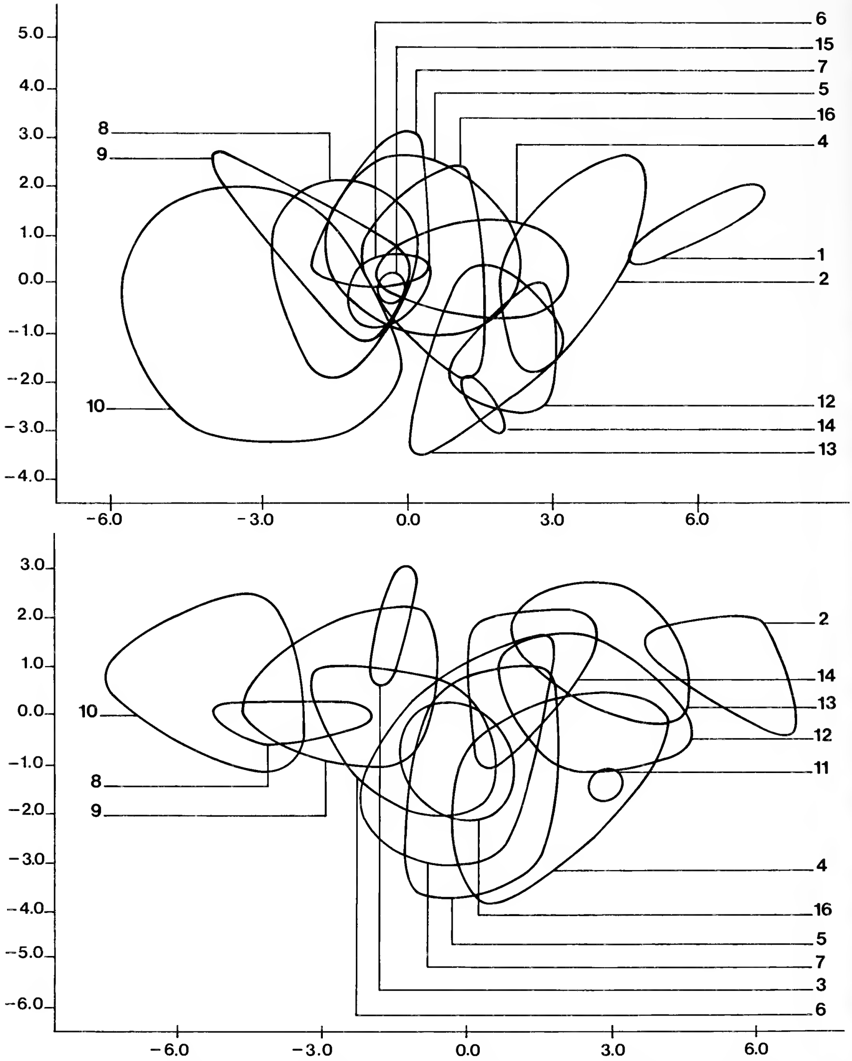

Fig. 4.—Plots (males above; females below) of first two canonical variates, showing phenetic relationships among samples of *Geomys personatus*. See Fig. 1 and text for key to samples.

Diagnosis.—Among smaller member of species, being similar to *G. p. fallax* in size; pale brown in coloration.

Description.—Externally, size medium or slightly smaller for the species (Table 2). Dorsal hair coloration is Buffy Brown on tips (capitalized color terms from Ridgeway,

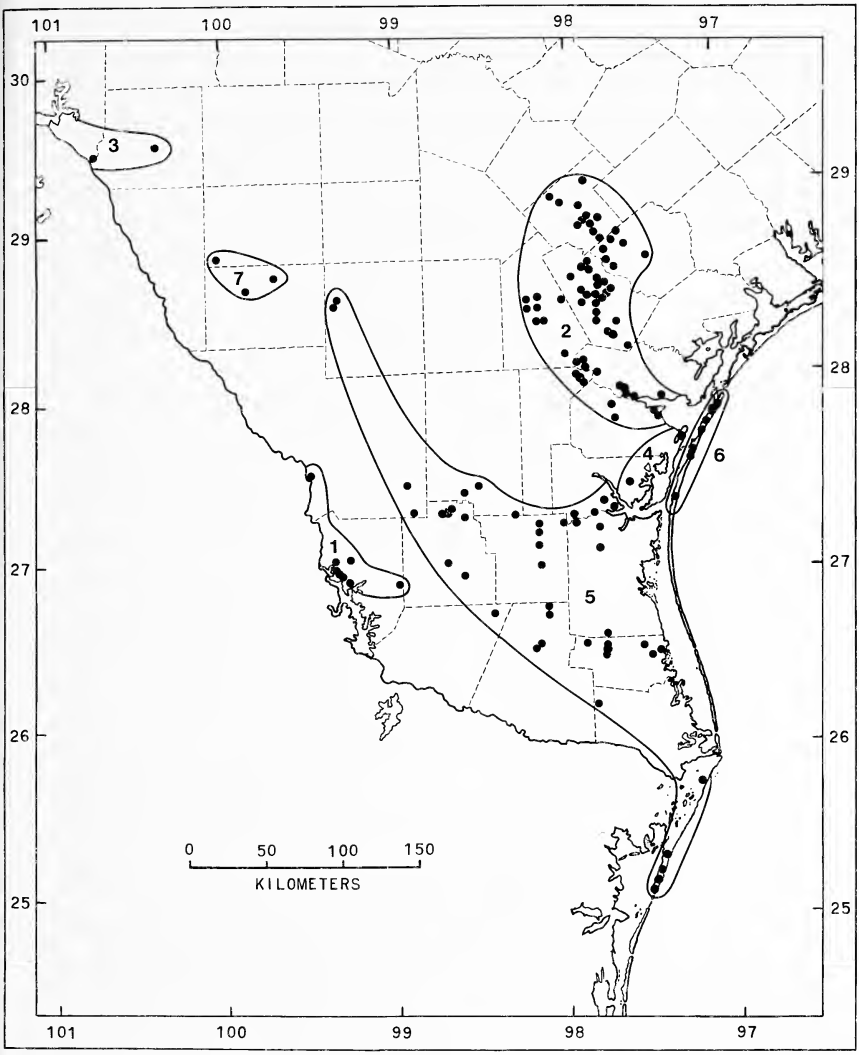

Fig. 5.—Geographic distribution of subspecies of *Geomys personatus*: 1) *G. p. davisi*; 2) *G. p. fallax*; 3) *G. p. fuscus*; 4) *G. p. maritimus*; 5) *G. p. megapotamus*; 6) *G. p. personatus*; 7) *G. p. streckeri*.

1912) and gray on bases. Coloration extends laterally and ventrally where white-tipped hairs are dispersed in the pelage, resulting in a paler ventral coloration. Some areas on venter are covered with pure white hair.

Cranially, the basioccipital is longer than the rostral breadth. Sagittal and lamdoidal crests are well developed. Zygomatic arches are expanded anteriorly.

Measurements.—Measurements of *G. p. davisi* (sample 4) are given in Table 2. External and cranial measurements (in millimeters) of the holotype are as follows: total length, 269; length of tail, 84; length of hind foot, 35; greatest length of skull, 44.8; condylobasal length, 43.7; basal length, 41.1; palatal length, 28.4; palatofrontal depth, 17.0; length of nasals, 16.1; diastema, 15.2; zygomatic breadth, 26.8; mastoid breadth, 26.7; squamosal breadth, 20.3; rostral breadth, 9.1; interorbital constriction, 6.1; breadth across maxillaries, 8.9.

Comparisons.—Geographically, *G. p. davisi* is closest to *G. p. megapotamus,* which virtually blocks contact with *G. p. fallax, G. p. maritimus,* and *G. p. personatus. G. p. davisi* differs from *G. p. megapotamus* in being smaller. Comparing the greatest length of the skull, males and females of *G. p. davisi* averaged 49.9 and 44.1 mm, respectively, whereas those of *G. p. megapotamus* (sample 5) averaged 51.7 and 46.3 mm. It is also much smaller than *G. p. maritimus* (mean greatest length of skull of specimens in sample 9—males, 55.3; females, 49.5) and *G. p. personatus* (mean greatest length of skull—males, 57.9; females, 52.9). Although it might be possible for *G. p. davisi* to come into contact with *G. p. fuscus* (mean greatest length of skull—males, 41.4; females, —) and *G. p. streckeri* (mean greatest length of skull—males, 45.1; females, 40.0) both subspecies are distinctly smaller than *G. p. davisi.* The subspecies most closely approximating *G. p. davisi* in size is *G. p. fallax* (mean greatest length of skull of specimens in sample 12—males, 49.8; females, 43.9). However, they are isolated from each other and most obviously differ in color (*G. p. davisi* being paler).

Remarks.—The geographic distribution of *G. p. davisi* generally borders the Rio Grande River. However, one individual (TNHC 176) from 20 mi E Zapata also may belong to this subspecies. The primary reason for this assignment is that it probably occurs in the same type of soil as other members of the taxon, based on the state soil map (Godfrey et al., 1973). Because this individual was not an adult it was not incorporated in statistical analyses that could have provided a more definite identification. It is possible that additional investigations will show that specimens from this geographical area belong to the subspecies *G. p. megapotamus.*

Etymology.—The subspecific name honors Dr. William B. Davis for his contributions to the knowledge of *Geomys personatus* as well as other species of pocket gophers.

Specimens examined (55).—TEXAS. *Webb Co.:* Laredo, 1 (USNM). *Zapata Co.*: 5 mi E San Ignacio, 1 (TNHC); 10 mi N Zapata, 33 (31 TNHC, 2 UIMNH); 10 mi NW Zapata, 3 (TCWC); 6 mi NW Zapata, 1 (CM); 3 mi N, 4.2 mi W Zapata, 1 (CM); 3 mi N, 2.8 mi W Zapata, 13 (CM); Carrizo (=Zapata), 1 (USNM); 20 mi E Zapata, 1 (TNHC).

Geomys personatus fallax Merriam, 1895

Geomys personatus fallax Merriam, N. Amer. Fauna, 8:144, 31 January 1895.

Holotype.—Adult male, skin and skull, USNM 32031/43845; from

S side Nueces Bay, Nueces Co., Texas; collected on 30 November 1891 by William Lloyd, original no. 949.

Measurements of holotype.—Total length, 250; length of tail, 80; length of hind foot, 35; greatest length of skull, 46.7; condylobasal length, 45.4; basal length, 43.1; palatal length, 29.8; palatofrontal depth, 16.1; length of nasals, 16.8; diastema, 16.6; zygomatic breadth, 30.2; mastoid breadth, 27.5; squamosal breadth, 20.2; rostral breadth, 10.0; interorbital constriction, 6.4; breadth across maxillaries, 8.2.

Distribution.—Occurring in the vicinity of Nueces Bay, northwestward along the Nueces River and north as far as the vicinity of Falls City. Collecting localities include Bee, Goliad, Jim Wells, Karnes, Live Oak, Nueces, and San Patricio counties, Texas.

Remarks.—Kennerly (1959) reported that the distribution of *G. p. fallax* comes into contact with that of *Geomys bursarius attwateri* between Skidmore, Bee Co., and Falls City, Karnes Co. Because both species occur in the same geographic region, it was necessary to differentiate between the taxa to avoid using specimens of *G. bursarius* in any analyses. Most characteristics of the species are similar enough to make identification difficult. Kennerly (1958*b*) noted minor bacular differences. Timm and Price (1980) found each species to have different types of lice. Although *G. b. attwateri* possesses a karyotype of 2N = 70 and FN = 72 (Hart, 1978, Honeycutt and Schmidly, 1979), the karyotype of *G. p. fallax* (2N = 68, 70 and FN = 70, 71; Davis et al., 1971) is variable and the possibility that some individuals of the two taxa have the same diploid and fundamental numbers cannot be ruled out. These methods of differentiating species can be useful, but they have limited application in identifying museum study specimens. Davis (1940) distinguished *G. personatus* and *G. bursarius* by comparing the length of the basioccipital to the width of the rostrum. Although this method proved useful in most cases, it emphasized the necessity of employing additional methods, because 1) some localities (for example—Bee Co.: 5–8 mi NE Beeville, 1.5 mi S Skidmore; Karnes Co.: ½ mi S Falls City) yielded specimens of both taxa, 2) some specimens had a rostral breadth and basioccipital length that are essentially equal, thus leaving any identification questionable, and 3) a few specimens that were definitely one of the two species, based on geographical criteria, did not comply with the expected cranial characters. It is uncertain whether specimens, for which the final comment applies, represent cases of character displacement or erroneous information on associated labels; therefore, they were not used in this study.

To help differentiate and identify *Geomys personatus* and *attwateri,* a discriminant function analysis was performed. Table 5 gives the discriminant function coefficients resulting from the comparison of reference samples of male and female *G. p. fallax* and *G. attwateri.* The

Table 5.—*Discriminant function coefficients resulting from a discriminant function analysis comparing reference samples of* Geomys personatus fallax *and* G. attwateri.

Character	Discriminant function coefficients	
	Male	Female
Greatest length of skull	0.17075	0.95361
Condylobasal length	−0.71121	−1.36357
Basal length	0.03878	0.33446
Palatal length	0.52366	0.13603
Palatofrontal depth	−0.34221	0.11252
Length of nasals	−0.18011	−0.28420
Diastema	0.25139	0.07742
Zygomatic breadth	0.00213	0.22745
Mastoid breadth	0.20445	−0.03256
Squamosal breadth	−0.18248	−0.40644
Rostral breadth	0.40461	−0.00295
Interorbital constriction	0.24765	0.58744
Breadth of maxillaries	−0.20965	−0.23906

discriminant scores of male *G. p. fallax* ranged from −6.135 to −6.652; male *G. attwateri* ranged from −4.567 to −5.372. The discriminant scores of female *G. p. fallax* ranged from −1.761 to −2.334; female *G. attwateri* ranged from −0.162 to −1.000. In this study most specimens identified by discriminant function analysis were in agreement with expected geographic ranges of the respective species, with areas of potential contact being in general agreement with findings of Kennerly (1959). However, at least three specimens received discriminant scores that are between the ranges of scores of both species. These specimens were from 9 mi SE Runge, Goliad Co. (TNHC 4923, ♀); 7 mi NE Beeville, Bee Co. (TNHC 4827, ♀); 5.6 mi S Beeville, Bee Co. (TNHC 4816, ♂). Because the three specimens originated from areas of potential contact, it is possible that they may represent hybrids between *G. p. fallax* and *G. attwateri*; however, considerably more data are needed before this can be confirmed.

The contact between *G. bursarius* and *G. personatus* is truely a unique situation. It is one of the few areas in North America where two species of *Geomys* coexist (see Tucker and Schmidly, 1981). Although Kennerly (1958*a*, 1959) reported observations of *G. personatus* and *G. attwateri* in the area of contact, considerably more investigation is needed in order to better understand this interesting phenomenon, as well as the biology of the genus *Geomys*.

Specimens examined (301).—TEXAS. *Bee Co.:* 8.4 mi N, 1.7 mi E Beeville, 3 (TTU); 8 mi N Beeville, 5 (TTU); 8 mi NW Beeville, 1 (TNHC); 8 mi NE Beeville, 1 (TNHC); 7.6 mi NNE Beeville, 1 (TNHC); 7.3 mi N, 0.6 mi E Beeville, 1 (TTU); 5 mi NE

Beeville, 1 (TNHC); 0.1 mi W US Hwy. 181 on Fm. Rd. 2824, 2 (TTU); 3 mi N Beeville, 1 (TNHC); 2.8 mi N, 5.1 mi W Beeville, 1 (TTU); 2.7 mi N, 4.6 mi W Beeville, 2 (TTU); 2.5 mi NE Beeville, 1 (TNHC); 2 mi N Beeville, 1 (TNHC); 1.1 mi N, 3.6 mi W Beeville, 1 (TTU); 0.8 mi N, 4.3 mi W Beeville, 16 (TTU); Bates Ranch near Beeville, 4 (TTU); 0.6 mi NW Beeville, 1 (TNHC); 6.2 mi W Beeville, 1 (TNHC); Beeville, 38 (29 TNHC, 9 TTU); E of Beeville, 1 (TNHC); 2.1 mi S Beeville, 1 (TNHC); 3 mi S Beeville, 1 (TNHC); 5 mi S Beeville, 1 (TNHC); 5.45 mi S Beeville, 1 (TNHC); 5.6 mi S Beeville, 1 (TNHC); 21 mi SE Beeville, 1 (TNHC); 2 mi E Cadiz, 1 (TNHC); 4.1 mi NE Mineral, 1 (TNHC); 0.3 mi W Mineral, 1 (TNHC); 0.7 mi S Mineral, 1 (TNHC); 1.3 mi E Normanna, 1 (TNHC); ½ mi S Normanna, 1 (TNHC); 2.9 mi SE Normanna, 1 (TNHC); 2.5 mi W Orangedale, 1 (TNHC); 0.2 mi S Orangedale, 1 (TNHC); 0.3 mi W Pettus, 1 (TNHC); 2 mi S Pettus, 1 (TNHC); 4.3 mi NE Skidmore, 1 (TNHC); 1 mi W Skidmore, 1 (TNHC); ¼ mi S Skidmore curve, 1 (TNHC); ½ mi SW Skidmore, 1 (TNHC); 1 mi SE Skidmore, 1 (TNHC); 1.1 mi S Skidmore, 2 (TNHC); 1.5 mi S Skidmore, 3 (TNHC); 0.5 mi W Tulsuta, 1 (TNHC). *Goliad Co.:* 10.4 mi NW Berclaire, 1 (TNHC); 5 mi NW Berclaire, 1 (TNHC); 2.1 mi W Charco, 2 (TNHC); 2 mi SE Charco, 1 (TNHC); 2.95 mi NNE bridge over Hord Creek, 1 (TNHC); 6 mi E Pettus, 1 (TNHC); 8 mi E Pettus, 1 (TNHC); 9 mi SE Runge, 1 (TNHC); 1 mi SSW San Antonio R., 1 (TNHC). *Jim Wells Co.:* Sandia 4 (3 TCWC, 1 TTU); 0.3 mi S, 0.4 mi E Sandia, 1 (TTU); 1.3 mi S, 1.6 mi E Sandia, 1 (TTU); 1.5 mi S, 1.9 mi E Sandia, 1 (TTU); 1.8 mi S, 2.3 mi E Sandia, 1 (TTU); 2 mi S, 2.4 mi E Sandia, 1 (TTU); 2.1 mi S, 2.3 mi E Sandia, 1 (TTU). *Karnes Co.:* 2 mi NE Choate, 1 (TNHC); 2.1 mi SE Choate, 1 (TNHC); 2.3 mi SE Choate, 1 (TNHC); ½ mi S Falls City, 1 (TNHC); 8.4 mi N Helena, 1 (TNHC); Helena, 1 (TNHC); 2.2 mi S Helena, 1 (TNHC); ¼ mi E Hobson, 1 (TNHC); 3 mi NE Karnes City, 2 (TNHC); 4.7 mi NE Kenedy, 1 (TNHC); 4.5 mi NE Kenedy, 1 (TNHC); 4 mi NE Kenedy, 1 (TNHC); 3.4 mi NE Kenedy, 1 (TNHC); 2.1 mi NE Kenedy, 2 (TNHC); 1.2 mi NE Kenedy, 1 (TNHC); 0.8 mi NE Kenedy, 1 (TNHC); 4 mi E Kenedy, 1 (TNHC); 4.5 mi E Kenedy, 2 (TNHC); 5.5 mi E Kenedy, 1 (TNHC); 6.0 mi SE Kenedy, 1 (TNHC); 2 mi SW Runge, 1 (TNHC). *Live Oak Co.:* 13.5 mi W Beeville, 1 (TNHC); 8 mi N George West, 4 (TNHC); 8 mi NW George West, 15 (TNHC); 5 mi NW George West, 7 (TNHC); 4 mi N George West, 3 (TTU); 3 mi N George West, 42 (40 TNHC, 2 UIMNH); 1½ mi S George West, 1 (TCWC); 3 mi SE George West, 1 (TNHC); 0.8 mi S, 0.3 mi E Lagarto, 2 (TTU); 1.5 mi S, 0.6 mi E Lagarto, 1 (TTU); 5 mi S Three Rivers, 2 (TCWC); 3 mi E Nueces R. on Hwy. 202, 1 (TNHC). *Nueces Co.:* Calallen, 8 (5 LACM, 3 UIMNH); 1 mi E Calallen, 3 (TCWC); Corpus Christi, 1 (USNM); near Corpus Christi, 15 (AMNH); port area of Corpus Christi, 1 (TAIU); 17 mi W Corpus Christi, 8 (TTU); Las Mottes, 1 (USNM); specific locality unknown, 2 (BM). *San Patricio Co.:* 4 mi SE Edroy, 4 (TCWC); 5.3 mi SE Edroy, 1 (TNHC); 5.5 mi W Mathis, 2 (CM); 2 mi W Mathis, 1 (TNHC); 3 mi SW Mathis, 2 (TCWC); 5 mi SE Mathis, 1 (TNHC); 2 mi N Odem, 2 (TNHC); 1.5 mi N Odem, 1 (TNHC); 1.3 mi N Odem, 1 (TNHC); ½ mi N Odem, 1 (TNHC); ¼ mi SE Odem, 1 (TNHC); 2.6 mi SW Odem, 1 (TNHC); 5 mi SE Odem, 3 (TNHC); 8 mi S Taft, 1 (TNHC). *County unknown:* 10 mi from mouth of Nueces R., 2 (USNM); near mouth of Nueces R., 1 (AMNH); Nueces Bay, 2 (USNM).

Geomys personatus fuscus Davis, 1940

Geomys personatus fuscus Davis, Texas Agric. Exp. Station Bull., 590:30, 23 October 1940.

Holotype.—Subadult male, skin and skull, AMNH 12691/10985; from Fort Clark (Bracketville), Kenney Co., Texas; collected on 6 February 1893 by Edgar A. Mearns, original no. 2274.

Measurements of holotype.—Total length, 229; length of tail, 68; length of hind foot, 33.5; greatest length of skull, 40.5; condylobasal length, 39.4; basal length, 36.7; palatal length, 24.8; palatofrontal depth, 13.4; length of nasals, 14.7; diastema, 13.5; zygomatic breadth, 22.3; mastoid breadth, 21.0; squamosal breadth, 16.7; rostral breadth, 8.4; interorbital breadth, 5.5; breadth across maxillaries, 7.2.

Distribution.—Occurring near the Rio Grande River in Kinney and Val Verde counties, Texas.

Remarks.—*G. p. fuscus* is the northernmost taxon of the species. Geographically, it is closest to *G. p. streckeri* which occurs about 50 miles to the southeast in the vicinity of Carrizo Springs. Our data indicate that these two taxa are similar. If *G. p. streckeri* ever should be elevated to a distinct species (see account for *G. p. streckeri*) then *G. p. fuscus* also would be included, either as a synonym or as a subspecies of *streckeri*. The exact relationship between *G. p. fuscus* and *G. p. streckeri* is difficult to understand at this time because each taxon has unique ectoparasites (Timm and Price, 1979) and there is unsuitable habitat between their respective distributions. Furthermore, until additional material of *G. p. fuscus* can be obtained, no proper evaluation of the relationship of the two taxa can be made.

Efforts to acquire additional specimens of *G. p. fuscus* were unsuccessful. Localities of known records (Del Rio, Fort Clark, and mouth of Sycamore Creek) were visited. Generally, most of the habitat at these localities appears unsuitable for *G. personatus*. One series of mounds were located on the grounds of Fort Clark in Bracketville. However, because the pocket gopher never responded to trapping efforts, it was not confirmed whether the mounds were made by *G. personatus* or *Pappogeomys castanops* (see Russell, 1968). Russell (1968) commented that *G. p. fuscus* is common in the vicinity of Eagle Pass, Maverick Co., Texas. However, we have not examined, nor do we know of any specimens in museum collections from this locality. Because this area is about 100 kilometers (60 miles) southeast of previous records of *G. p. fuscus* and approaching midway between the distributions of *G. p. fuscus* and *G. p. davisi*, pocket gophers occurring in the vicinity of Eagle Pass are certainly worthy of further investigation to verify their taxonomic status.

Specimens examined (5).—TEXAS. *Kinney Co.:* Fort Clark, 5 (4 AMNH, 1 FMNH).

Geomys personatus maritimus Davis, 1940

Geomys personatus maritimus Davis, Texas Agric. Exp. Station Bull., 590:26, 23 October 1940.

Holotype.—Young adult (basioccipital and basisphenoid not completely fused) female, skin and skull, TCWC 608; from Flour Bluff, 11 mi SE Corpus Christi, Nueces Co., Texas; collected on 21 April 1938 by William B. Davis, original no. 3059.

Measurements of holotype.—Total length, 278; length of tail, 80; length of hind foot, 36; greatest length of skull, 51.2; condylobasal length, 48.9; basal length, 45.6; palatal length, 32.1; palatofrontal depth, 19.1; length of nasals, 18.0; diastema, 17.0; zygomatic breadth, 29.7; mastoid breadth, 28.1; squamosal breadth, 21.7; rostral breadth, 11.4; interorbital constriction 6.6; breadth across maxillaries, 9.6.

Distribution.—Restricted to sandy soils of the mainland in Kleberg and Nueces counties, between Baffin Bay and Flour Bluff.

Remarks.—The range of *G. p. maritimus* lies between that of *G. p. fallax, G. p. megapotamus,* and *G. p. personatus.* However, *G. p. maritimus* more closely resembles the latter two taxa by being intermediate in size and having similar coloration. Davis (1940) provided further comments on the relationship between *G. p. maritimus* and other subspecies of *G. personatus.*

Specimens examined (130).—TEXAS. *Kleberg Co.:* NE King Ranch, 45 (43 TNHC, 2 UIMNH). *Nueces Co.:* 8.0 mi S, 8.3 mi E Corpus Christi, 5 (TTU); 11 mi SE Corpus Christi, 6 (2 KU, 3 TCWC, 1 UIMNH); 14 mi SE Corpus Christi, 3 (KU); Corpus Christi Bay, Flour Bluff, 6 (ANSP); Flour Bluff, 65 (8 TNHC, 53 TTU, 4 UIMNH).

Geomys personatus megapotamus Davis, 1940

Geomys personatus megapotamus Davis, Texas Agric. Exp. Station Bull., 590:27, 23 October 1940.

Holotype.—Adult female, skin and skull, TCWC 794; from 4 mi SE Oilton, Webb County, Texas; collected on 25 November 1938 by William B. Davis, original no. 3254.

Measurements of holotype.—Total length, 250; length of tail, 67; length of hind foot, 35; greatest length of skull, 44.5; condylobasal length, 43.3; basal length, 41.1; palatal length, 28.3; palatofrontal depth, 17.1; length of nasals, 15.5; diastema, 15.1; zygomatic breadth, 26.7; mastoid breadth, 25.5; squamosal breadth, 19.6; rostral breadth, 9.7; interorbital constriction, 6.7; breadth across maxillaries, 9.2.

Distribution.—Occurring in sandy soils of southern Texas and extreme northeastern Tamaulipas. In Texas, specimens have been collected in Brooks, Cameron, southern Duval, northern Hidalgo, Jim Hogg, Kenedy, southern Kleberg, eastern Starr, eastern Webb, and Willacy counties. The northernmost record is 6 mi W Cotulla, La Salle Co., Texas; the southernmost record is Boca Santa Maria (barrier island), Tamaulipas.

Remarks.—Even in the original description by Davis (1940), *G. p. megapotamus* had the most extensive distribution of all the subspecies of *G. personatus.* Until the current study, the southern extent of the distribution of this subspecies was thought to be Cameron County, Texas. The population of *G. personatus* in Tamaulipas, reported by Selander et al. (1962), was assumed to be an extension of the population occurring on the Texas barrier islands, and was assigned to *G. p. personatus* (Hall, 1981). However, our data indicate that these populations belong to *G. p. megapotamus*. Furthermore, the lack of pocket gophers (or sign thereof) from South Padre Island, as indicated by fieldwork (by Williams) and lack of material in museum collections, suggest that *G. p. megapotamus* in Texas (as described by Davis, 1940) is geographically the nearest population.

The southern limit of the geographic range of *G. p. megapotamus* is questionable at the present time. Fieldwork conducted by Selander et al. (1962) and Williams has revealed pocket gophers occurring as far south as Boca Santa Maria on the coastal beaches of Tamaulipas. However, both field parties were unable to cross the strait of Boca Santa Maria to determine if the population continues. The presence of the closely related *G. tropicalis,* about 325 kilometers south of this locality, certainly strengthens the possibility of pocket gophers continuing further south along the beach. However, fieldwork (by Williams) determined that *G. personatus* probably does not get as far south as La Pesca, Tamaulipas (about 140 kilometers south of Boca Santa Maria). In addition to the absence of pocket gophers along the coastal beaches in this area, it is unlikely that they would inhabit these beaches because of their restricted size and predominate sea shell composition.

Specimens examined (288).—TAMAULIPAS. 10 mi N Boca Santa Maria, 18 (TTU); 45 mi S Rio Grande, Boca Santa Maria, 28 (TTU); 35 mi SSE Matamoros, 8 (KU); 5 mi S road to Washington Beach (on Washington Beach), 1 (TTU); 33 mi S Washington Beach, 1 (KU); 73 mi S Washington Beach, 8 (KU). TEXAS. *Brooks Co.:* Falfurrias, 6 (LACM); 10.5 mi E Falfurrias, 5 (TTU); 3 mi S Falfurrias, 3 (TCWC); 8.25 mi S Falfurrias, 5 (TTU); 15 mi S Falfurrias, 2 (TTU). *Cameron Co.:* Juarez Rancho, 1 (USNM); Santa Rosa, 1 (USNM). *Duval Co.:* 3 mi S, 24.6 mi E Hebbronville, 7 (TTU); 3 mi E Realitos, 4 (TNHC); 3½ mi SW Realitos, 2 (TCWC). *Hidalgo Co.:* 2 mi S County Mark on Hwy. 281, 1 (TTU); 5 mi S County Mark on Hwy. 281, 2 (TTU); 3 mi NW Linn, 2 (TTU); 4 mi W Linn, 2 (TTU). *Jim Hogg Co.:* 26.8 mi N Agua Nueva, 3 (TTU); 3 mi N Agua Nueva, 1 (TCWC); 1 mi NE Hebbronville, 1 (TCWC); 1.5 mi W Hebbronville, 2 (TTU); Hebbronville, 39 (2 LACM, 37 TNHC); 20 mi S Hebbronville, 9 (TNHC). *Kenedy Co.:* 3.5 mi S Mifflen, 1 (TAIU); Norias Ranch, 9 (FMNH); 10 mi N, 0.8 mi E Raymondville, 6 (TTU); 11 mi S Riviera, 1 (TAIU); La Paloma Ranch, 10 mi W Sarita, 2 (TAIU); La Paloma Ranch, 9½ mi W Sarita, 1 (TAIU); 6 mi E Sarita, 2 (ANSP); 3.8 mi S Sarita, 3 (TTU). *Kleberg Co.:* 7.7 mi E Riviera, 4 (TAIU); 8.7 mi E Riviera, 1 (TAIU); 1 mi S Jct. Fm. Rd. 2775 and 628, 1 (TAIU); Jct. Fm. Rd. 1546 and 2510, 9 (TTU); 2 mi S Riviera, 2 (TCWC); 2.8 mi S, 8.8 mi W Riviera, 4 (TTU). *La Salle Co.:* 6 mi W Cotulla, 1 (TCWC); 7 mi WSW Cotulla, 1 (TCWC). *Starr Co.:* 2 mi N La Gloria, 1 (TAIU). *Webb Co.:* 14 mi W Hebbronville, 1 (TTU); 4 mi SE Oilton, 8 (2 KU, 6 TCWC). *Willacy Co.:* 8 mi W Port Mansfield, 2 (TTU); 5 mi W Port Mansfield, 3 (TTU); 4 mi W Port Mansfield, 9 (TTU); 10 mi NW Raymondville, 1 (TNHC); 8 mi N Raymondville, 16 (TTU); 7 mi N Raymondville, 1 (TNHC); 5.4 mi N Raymondville, 1 (TAIU); 3 mi N Raymondville, 34 (TNHC); 16 mi W San Perlita, 1 (TCWC).

Geomys personatus personatus True, 1889

Geomys personatus True, Proc. U.S. Nat. Mus., 11:159 (for 1888), 5 January 1889.

Lectotype.—Female, age undetermined, skin and skull (damaged), USNM 19668/38000; from Padre Island, Texas (herein restricted to Padre Island, 6.1 mi S Nueces County Park [27°32′N, 97°15′W], Kleberg Co., Texas); collected on 11 April 1888 by Mr. C. K. Worthen, no original number.

Paralectotype.—Male, age undetermined, skin and skull (damaged), USNM 19667/37999; from Padre Island, Texas; collected on 11 April 1888 by Mr. C. K. Worthen, no original number.

Measurements (lectotype followed by paralectotype).—Total length, 294, 283; length of tail, 78, 73; length of hind foot, 33, 32. Cranial measurements were not taken because of damaged skulls.

Distribution.—Restricted to Mustang and Padre islands in Kleberg and Nueces counties, Texas.

Remarks.—The original description of *G. personatus* (True, 1889) was based on two specimens from Padre Island, Texas (Poole and Schantz, 1942). To the best of our knowledge, the status of the type specimens has not changed since that time. Therefore, we have designated a lectotype and a paralectotype. The lectotype selected has a cranium with less damage than that of the paralectotype and is the more mature individual.

The southern limit of the distribution of *G. p. personatus* is not certain. We found all records of *G. p. personatus* to occur either on Mustang Island or northern Padre Island. Past and recent field investigations (by W. Lloyd in 1891 and Williams in 1973) on southern Padre Island failed to find any evidence of pocket gophers. Bailey (1905) and Davis (1940) suggested that *G. p. personatus* occurs as far south as the central part of Padre Island. Our findings are in agreement with both studies. Because Mustang Island and Padre Island are more or less continuous along the southern coastline of Texas, it is not known why the pocket gophers have not moved into the habitats of South Padre Island. Assuming that currently existing waterways along the coastline have not been permanent enough to hinder dispersal by pocket gophers, it is possible that the soil type restricts the southern distribution of *G. p. personatus*. According to the state soil map (Godfrey et al., 1973) the soil on Padre Island becomes more calcareous south of Baffin Bay. However, it is not yet known whether such a physical change in soil, or resulting changes in vegetation and other factors, or combination of effects, would serve as a barrier to further dispersal.

Although True (1889) did not list the county of the collecting locality of the cotypes in the original description, subsequent authors (Hall, 1981; Hall and Kelson, 1959; Miller, 1912, 1924; Poole and Schantz, 1942) have given "Cameron Co." as part of the type locality. We believe that this subspecies occurs only on North Padre Island (north of Baffin Bay) and therefore the type specimens were not taken in Cameron Co. It is possible that the use of Cameron Co. resulted from the fact that the county at one time encompassed the entire coastal region of Texas from the Rio Grande to Baffin Bay. This area was subsequently divided (from north to south) into Kenedy, Willacy, and Cameron counties. In order to prevent future taxonomic confusion, we herein restrict the type locality of *G. p. personatus* to Padre Island, 6.1 mi S Nueces County Park (27°32′N, 97°15′W), Kleberg Co., Texas.

Specimens examined (203).—TEXAS. *Kleberg Co.:* Padre Island, 6.1 mi S Nueces County Park, 5 (TTU); N Padre Island, 26 (24 TNHC, 2 UIMNH); 23 mi S Port Aransas, 1 (TCWC); ¼ mi N Entrance Padre Island National Park, 1 (TAIU); 19 mi S Mustang Island, 1 (TCWC). *Nueces Co.:* Mustang Island, Port Aransas, 20 (TTU); Mustang Island, 2½ mi S Port Aransas, 8 (UIMNH); Mustang Island, 4.8 mi S Port Aransas, 1 (TTU); Mustang Island, 4.5 mi N Access Road No. 2 on Park Road 53, 8 (TTU); Mustang Island, Access Road No. 2, 7 mi S, 4 mi W Port Aransas, 34 (TTU); Mustang Island, 9 mi S, 5 mi W Port Aransas, 11 (TTU); Mustang Island, 13 mi S Port Aransas, 1 (KU); Mustang Island, 14 mi SW Port Aransas, 5 (KU); Mustang Island, 15 mi SW Port Aransas, 5 (TCWC); Mustang Island, 19 mi S Port Aransas, 6 (TCWC); N end Padre Island, 4 (2 TCWC, 2 UIMNH); Mustang Island, 39 (7 LACM, 2 USNM, 30 TCWC). *County unknown:* Padre Island, 27 (5 AMNH, 1 BM, 13 USNM, 8 TCWC).

Geomys personatus streckeri Davis, 1940

Geomys personatus minor Davis, Texas Agric. Exp. Station Bull., 590:29, 23 October 1940 (name preoccupied by *Geomys minor* Gidley, Dept. Interior, Prof. Paper 131-E, p. 123, Dec. 26, 1922).

Geomys personatus streckeri Davis, J. Mamm., 24:508, 20 November 1943.

Holotype.—Adult female, skin and skull, TCWC 787; from Carrizo Springs, Dimmit County, Texas; collected on 24 November 1938 by William B. Davis, original no. 3239.

Measurements of holotype.—Total length, 225; length of tail, 75; length of hind foot, 30; greatest length of skull, 37.9; condylobasal length, 37.3; basal length, 34.7; palatal length, 23.5; palatofrontal depth, 13.9; length of nasals, 13.1; diastema, 11.9; zygomatic breadth, 22.3; mastoid breadth, 21.4; squamosal breadth, 17.5; rostral breadth, 8.7; interorbital constriction, 6.6; breadth across maxillaries, 7.2.

Distribution.—Restricted to Dimmit and Zavala counties, Texas, in the vicinity of Carrizo Springs and Crystal City.

Remarks.—Recent data concerning *G. p. streckeri* indicate that this taxon is unique within the species. Davis et al. (1971) reported *G. p. streckeri* to be the only subspecies of *G. personatus* to have a diploid number of 72. *G. p. streckeri* also is unique by being the only known host to the louse *Geomydoecus truncatus*; other members of *G. personatus* are parasitized by two other species of *Geomydoecus* (Price and Emerson, 1971; Timm and Price, 1979). Perhaps the most distinguishing character of *G. p. streckeri* is its small size. Williams (1982) found phallic and bacular dimensions to be smaller than those of *G. p. davisi*, *G. p. maritimus*, and *G. p. personatus*. Our study showed almost half of the cranial characters of both sexes to be significantly different from all other samples examined (see Table 2). These metrical differences clearly showed the uniqueness of this taxa with the MINT multivariate analysis (see sample 2 in Figs. 2 and 3). The combination of data concerning karyotypes, parasites, phalli and bacula, in addition to the univariate and multivariate (MINT) analyses, poses some interesting questions about the taxonomic status of *G. p. streckeri*. However, the BMDP-7M discriminant and canonical analyses indicate *G. p. streckeri* to be small but to have no more distinctness as a taxon than other subspecies of *G. personatus* (Fig. 4). Because these analyses involve the multivariate examination of individual specimens (instead of sample means as used by the MINT program) we have placed more value on this procedure for determining the taxonomic status of *G. p. streckeri*. Therefore, we have chosen to maintain its subspecific status at this time. Although this decision could be argued, additional data are needed to substantiate or refute our findings.

Davis (1940) reported *G. p. streckeri* to occur on a western tributary of the Nueces River at Carrizo Springs. Because *G. p. megapotamus* has been reported from the Nueces River in La Salle Co., Davis (1940) suggested that *G. p. streckeri* and *G. p. megapotamus* might come into contact along the Nueces River. Davis et al. (1971) reported additional records of *G. p. streckeri* from the east side of the Nueces River in Zavala Co. (the identification of these specimens was confirmed by karyotypic data; Davis et al., 1971). Therefore, *G. p. streckeri* and *G. p. megapotamus* currently are known to be separated by about 40 kilometers (25 miles) along the Nueces River. Further investigation is needed in Dimmit and LaSalle counties to determine if these taxa are in contact. Although our study indicated *G. personatus* in La Salle Co. to be definitely of the *megapotamus*-type, it also would be useful to learn more about that sample. Such investigations could provide information relevant to the taxonomic status of *G. p. streckeri*.

Specimens examined (74).—TEXAS. *Dimmit Co.:* 13 mi NE Carrizo Springs, 12 (TTU); Carrizo Springs, 39 (1 LACM, 31 TNHC, 7 TTU); near Carrizo Springs on Hwy. 277, 5 (TTU); 1.0 mi SW Carrizo Springs, 2 (TCWC). *Zavala Co.:* 14 mi W Crystal City, 10 (KU). *County unknown:* mouth of Sycamore Creek, 1 (USNM).

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INTRAISLAND AND INTERISLAND VARIATION IN ANTILLEAN POPULATIONS OF *MOLOSSUS MOLOSSUS* (MAMMALIA: MOLOSSIDAE)

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Abstract

Significant levels of secondary sexual variation and expected levels of individual variation were demonstrated in all samples of *Molossus molossus* from Jamaica, Guadeloupe, and Trinidad examined with univariate analyses. Significant morphometric differences were demonstrated among samples of *Molossus molossus* that originated from geographically close localities on the same island. Using multivariate techniques, broader patterns of geographic variation were demonstrated among the Antillean populations of *M. molossus*.

Introduction

The small members of the genus *Molossus* with pale-based hair occur throughout the Antilles and in adjacent areas of northern South America and Middle America. Recent authors (Husson, 1978; Jones

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et al., 1971; Koopman, 1978; Varona, 1974) have considered these populations as a single species *(Molossus molossus)*, whereas earlier authors (Miller, 1913; Hall and Kelson, 1959) have judged there to be as many as 10 species in this group.

These bats are badly in need of taxonomic revision. Earlier workers were confused by the high degree of local variation as well as geographic and secondary sexual variation. Jones et al. (1971) hypothesized that because populations were highly localized and presumably inbred, they may diverge morphologically "to a degree that mensural differences can be demonstrated even between samples from the same general geographic area." The presence of these localized populations may be at least partially responsible for the many names assigned to this group. The recently described subspecies *lambi* (Gardner, 1966) may be an example of such a local population.

Having samples of *Molossus molossus* available from the islands of Jamaica, Guadeloupe, and Trinidad in the Antilles led us to examine the degree of local as compared to geographic variation. Islands present an ideal situation for making these comparisons. Because populations on an island are potentially members of the same breeding population, demonstrable mensural differences among intraisland samples would indicate that these bats are exhibiting an unusual degree of local variation, possibly by forming local breeding demes. Presumably there is no opportunity for interbreeding among populations on widely separated islands in the Antilles; therefore, we would expect a greater variation among populations on different islands than among populations on the same island.

This paper should be viewed as the first phase of a study to clarify the systematic relationships of the small-sized members of the genus *Molossus*. The hypotheses that are tested in this study are: (1) there is no significant variation among intraisland populations of *Molossus molossus* and (2) the amount of interisland variation exceeds the amount of intraisland variation. An assessment of the amount of intraisland as compared to interisland variation should be important to future studies of geographic variation in this group, especially when mainland populations are studied.

We have not used subspecific names throughout this paper because of the taxonomic uncertainty in this group and because they are not necessary for the current study. However, currently the name *M. m. milleri* would apply to populations from Jamaica and *M. m. molossus* to populations from Guadeloupe and Trinidad (Hall, 1981:255–257).

METHODS AND MATERIALS

From all specimens, one external and nine cranial measurements were recorded. All measurements are given in millimeters and were taken by means of dial calipers as follows: *length of forearm,* from posteriormost projection of the elbow to the anteriormost projecting portion of wrist joint with wing flexed; *greatest length of skull,* distance from posteriormost projection of the cranium to anteriormost surface of the upper incisors; *condylobasal length,* distance from posteriormost projection of exoccipital condyles to anteriormost projection of premaxillae; *zygomatic breadth,* greatest width across zygomatic arches at right angle to longitudinal axis of cranium; *mastoid breadth,* greatest width across mastoid processes, at right angle to longitudinal axis of skull; *breadth of braincase,* greatest width across braincase at widest point, at right angle to longitudinal axis of skull; *postorbital constriction,* least width across the postorbital constriction, at right angle to the longitudinal axis of cranium; *length of maxillary toothrow,* distance from posterior lip of alveolus of M^3 to anterior lip of alveolus of canine; *breadth across upper molars,* greatest distance from labial margins of upper molars at the widest point; *length of mandibular toothrow,* distance from posterior lip of alveolus of M_3 to anterior lip of alveolus of canine.

Only adult specimens (all specimens deposited in collection of The Museum, Texas Tech University) with phalangeal epiphyses completely fused were used in this study. Specimens were grouped into seven samples as follows for analysis: *Sample 1*—TRINIDAD: Blanchisseuse; Las Cuevas. *Sample 2*—TRINIDAD: Maracus Valley; Port of Spain; San Rafael. *Sample 3*—GUADELOUPE: 2 km N Ballif, Basse-Terre; 1 km S Basse-Terre, Basse-Terre. *Sample 4*—GUADELOUPE: 1 km N, 1 km W St. François, Grand-Terre. *Sample 5*—JAMAICA: Duanvale, Trelawny Parish. *Sample 6*—JAMAICA: ½ mi S, ½ mi W Runaway Bay, St. Ann Parish. *Sample 7*—JAMAICA: Queenhythe, St. Ann Parish.

Statistical procedures were performed on the IBM 370 computer at Texas Tech University. The univariate program yielded standard statistics (mean, range, standard deviations, standard error of the mean, variance, and coefficient of variation) and employed 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) was used to determine maximally nonsignificant subsets (Gabriel, 1964).

Cluster and principal component analyses were performed on standardized data using the NT-SYS program. A matrix of phenetic distance coefficients was computed and a cluster analysis was conducted using UPGMA (unweighted pair-groups method using arithmetic averages) on this matrix. The phenogram generated by the cluster analysis was compared with the original matrix, and a coefficient of cophenetic correlation was computed. A matrix of Pearson's product-moment correlation among characters was computed, and the first three principal components extracted. Projections of the OTUs onto the first three principal components were made.

Additional multivariate analyses were performed using the Statistical Analysis System (SAS) package developed by Barr and Goodnight (Service, 1972). A multivariate analysis of variance (MANOVA) and canonical analysis were performed to determine the degree of divergence among samples. Canonical analysis of data provides weighted combinations of characters, which maximizes the distinction among groups. This analysis extracts characteristic roots and vectors and computes a mean canonical variate for each sample. Additional orthogonal axes are constructed, which extract the next best combination of characters. This analysis emphasized those characters with the least within sample and greatest among sample variation, hence, providing the best combinations of characters to discriminate among samples. Each eigenvalue and its corresponding canonical variate represents an identifiable fraction of the total variation. Sample means and individuals were plotted on the first three canonical variates. The relative importance of each original variable to the first two canonical variates was computed. These techniques have recently been used in the study of mammals by Schmidly and Hendricks (1976), Yates and Schmidly (1977), and Swanepoel and Genoways (1978).

RESULTS

Univariate Analyses

Secondary sexual and individual variation were assessed in order to understand these two types of non-geographic variation in Antillean populations of *Molossus molossus*. Intraisland and interisland variation were also examined to determine if significant variation was present.

Secondary sexual variation.—Males and females from each sample were compared to determine the amount of secondary sexual variation present (Table 1). Two or more samples were significantly different for all measurements. Length of forearm exhibited the least amount of secondary sexual variation with only the two samples from Guadeloupe showing significant variation. Postorbital constriction revealed significant secondary sexual variation in only three samples (3, 4, and 7). In three measurements (greatest length of skull, condylobasal length, and mastoid breadth), the sexes were significantly different for all seven samples. Only one sample (5) did not show significant secondary sexual variation for zygomatic breadth and only two samples did not differ significantly for breadth across upper molars (1 and 7) and length of mandibular toothrow (2 and 5).

The greatest amount of secondary sexual variation was exhibited by the two samples from Guadeloupe. Males and females differed in all measurements for sample 3 and all but breadth of braincase for sample 4. Samples 1 and 5 revealed the least amount of secondary sexual variation differing in only five measurements.

In all subsequent analyses, males and females have been handled separately.

Individual variation.—The amount of individual variation present in these samples is small, indicating that each probably represents a single population (Table 1). Highest coefficients of variation for males were recorded for postorbital constriction in sample 4 (7.7) and mastoid breadth in sample 5 (4.2), whereas for females highest values were for length of maxillary toothrow in sample 6 (5.8) and postorbital constriction in sample 1 (5.5). Generally, amount of individual variation was comparable between the sexes and among the seven samples.

Intraisland variation.—Males and females were compared separately from two samples from Guadeloupe (3 and 4) and the three from Jamaica (5–7) to determine if significant differences occur between or among samples from a single island (Table 1). The samples from Trinidad were not considered in this portion of the analyses because these samples were formed by grouping material from adjacent localities.

Table 1.—*Variation in external and cranial measurements of* Molossus molossus *from Jamaica, Guadeloupe, and Trinidad. Samples are defined in text.*

Sample	Sample size	Mean	(Range)	±2 SE	CV
			Males		
Length of forearm					
1	4	38.1	(36.8–39.3)	±1.10	2.9
2	11	37.4	(36.7–38.4)	±0.37	1.6
3	23	38.7	(37.8–40.3)	±0.27	1.7
4	20	38.9	(37.1–40.7)	±0.40	2.3
5	3	38.8	(38.6–39.2)	±0.40	0.9
6	9	39.0	(38.3–39.8)	±0.31	1.2
7	24	39.0	(38.0–40.3)	±0.24	1.5
Greatest length of skull					
1	4	17.6	(17.4–17.7)	±0.13	0.7
2	11	17.3	(16.6–17.7)	±0.22	2.1
3	23	17.0	(16.4–17.4)	±0.11	1.5
4	20	17.0	(16.1–17.7)	±0.19	2.5
5	3	17.8	(17.8–17.9)	±0.07	0.3
6	9	17.3	(16.8–17.5)	±0.17	1.4
7	24	17.8	(17.2–18.5)	±0.13	1.8
Condylobasal length					
1	4	17.0	(16.8–17.3)	±0.22	1.3
2	11	16.7	(16.3–17.3)	±0.17	1.7
3	23	16.5	(15.9–17.1)	±0.11	1.6
4	20	16.5	(15.7–17.4)	±0.19	2.5
5	3	17.4	(17.1–17.8)	±0.43	2.2
6	9	17.0	(16.7–17.3)	±0.14	1.2
7	24	17.3	(16.8–17.5)	±0.22	2.1
Zygomatic breadth					
1	4	10.9	(10.4–11.0)	±0.30	2.8
2	11	10.7	(10.3–11.0)	±0.15	2.3
3	23	10.6	(10.3–10.8)	±0.06	1.4
4	20	10.8	(10.2–11.0)	±0.10	2.1
5	3	10.7	(10.2–11.1)	±0.52	4.2
6	9	11.1	(10.8–11.4)	±0.11	1.5
7	24	11.0	(10.7–11.4)	±0.08	1.8
Postorbital constriction					
1	4	3.7	(3.6–3.8)	±0.10	2.6
2	11	3.6	(3.4–3.9)	±0.09	3.9
3	23	3.4	(3.2–3.7)	±0.05	3.5
4	20	3.7	(3.4–4.8)	±0.13	7.7
5	3	4.0	(3.9–4.0)	±0.07	1.5
6	9	4.1	(4.0–4.2)	±0.05	1.8
7	24	4.1	(3.9–4.4)	±0.05	2.9

Table 1.—*Continued.*

Sample	Sample size	Mean	(Range)	±2 SE	CV
Breadth of braincase					
1	4	8.9	(8.7–9.1)	±0.16	1.8
2	11	8.9	(8.5–9.3)	±0.14	2.7
3	23	8.6	(8.4–8.9)	±0.05	1.5
4	20	8.7	(8.4–9.0)	±0.08	2.0
5	3	9.0	(8.9–9.1)	±0.12	1.1
6	9	8.9	(8.7–9.1)	±0.09	1.6
7	24	9.0	(8.6–9.9)	±0.10	2.8
Mastoid breadth					
1	4	10.4	(10.2–10.8)	±0.28	2.7
2	11	10.2	(10.0–10.5)	±0.10	1.6
3	23	10.2	(9.6–10.6)	±0.11	2.5
4	20	10.3	(9.9–10.6)	±0.10	2.2
5	3	10.7	(10.2–11.0)	±0.52	4.2
6	9	10.8	(10.5–11.1)	±0.14	1.9
7	24	10.7	(10.2–11.1)	±0.09	2.0
Length of maxillary toothrow					
1	4	6.0	(5.9–6.1)	±0.10	1.6
2	11	5.9	(5.6–6.1)	±0.08	2.3
3	23	5.7	(5.3–6.4)	±0.10	4.2
4	20	5.8	(5.5–6.2)	±0.08	3.3
5	3	5.7	(5.7–5.8)	±0.07	1.0
6	9	6.0	(5.8–6.4)	±0.12	3.0
7	24	5.9	(5.6–6.2)	±0.07	2.8
Breadth across upper molars					
1	4	7.7	(7.3–8.0)	±0.29	3.8
2	11	7.9	(7.6–8.2)	±0.13	2.7
3	23	7.7	(7.4–8.0)	±0.06	2.0
4	20	7.7	(7.3–8.2)	±0.11	3.2
5	3	8.0	(7.9–8.0)	±0.07	0.7
6	9	7.9	(7.7–8.0)	±0.07	1.3
7	24	7.9	(7.5–8.2)	±0.07	2.3
Length of mandibular toothrow					
1	4	6.7	(6.6–6.9)	±0.15	2.2
2	11	6.6	(6.3–7.0)	±0.15	3.6
3	23	6.4	(6.2–6.7)	±0.05	2.0
4	20	6.5	(5.9–6.7)	±0.08	2.8
5	3	6.7	(6.6–6.7)	±0.07	0.9
6	9	6.7	(6.5–6.9)	±0.09	2.0
7	24	6.7	(6.5–7.0)	±0.05	1.9
Length of forearm					
1	5	37.8	(36.6–38.8)	±0.74	2.2
2	15	37.8	(35.4–40.2)	±0.62	3.2
3	22	38.1	(36.1–39.3)	±0.34	2.1
4	20	37.9	(36.0–38.9)	±0.32	1.9
5	10	38.7	(38.1–40.3)	±0.40	1.6
6	10	38.5	(37.4–39.0)	±0.33	1.4
7	22	38.7	(37.3–40.2)	±0.31	1.9

Table 1.—*Continued.*

Sample	Sample size	Mean	(Range)	±2 SE	CV
Greatest length of skull					
1	5	16.5	(16.2–16.6)	±0.14	0.9
2	16	16.5	(15.9–17.3)	±0.17	2.0
3	22	16.1	(15.5–16.5)	±0.12	1.7
4	20	16.3	(15.8–17.0)	±0.13	1.7
5	10	16.8	(16.3–17.1)	±0.15	1.4
6	10	16.7	(16.5–16.9)	±0.09	0.9
7	22	16.9	(16.3–17.6)	±0.12	1.7
Condylobasal length					
1	5	15.9	(15.7–16.0)	±0.12	0.8
2	16	16.0	(15.5–16.6)	±0.16	1.9
3	22	15.7	(14.8–16.0)	±0.13	2.0
4	20	15.9	(15.4–16.7)	±0.14	2.0
5	10	16.4	(16.3–16.7)	±0.13	1.3
6	10	16.5	(16.3–16.7)	±0.08	0.8
7	22	16.5	(16.0–16.9)	±0.09	1.3
Zygomatic breadth					
1	5	10.2	(10.0–10.4)	±0.15	1.6
2	16	10.2	(9.9–10.6)	±0.10	2.0
3	22	10.1	(9.7–10.4)	±0.08	1.8
4	20	10.3	(9.9–10.9)	±0.10	2.1
5	10	10.6	(10.4–10.9)	±0.10	1.5
6	10	10.6	(10.3–10.8)	±0.09	1.4
7	22	10.6	(10.3–10.9)	±0.06	1.3
Postorbital constriction					
1	5	3.5	(3.2–3.7)	±0.17	5.5
2	16	3.5	(3.3–3.8)	±0.06	3.3
3	22	3.4	(3.1–3.5)	±0.04	3.1
4	20	3.3	(3.2–3.7)	±0.04	2.9
5	10	4.0	(3.9–4.1)	±0.04	1.7
6	10	4.0	(3.8–4.1)	±0.06	2.3
7	22	4.0	(3.8–4.1)	±0.03	2.0
Breadth of braincase					
1	5	8.9	(8.6–9.4)	±0.28	3.5
2	16	8.5	(8.1–8.8)	±0.09	2.2
3	22	8.4	(8.1–8.6)	±0.06	1.7
4	20	8.5	(8.2–8.9)	±0.08	2.0
5	10	8.8	(8.6–8.9)	±0.05	1.0
6	10	8.8	(8.5–9.8)	±0.24	4.4
7	22	8.7	(8.5–9.0)	±0.05	1.3
Mastoid breadth					
1	5	9.7	(9.6–10.0)	±0.15	1.7
2	16	9.8	(9.2–10.2)	±0.13	2.7
3	22	9.6	(8.2–10.0)	±0.16	3.9
4	20	9.8	(9.4–10.3)	±0.10	2.2
5	10	10.3	(10.0–10.4)	±0.08	1.3
6	10	10.3	(10.0–10.5)	±0.10	1.5
7	22	10.3	(9.9–10.6)	±0.07	1.6

Table 1.—*Continued.*

Sample	Sample size	Mean	(Range)	±2 SE	CV
Length of maxillary toothrow					
1	5	5.7	(5.5–5.8)	±0.12	2.3
2	16	5.7	(5.4–6.2)	±0.09	3.1
3	22	5.5	(5.3–5.9)	±0.06	2.4
4	20	5.5	(4.7–5.8)	±0.07	4.4
5	10	5.6	(5.5–5.8)	±0.07	2.1
6	10	5.8	(5.6–6.7)	±0.21	5.8
7	22	5.7	(5.5–5.9)	±0.05	2.3
Breadth across upper molars					
1	5	7.6	(7.5–7.8)	±0.12	1.7
2	16	7.5	(7.2–8.2)	±0.13	3.3
3	22	7.4	(7.2–7.6)	±0.06	1.9
4	20	7.4	(7.0–7.7)	±0.09	2.9
5	10	7.7	(7.5–7.9)	±0.11	2.2
6	10	7.6	(7.3–7.9)	±0.11	2.3
7	22	7.8	(7.4–8.9)	±0.15	4.6
Length of mandibular toothrow					
1	5	6.4	(6.2–6.5)	±0.12	2.0
2	16	6.5	(6.2–7.0)	±0.10	3.2
3	22	6.2	(6.0–6.4)	±0.05	1.9
4	20	6.3	(6.1–6.5)	±0.05	1.8
5	10	6.4	(6.2–6.9)	±0.12	3.2
6	10	6.4	(6.3–6.6)	±0.06	1.6
7	22	6.5	(6.3–6.9)	±0.07	2.6

Males from Guadeloupe (samples 3 and 4) differed significantly in two measurements—zygomatic breadth and postorbital breadth. Female samples from the island were significantly different in these two measurements as well as mastoid breadth. On Jamaica, the three samples of males exhibited significant differences in greatest length of skull, zygomatic breadth, and length of maxillary toothrow. In greatest length of skull, samples 5 and 7 differed significantly from sample 6, whereas in zygomatic breadth, samples 6 and 7 differed significantly from sample 5. Female samples from Jamaica differed in greatest length of skull.

Interisland variation.—The seven samples from the three islands were compared for both sexes to determine if significant variation occurred among the samples and islands. All measurements for both sexes exhibited significant differences among the samples (Table 1). However, in only two measurements (mastoid breadth and postorbital constriction) did samples from one island form a subset significantly different from those of the other island. In both of these measurements, the three samples of females from Jamaica formed a subset that did not overlap samples from Trinidad and Guadeloupe. The samples formed two to four overlapping subsets in all of the other measurements for both sexes.

Conclusions.—In any analysis of variation in *Molossus molossus,* the sexes must be considered separately. The analyses have shown that there is significant intraisland and interisland variation. The interisland variation, however, was of such a nature that the populations from the three islands cannot be distinguished on the basis of a single measurement. The degree of intraisland and interisland variation cannot be compared using these methods, but with significant variation present at both levels, multivariate analyses should be useful in making such comparisons.

Multivariate Analyses

Fig. 1 shows the results of the cluster analyses of the distance coefficients for males and females. The cluster analysis for females (cophenetic correlation coefficient, 89.1%) has the seven samples divided into three clusters which correspond to the three islands. The samples from Trinidad and Guadeloupe, although widely separated, are grouped more closely to each other than to the Jamaican samples. In the analysis for males (cophenetic correlation coefficient, 83.5%), the samples are also grouped into three clusters. However, in this analysis, sample 2 from Trinidad is grouped with the two samples from Guadeloupe. The remaining portions of the clusters are identical with those of the females.

Comparing the individual distance coefficients reveals some interesting results. Among the three samples on Jamaica the highest distance coefficient is 1.176 between male samples 5 and 6. The lowest coefficient is between female samples 5 and 7 (0.513). The distance coefficients between the two samples on Guadeloupe were 0.564 (females) and 0.668 (males) and on Trinidad were 0.622 (females) and 1.262 (males). These values, at least in some cases, are higher than would be expected of intraisland comparisons of populations of the same species; however, the interisland comparisons reveal values that are generally higher. The lowest distance coefficient among samples on Jamaica and Guadeloupe was 1.277 for males in samples 4 and 6 and among samples on Jamaica and Trinidad was 1.307 for females in samples 1 and 5. These low values for the interisland comparisons are higher than any of the intraisland comparisons. The lowest interisland value between Guadeloupe and Trinidad was 1.017 between female samples 2 and 4. This value is slightly lower than the intraisland value found for males on Trinidad (1.262).

The first three principal components extracted from the matrix of

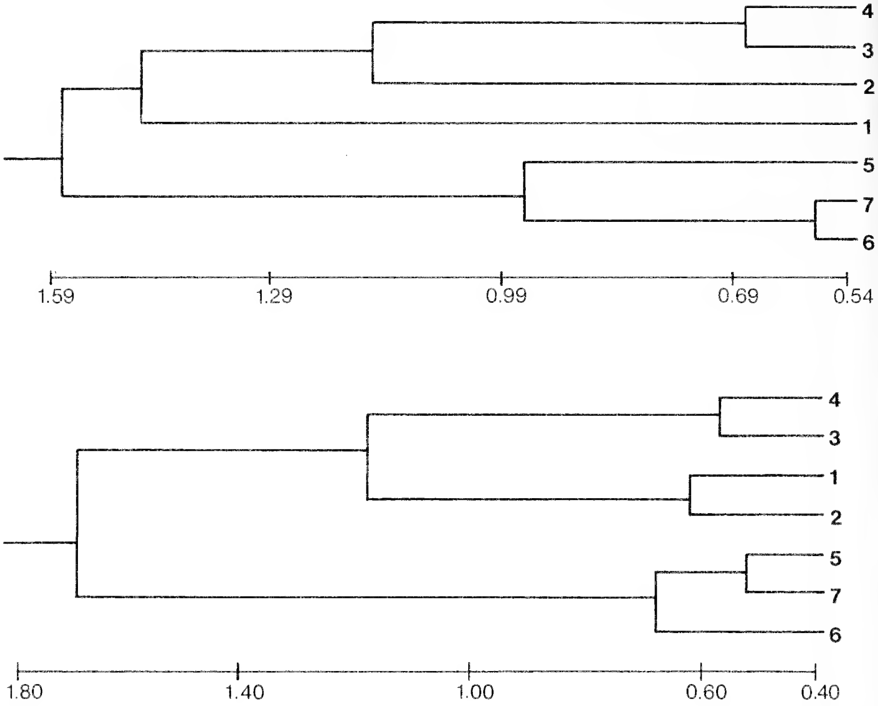

Fig. 1.—Phenograms of numbered samples (see text for key to numbers) of *Molossus molossus* (males, top; females, bottom) from the Antilles computed from matrices based upon 10 characters and clustered by unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient for males is 83.5% and for females 89.1%.

correlation among characters are shown for males and females in Fig. 2. The percent of phenetic variation explained by the first three principal components for males and females, respectively, were 51.5 and 75.6 for component I, 28.1 and 13.5 for component II, and 12.5 and 5.5 for component III. Results of principal components analyses showing the influence of each character for the first three components are given in Table 2.

Most characters are heavily weighted in the first component for both sexes. However, rather low values were found for length of forearm, length of maxillary toothrow, and breadth across upper molars for males; length of mandibular toothrow is lowest for females. In component II, characters with heavy weighting in males were greatest length of skull, mastoid breadth, length of maxillary toothrow, and

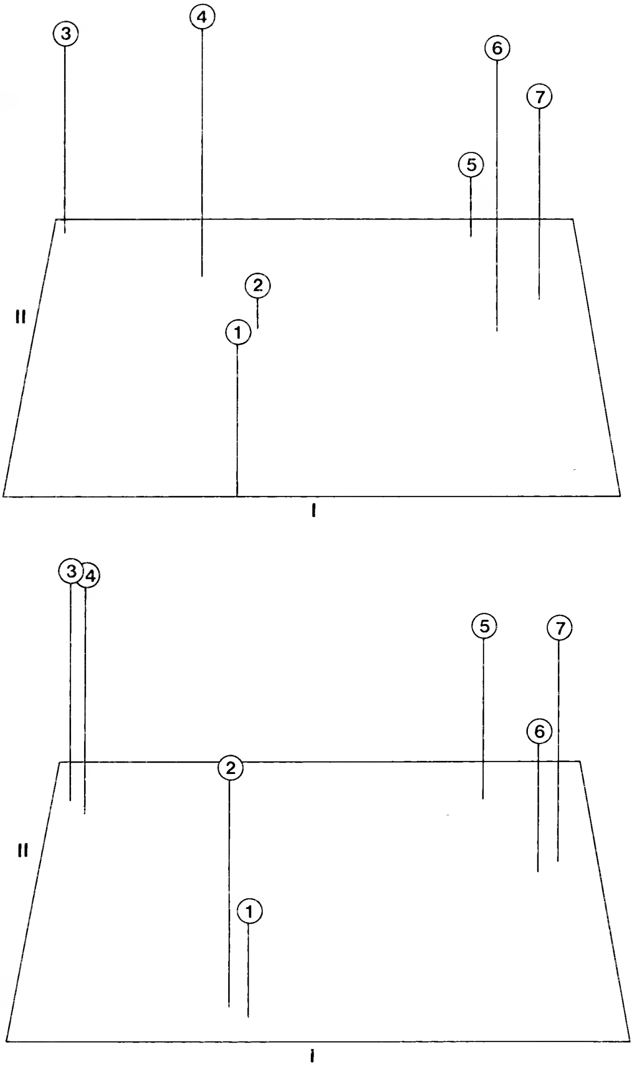

Fig. 2.—Three-dimensional projections of samples (see text for key to numbers) of *Molossus molossus* from the Antilles (males, top; females, bottom) onto the first three principal components based on matrices of correlation among one external and nine cranial measurements. Components I and II are indicated in the figure and component III is represented by height.

Table 2.—*Principal component loadings for 10 characters of* Molossus molossus.

Characters	Males			Females		
	Component I	Component II	Component III	Component I	Component II	Component III
Length of forearm	0.379	−0.448	0.691	0.802	−0.566	−0.053
Greatest length of skull	0.758	−0.567	−0.272	0.962	0.078	0.178
Condylobasal length	0.872	0.106	−0.267	0.986	−0.035	−0.018
Zygomatic breadth	0.663	0.471	0.561	0.915	−0.325	0.177
Mastoid breadth	0.747	−0.601	0.207	0.876	−0.221	−0.036
Breadth of braincase	0.861	0.299	−0.407	0.738	0.360	−0.525
Postorbital breadth	0.986	0.040	0.107	0.970	−0.237	−0.030
Length of maxillary toothrow	0.309	0.839	0.242	0.723	0.597	−0.100
Breadth across upper molars	0.396	−0.814	−0.059	0.972	0.054	−0.058
Length of mandibular toothrow	0.842	0.487	−0.184	0.683	0.563	0.444

breadth across upper molars, and for females were length of forearm, length of maxillary toothrow, and length of mandibular toothrow. Length of forearm for males and breadth of braincase for females were the only characters weighting heavily in component III.

In both of the three-dimensional projections (Fig. 2), the intraisland groups appear to be grouped closer to each other than any interisland comparisons. The only possible exception would be samples 2 (Trinidad) and 4 (Guadeloupe) for males. The other intraisland groups are tightly clustered. In both sexes from Jamaica, samples 6 and 7 are closer to each other than either is to sample 5.

In both male and female *Molossus molossus,* multivariate analyses of variance showed that there were significant ($P < .0001$) morphological differences among geographic samples in the following tests: Hotelling-Lawley's Trace; Pillai's Trace; Wilk's Criterion; Roy's Maximum Root Criterion. Two-dimensional plots of the seven samples onto the first two canonical variates based on a matrix of variance-covariance among length of forearm and nine cranial characters are presented in Fig. 3. The percentages of phenetic variation represented in the first two canonical variates for males and females, respectively, were 60.1 and 84.5 for variate I and 22.5 and 9.8 for variate II.

Length of forearm in males (18.4%) and postorbital constriction in females (41.09%) contributed the most toward separating the samples on the first variate (Table 3). Other characters that contributed more than 10% on the first variate include postorbital constriction, mastoid breadth, greatest length of skull, and breadth across upper molars for males, and condylobasal length, zygomatic breadth, and length of forearm for females. Three characters in males contributed more than 10% to the separation on the second variate, namely, greatest length of skull, length of forearm and zygomatic breadth, whereas four characters in females (greatest length of skull, zygomatic breadth, condylobasal length, length of mandibular toothrow) contributed more than 10% to the separation on the second variate.

Examination of the two-dimensional plot for females reveals the three intraisland groups cluster together and show no interisland overlap. The three Jamaican samples and the two Trinidad samples are broadly overlapping. However, the means for the two samples from Guadeloupe fall outside of one standard deviation of the other sample.

Examination of the two-dimensional plot for males reveals the intraisland groups are not nearly as tightly clustered as was seen for females; however, no interisland samples were found to overlap. Sample 6, from Jamaica, is totally separated from all other samples studied. The other two Jamaican samples (5 and 7) do overlap, but the means are outside of one standard deviation. The one standard deviation ellipses for the two samples from Guadeloupe are just touching. The two intraisland samples with the most overlap are from Trinidad; however, even here the means fall outside the one standard deviation ellipse of the other sample.

DISCUSSION

Significant morphological differences can be demonstrated among samples of *M. molossus* that originate from geographic areas in close proximity on the same island. From collecting sites about 55 kilometers apart on Guadeloupe, two samples of males differed significantly in two measurements and the females in three. Among the three samples from Jamaica (total distance separating sample sites of 30 kilometers), males differed in three measurements and females in one. Interpretation of these results could indicate that taxonomic recognition be given to populations on a single island. Therefore, our first hypothesis—no significant differences among intraisland samples—is rejected.

The best methods for comparing intraisland and interisland variation in *Molossus molossus* are multivariate techniques, but no one analysis seemed better than another. Each analysis gave a slightly different view of the data. We would suggest that as many types of analyses as possible be used when studying morphometric variation in *Molossus molossus*.

In the cluster analyses of distance coefficients, the females formed three clusters corresponding to the islands. In males there were also three clusters, but one of the samples from Trinidad grouped with the samples from Guadeloupe. The intraisland distance coefficients are generally higher than would be expected for samples of other species from such close geographic proximity. However, the interisland values were generally higher than the intraisland comparisons. The one exception was between the samples of males on Trinidad, which would account for the grouping in the cluster analysis.

The samples of females form tight clusters based upon their island of origin in the principal component analysis. The males from Jamaica also form a tight cluster in the principal component analysis; however, the samples of males from Trinidad and Guadeloupe are fairly widely separated. It would be difficult to determine the geographic relationships of the samples from the latter two islands based only on study of Fig. 2.

The two former multivariate analyses give a picture of the relationships of the populations without weighting the characters; therefore, a canonical analysis weighting the characters was also conducted. The female samples again are closely clustered based upon their geographic origin, especially those from Jamaica and Trinidad. The two populations of females from Guadeloupe are somewhat more separated in this analysis than in the others. There is no interisland overlap and the

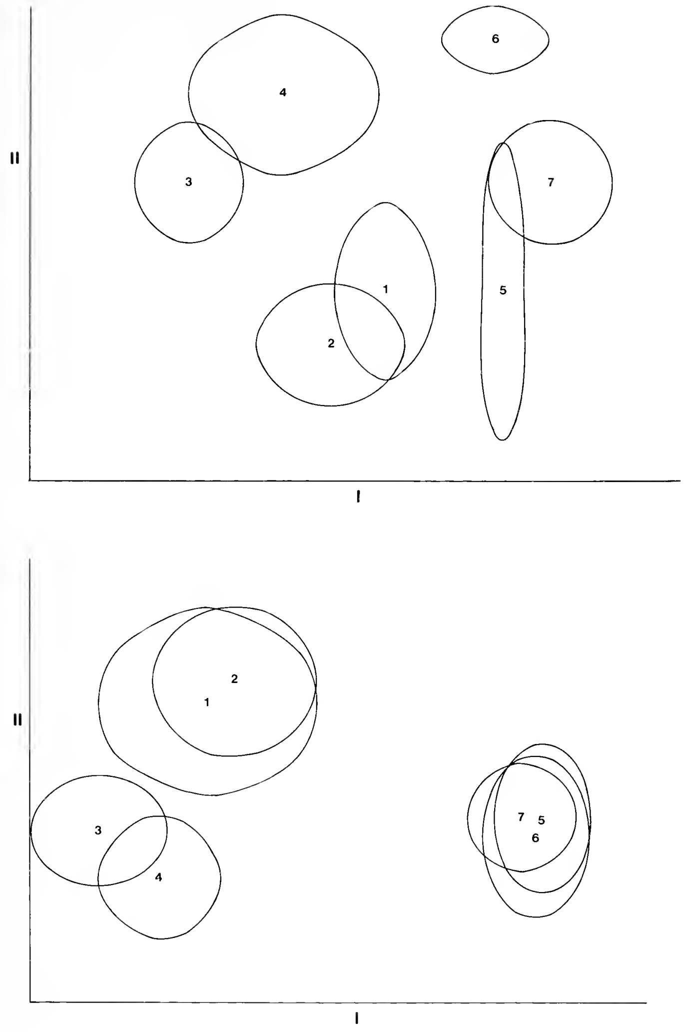

Fig. 3—Two-dimensional projections of samples (see text for key to numbers) of *Molossus molossus* from the Antilles onto the first two canonical variates based on a matrix of variance-covariance among one external and nine cranial measurements.

intraisland relationships are quite clear. For males the picture is quite different. The only overlap present is intraisland, but there is even little of this. The interisland relationships are not clear, particularly because of the isolated position of sample 6 from Jamaica.

Table 3.—*Eigenvalues of canonical variates showing the percentage influence among the one external and nine cranial characters of* Molossus molossus.

	Males				Females			
	I		II		I		II	
Characters	Normalized score	Percent influence	Normalized score	Percent influence	Normalized score	Percent influence	Normalized score	Percent influence
Length of forearm	−0.05412546	18.40	−0.11802628	24.24	−0.02285794	10.18	0.01896076	3.54
Greatest length of skull	0.08893837	13.54	0.28601946	26.31	0.02581785	4.96	−0.38688084	31.20
Condylobasal length	0.05589704	8.28	0.00171426	0.15	0.07652449	14.34	0.19524167	15.36
Zygomatic breadth	0.04423315	0.04	−0.29602578	16.98	−0.11002061	13.29	0.46939735	23.80
Mastoid breadth	0.14871458	13.65	−0.11420466	6.33	0.08500490	9.86	0.09280756	4.52
Breadth of braincase	0.06342258	4.92	0.19351566	9.06	−0.00999643	1.00	−0.04364188	1.82
Postorbital constriction	0.49822111	16.47	0.25092000	5.01	0.96659557	41.09	−0.05246146	0.94
Length of maxillary toothrow	−0.14342332	7.34	0.19524290	1.04	−0.03726515	2.45	−0.17354938	4.78
Breadth across upper molars	−0.16031757	10.98	0.10709512	4.43	−0.00042139	0.04	−0.09957419	3.69
Length of mandibular toothrow	0.11032667	6.38	0.18462909	6.45	0.03771688	2.79	−0.33335310	10.35

This study has shown that significant morphological variation can exist between intraisland populations of *Molossus molossus*. A similar type of study (Swanepoel and Genoways, 1978) of Antillean bats of the genus *Brachyphylla* did not reveal this level of intraisland variation. The current study has also demonstrated that patterns of geographic variation on a broader scale can be shown in *Molossus molossus* by using multivariate analyses. The local variation is more than would be expected in most other species of mammals (pocket gophers, especially *Thomomys*, are probably similar) but there are broader overriding patterns of geographic variation that exceed this local variation; therefore, the second hypothesis—interisland variation exceeds intraisland variation—can be accepted. Clearly, analyses of geographic variation can be performed on these small *Molossus*, but an understanding of local variation will aid in the appreciation of the broader geographic patterns.

The reasons this species has high levels of local geographic variation cannot be answered by the current study. Possibly as suggested by Jones et al. (1971), these local populations show a high degree of philopatry and inbreeding leading to morphological divergence on very local levels. We believe that genic analyses and ecological studies, particularly dealing with the breeding structure of these populations, would be very informative.

Specimens examined (200).—GUADELOUPE. Basse-Terre: 2 km N Ballif, 35; 1 km S Basse-Terre, 10. Grand-Terre: 1 km N, 1 km W St. François, 40. JAMAICA. St. Ann Parish: Queenhythe, 46; ½ mi S, ½ mi W Runaway Bay, 20. Trelawny Parish: Duanvale, 13. TRINIDAD. St. George Co.: Blanchisseuse, 6; Las Cuevas, 3; Maracas Valley, 10; Port-of-Spain, 7; San Rafael, 10.

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DISTRIBUTION AND TAXONOMIC STATUS OF *BLARINA HYLOPHAGA* ELLIOT (INSECTIVORA: SORICIDAE)

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Abstract

Systematic relationships of southern populations of short-tailed shrews (genus *Blarina*) are assessed on the basis of univariate and multivariate statistics. Populations are separated into two phena; southwestern short-tailed shrews are significantly larger morphometrically than southeastern forms. The two phena apparently represent distinct species. The name *Blarina hylophaga* is available for southwestern populations, and the name *Blarina carolinensis* is here restricted to short-tailed shrews in the southeastern United States.

Introduction

Short-tailed shrews of the genus *Blarina*, excepting those from the Dismal Swamp of Virginia and North Carolina, formerly were assigned to the species *B. brevicauda* (Hall and Kelson, 1959:52; Hall, 1981). The only subspecies of short-tailed shrew recognized on the southern

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Great Plains was *B. b. carolinensis* until Elliot (1899) named *B. b. hylophaga* based on two specimens from Dougherty, Murray Co., Oklahoma. Blair (1939) described the latter subspecies as ". . . a slight local race, developed through partial isolation in the Arbuckle Mountains." Subsequently, Jones and Glass (1960) examined specimens of *Blarina brevicauda* from Oklahoma and found no appreciable differences between the two subspecies. They therefore assigned all short-tailed shrews from Oklahoma to the subspecies *B. b. carolinensis* and relegated *B. b. hylophaga* as a junior synonym of *B. b. carolinensis*. In the same paper, Jones and Glass noted a difference in size between specimens of *carolinensis* from Oklahoma and specimens from near the type locality of *carolinensis* in South Carolina; western shrews were described as appreciably larger than eastern shrews. This difference was attributed to clinal variation in size although the authors examined no specimens between South Carolina and Oklahoma.

Cockrum (1952), Jones and Findley (1954), and Jones (1964) all noted that the genus *Blarina* exhibits clinal variation in size, from north to south, with a large step in southern Nebraska. On the basis of these observations, Genoways and Choate (1972) examined specimens from Nebraska to ascertain whether that step represented a subspecific or specific boundary. The results of their study, plus karyotypic data obtained later (Genoways et al., 1977), suggested that the latter was the case and two species of *Blarina* exist on the Great Plains—*B. brevicauda* in the north, and *B. carolinensis* in the south. George et al. (1982) compared the karyotypes of populations presently assigned to *Blarina carolinensis* in the southern United States and concluded that they represent distinct eastern and western species. This study was undertaken to assess variation between those eastern and western populations and to ascertain the distribution and taxonomic status of the southwestern taxon, for which the name *B. hylophaga* is available.

MATERIALS AND METHODS

A total of 380 specimens was examined from Alabama, Arkansas, Georgia, Kansas, Louisiana, Mississippi, Missouri, Oklahoma, South Carolina, Tennessee, and Texas. These specimens are deposited in the collections listed in the Acknowledgments.

Specimens were aged on the basis of toothwear and condition of pelage (Choate, 1972). For statistical analyses, all age and sex groups were pooled because no appreciable secondary sexual or age variation has been found in the genus (Guilday, 1957; Choate, 1972; Schmidly and Brown, 1979). Nine cranial and mandibular measurements (described by Choate, 1972) were recorded in mm from each specimen: occipitopremaxillary length (OPLEN); P^4–M^3 length (PMLEN); cranial breadth (CRNBR); breadth of zygomatic plate (ZYPBR); maxillary breadth (MAXBR); interorbital breadth (INOBR); mandibular length (LENMA); mandibular height (HEMAN); articular breadth (ARTBR). All measurements were taken with dial calipers accurate to 0.1 mm. Only specimens with complete data were used in statistical analyses.

Discriminant analysis was performed with a computer program from the Statistical

Package for the Social Sciences (Nie et al., 1975). Reference samples were from western Kansas (sample number 1, below) and the southeastern United States (sample 19, below). Because of the paucity of specimens from the Southeast and the need for a relatively large reference sample, all specimens available from Alabama, Georgia, Mississippi, South Carolina, and Tennessee were included in the southeastern reference sample. All specimens measured from Arkansas, southern Kansas, Louisiana, southern Missouri, Oklahoma, and Texas were evaluated with the discriminant equation generated from the reference samples, and the resulting scores were plotted to determine taxonomic affinities.

Standard statistics (mean, standard deviation, standard error, and coefficient of variation) were calculated for sample measurements using a computer program of the Statistical Analysis System, SAS (Helwig and Council, 1979). Nineteen samples (Fig. 1) were pooled on the basis of geographic locality and results of the discriminant analysis, as follows (sample sizes in parentheses): 1) Kansas—Ellis, Graham, Norton, Phillips, Rooks, Rush, Sheridan, and Trego counties (46 specimens); 2) Kansas—Greenwood County (21); 3) Oklahoma—Payne County (11); 4) Oklahoma—Osage County (17); 5) Arkansas—Benton, Fulton, Stone, and Washington counties, and Missouri—Camden, Greene, and Wright counties (13); 6) Arkansas—Craighead, Cross, Greene, and Mississippi counties (98); 7) Oklahoma—Cleveland County (5); 8) Oklahoma—Murray County (9); 9) Arkansas—Jefferson, Prairie, Pulaski, and Saline counties (11); 10) Arkansas—Howard, Little River, Polk, and Union counties (5); 11) Arkansas—Ashley and Drew counties (14); 12) Louisiana—near Blanchard, Caddo Parish (4); 13) Louisiana—near Greenwood, Caddo Parish (16); 14) Louisiana—Bienville, Grant, Lincoln, and Winn parishes (8); 15) Texas—Nacogdoches County (6); 16) Texas—Hardin, Newton, Tyler, and Walker counties (49); 17) Louisiana—Calcasieu, Evangeline, Sabine, Vernon, and West Baton Rouge parishes (8); 18) Texas—Aransas County (2); 19) Alabama—Cullman, Etowah, Hale, Russell, and Sumter counties, Georgia—Dodge, Earl, Grady, Liberty, and Thomas counties, Mississippi—Adams, Harrison, Marshall, Scott, and Tishomingo counties, South Carolina—Charleston and Georgetown counties, and Tennessee—Decatur, Madison, and Shelby counties (37).

Using SAS, a one-way analysis of variance (F test) and Duncan's multiple range test were used to test for significant differences among means and to identify maximal nonsignificant subsets. A multivariate analysis of variance (MANOVA) and canonical analysis were performed with SAS to assess the extent of morphometric divergence among samples.

RESULTS

Standard statistics, results of Duncan's multiple range test, and analysis of variance are shown in Table 1. For all characters, analysis of variance revealed highly significant differences among samples ($P <$ 0.0001). Duncan's multiple range test showed significant differences between, on the one hand, samples from Kansas (1 and 2), Oklahoma (3, 4, 7, and 8), the Ozarks of Arkansas and Missouri (5), Greenwood, Caddo Parish, Louisiana (13), and Aransas County, Texas (18) and, on the other hand, samples from Arkansas (6, 9, 10, and 11), Louisiana (12, 14, and 17), eastern Texas (15 and 16), and east of the Mississippi River (19) for two of the nine measurements (OPLEN and CRNBR). For PMLEN, MAXBR, LENMA, and ARTBR, a similar relationship was found; however, there was some overlap between the two groups. Sample 15 did not differ significantly from sample 8 for LENMA, and

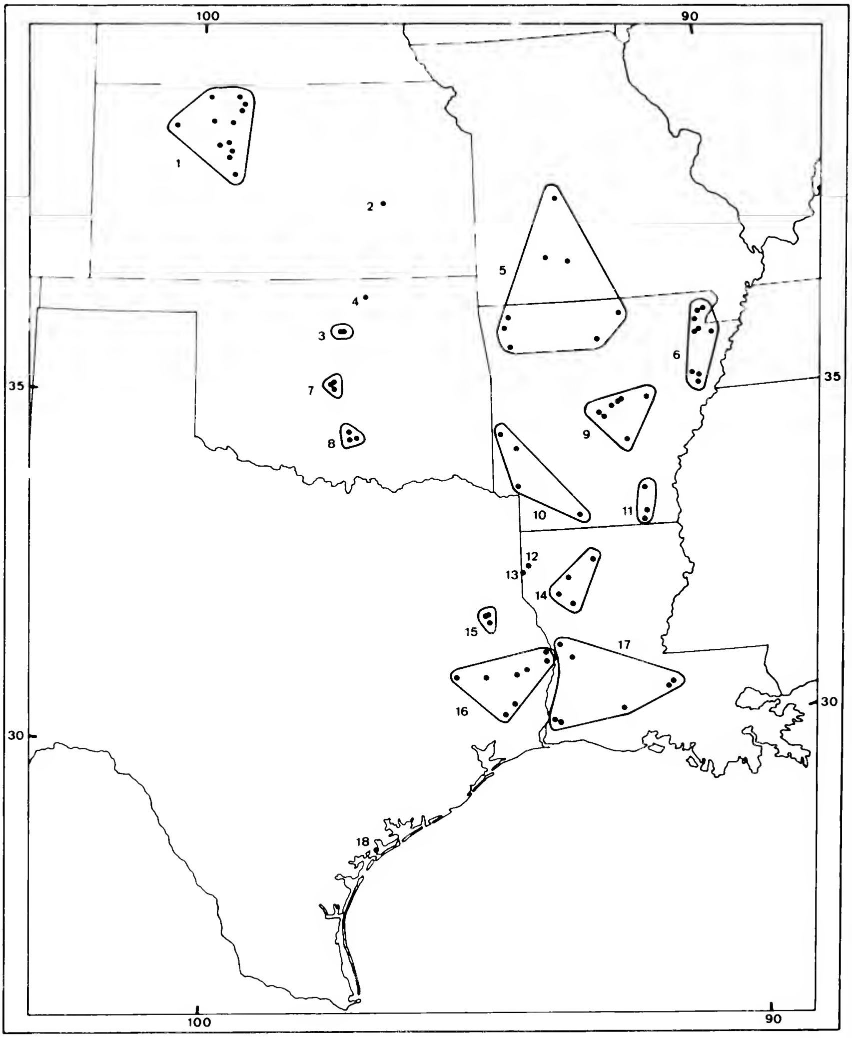

Fig. 1.—Geographic distribution of samples of *Blarina*. Numbers refer to samples described in text.

from 8, 13, and 18 for PMLEN. Sample 18 did not differ significantly from 15 and 6 for MAXBR. Samples 18, 13, and 8 did not differ significantly from 6, 9, 10, 11, 12, 14, 15, 16, 17, and 19 for ARTBR. For INOBR and HEMAN, sample 15 is placed with the former group described above, but for INOBR it did not differ significantly from sam-

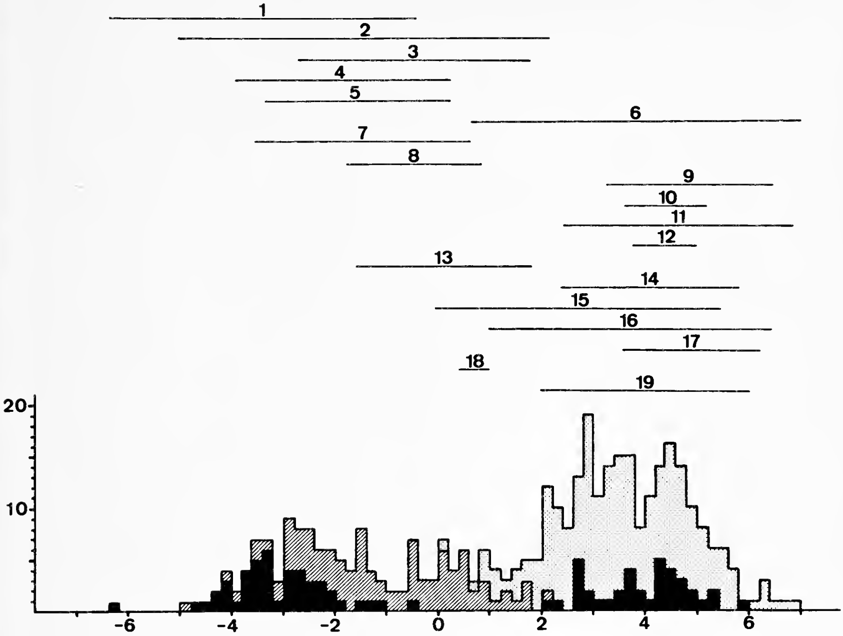

Fig. 2.—Histogram of linear discriminant scores for short-tailed shrews. Discriminant scores are indicated along the horizontal axis, and frequency of individuals is indicated along the vertical axis. Reference specimens are indicated by darkened areas, test specimens referred to the southwestern phenon (referred to as "*hylophaga*") are indicated by crosshatched areas, test specimens referred to the southeastern phenon (referred to as "*carolinensis*") are indicated by stippled areas. Horizontal lines above the histogram correspond to ranges of discriminant scores for samples described in text.

ple 6. For ZYPBR, the samples grouped in a different order, with a great deal of overlap among them; however, coefficients of variation for the character were high, thus reducing the probability of finding significant differences among samples.

Discriminant multipliers are given in Table 2, and discriminant scores for reference and test specimens are plotted in Fig. 2. The analysis clearly discriminated between eastern and western reference samples. Test specimens were discriminated as members of one or the other of these two phena, although scores of shrews from southern Oklahoma and northwestern Louisiana approached those of southeastern reference specimens. Likewise, scores of shrews from northeastern Arkansas approached those of the southeastern reference specimens and, in fact, overlapped with scores of specimens from

Table 1.—*Geographic variation in cranial characters of* Blarina. *Samples and measurements are explained in the text. Vertical lines alongside geographic samples indicate nonsignificant subsets. All F statistics were significant (*P < *0.0001).*

Sample	N	Mean	Range	2 SE	CV
Occipitopremaxillary length (F = 120.92)					
1	46	20.89	19.9–21.9	0.13	2.13
2	21	20.66	19.7–21.6	0.19	2.16
4	17	20.61	19.8–21.2	0.18	1.77
5	13	20.61	20.0–21.3	0.27	2.36
7	5	20.24	19.7–21.0	0.46	2.56
3	11	20.14	19.5–20.8	0.26	2.11
18	2	19.95	19.9–20.0	0.10	0.35
8	9	19.80	19.4–20.4	0.21	1.58
13	16	19.62	19.1–20.5	0.17	1.75
15	6	19.25	18.8–19.8	0.35	2.22
6	98	18.94	17.7–19.6	0.07	1.88
19	37	18.60	17.6–19.3	0.12	1.98
16	49	18.57	17.9–19.4	0.11	2.06
12	4	18.55	18.5–18.6	0.06	0.31
14	8	18.51	18.0–19.0	0.24	1.81
10	5	18.44	18.1–18.7	0.25	1.51
9	11	18.44	18.1–19.1	0.19	1.67
11	14	18.33	17.7–19.1	0.21	2.12
17	8	18.28	17.8–18.6	0.20	1.57
P^4-M^3 length (F = 52.50)					
1	46	5.77	5.3–6.2	0.05	3.18
5	13	5.75	5.4–6.0	0.10	3.14
2	21	5.70	5.4–6.0	0.08	3.30
4	17	5.67	5.5–5.9	0.07	2.40
7	5	5.62	5.5–5.9	0.16	3.18
3	11	5.59	5.4–5.9	0.10	2.82
18	2	5.55	5.5–5.6	0.10	1.27
13	16	5.48	5.2–5.8	0.07	2.60
8	9	5.48	5.3–5.7	0.08	2.19
15	6	5.37	5.2–5.5	0.08	1.92
6	98	5.26	4.9–5.6	0.03	2.75
12	4	5.20	5.1–5.3	0.16	2.22
16	49	5.18	4.9–5.5	0.04	2.96
14	8	5.16	5.0–5.3	0.64	1.77
19	37	5.16	4.6–5.6	0.05	3.21
9	11	5.15	4.9–5.3	0.08	2.51
10	5	5.10	5.0–5.3	0.11	2.40
11	14	5.07	4.9–5.3	0.07	2.61
17	8	5.05	4.9–5.3	0.09	2.59

Table 1.—*Continued.*

Sample				N	Mean	Range	2 SE	CV
				Cranial breadth (F = 69.86)				
5				13	11.59	10.9–12.2	0.23	3.62
1		┬		46	11.41	10.8–12.1	0.09	2.75
4	┬	┴		17	11.29	10.8–11.7	0.14	2.53
2	│	┬		21	11.15	10.6–11.7	0.14	2.97
7	┴	│	┬	5	11.10	10.7–11.6	0.34	3.43
3		│	│	11	11.00	10.3–11.5	0.20	2.99
18	┬	┴	│	2	11.00	10.7–11.3	0.60	3.86
8	│		┴	9	10.89	10.7–11.1	0.12	1.72
13	┴			16	10.70	10.2–11.3	0.16	2.96
15	┬			6	10.70	10.2–11.3	0.16	2.96
6	│			98	10.34	9.6–11.0	0.05	2.62
16	│	┬		49	10.22	9.6–10.6	0.69	2.36
17	│	│	┬	8	10.21	10.0–10.5	0.12	1.77
19	│	│	│	37	10.17	9.7–10.7	0.08	2.29
10	┴	│	│	5	10.12	9.8–10.3	0.18	2.03
9		│	│	11	10.06	9.6–10.4	0.16	2.68
14		┴	│	8	10.05	9.8–10.4	0.15	2.13
11			│	14	10.00	9.6–10.6	0.13	2.48
12			┴	4	9.95	9.9–10.0	0.06	0.58
				Breadth of zygomatic plate (F = 9.80)				
5		┬		13	2.32	2.0–2.5	0.08	6.32
1	┬	│		46	2.25	2.0–2.6	0.04	5.84
8	│	┴	┬	9	2.20	2.0–2.4	0.11	7.19
2	│	┬	│	21	2.18	1.8–2.5	0.07	6.90
18	┴	│	│	2	2.15	2.0–2.3	0.30	9.82
4		│	│	17	2.12	1.9–2.3	0.06	5.40
19		│	│	37	2.11	1.7–2.4	0.06	8.24
13		│	│	16	2.11	2.0–2.3	0.06	5.87
7		│	│	5	2.10	1.9–2.3	0.14	7.53
3		│	┴	11	2.09	1.8–2.4	0.10	8.13
6		│		98	2.04	1.7–2.3	0.03	6.92
15		│		6	2.02	1.9–2.2	0.10	5.80
14		│		8	1.99	1.7–2.1	0.10	6.82
16		│		49	1.98	1.6–2.2	0.04	7.62
10		│		5	1.96	1.7–2.1	0.15	8.54
9		│		11	1.96	1.5–2.2	0.14	11.75
12		│		4	1.95	1.9–2.0	0.06	2.96
11		│		14	1.94	1.8–2.2	0.08	7.48
17		┴		8	1.94	1.7–2.2	0.11	8.25

Table 1.—*Continued.*

Sample	N	Mean	Range	2 SE	CV
		Maxillary breadth (F = 85.23)			
1	46	7.58	7.1–8.0	0.06	2.57
4	17	7.42	7.2–7.6	0.06	1.55
5	13	7.38	7.0–7.7	0.14	3.36
2	21	7.30	6.6–7.7	0.11	3.53
7	5	7.28	7.0–7.8	0.28	4.28
3	11	7.19	6.9–7.6	0.13	3.02
13	16	7.08	6.7–7.3	0.09	2.61
8	9	7.07	6.9–7.4	0.11	2.24
18	2	6.95	6.8–7.1	0.30	3.05
15	6	6.75	6.2–7.1	0.16	4.66
6	98	6.70	6.1–7.0	0.04	2.62
19	37	6.58	6.3–7.7	0.06	2.92
14	8	6.58	6.3–6.9	0.15	3.12
16	49	6.53	6.2–7.0	0.05	2.51
11	14	6.51	6.1–6.8	0.12	3.49
9	11	6.49	6.1–7.0	0.14	3.61
17	8	6.49	6.3–6.7	0.10	2.25
10	5	6.46	6.3–6.7	0.14	2.35
12	4	6.45	6.4–6.5	0.06	0.90
		Interorbital breadth (F = 39.55)			
1	46	5.58	5.2–5.9	0.05	2.97
4	17	5.56	5.4–5.8	0.05	2.00
5	13	5.53	5.2–5.9	0.14	4.51
2	21	5.50	5.4–5.7	0.04	1.67
7	5	5.50	5.4–5.7	0.11	2.23
3	11	5.40	5.1–5.9	0.13	4.14
8	9	5.39	5.3–5.6	0.07	1.96
18	2	5.35	5.1–5.6	0.50	6.61
13	16	5.31	5.0–5.5	0.08	2.99
15	6	5.27	5.1–5.5	0.13	3.10
6	98	5.12	4.5–5.5	0.03	3.24
19	37	5.06	4.8–5.5	0.05	3.27
16	49	5.06	4.8–5.3	0.03	2.42
14	8	5.05	4.7–5.3	0.15	4.23
11	14	5.04	4.8–5.3	0.07	2.55
17	8	5.02	4.9–5.3	0.10	2.96
10	5	5.02	4.8–5.2	0.13	2.95
12	4	4.95	4.9–5.0	0.06	1.17
9	11	4.92	4.7–5.1	0.08	2.70

Table 1.—*Continued.*

Sample	N	Mean	Range	2 SE	CV
Mandibular length (F = 88.42)					
1	46	11.92	11.4–12.6	0.09	2.59
5	13	11.79	11.2–12.6	0.25	3.89
2	21	11.78	11.2–12.3	0.13	2.47
4	17	11.61	11.1–12.2	0.13	2.31
18	2	11.50	11.5	0	0
3	11	11.41	11.0–12.0	0.18	2.58
7	5	11.36	11.0–11.8	0.26	2.54
13	16	11.16	10.5–11.6	0.14	2.56
8	9	11.14	10.7–11.4	0.13	1.80
15	6	10.88	10.7–11.1	0.15	1.69
6	98	10.73	10.8–11.3	0.04	1.91
12	4	10.72	10.7–10.8	0.05	0.47
19	37	10.61	10.1–11.2	0.08	2.27
10	5	10.56	10.1–10.8	0.27	2.89
9	11	10.48	10.2–11.0	0.16	2.52
17	8	10.46	10.2–10.7	0.12	1.61
16	49	10.46	9.9–11.1	0.08	2.73
11	14	10.40	9.8–10.8	0.14	2.59
14	8	10.35	10.0–10.8	0.19	2.58
Mandibular height (F = 101.39)					
1	46	6.30	5.8–7.3	0.07	3.53
5	13	6.28	5.9–6.7	0.16	4.56
2	21	6.17	5.7–6.7	0.12	4.53
7	5	6.06	5.9–6.4	0.17	3.22
4	17	6.05	5.9–6.3	0.06	2.12
3	11	5.93	5.5–6.3	0.14	4.00
18	2	5.85	5.6–6.1	0.50	6.04
8	9	5.81	5.6–6.1	0.10	2.64
13	16	5.78	5.5–6.1	0.09	3.17
15	6	5.55	5.3–5.7	0.11	2.48
6	98	5.39	4.9–5.8	0.03	2.82
19	37	5.33	5.0–5.6	0.06	3.21
12	4	5.32	5.1–5.5	0.17	1.17
14	8	5.28	5.1–5.6	0.12	3.16
16	49	5.26	4.9–5.7	0.05	3.20
11	14	5.21	5.0–5.6	0.09	3.32
17	8	5.20	5.0–5.3	0.08	2.06
9	11	5.17	5.0–5.4	0.07	2.13
10	5	5.14	4.9–5.3	0.16	3.53

Table 1.—*Continued.*

Sample	N	Mean	Range	2 SE	CV
		Articular breadth (F = 51.69)			
5	13	2.28	2.0–2.5	0.08	6.50
1	46	2.27	2.1–2.5	0.03	4.88
2	21	2.27	2.0–2.5	0.05	5.81
4	17	2.22	2.0–2.4	0.05	4.91
7	4	2.22	2.1–2.4	0.15	7.40
3	11	2.11	2.0–2.3	0.06	4.95
13	16	2.06	1.9–2.2	0.05	4.71
18	2	2.05	2.0–2.1	0.10	3.45
8	9	2.04	2.0–2.1	0.04	2.58
15	6	1.95	1.9–2.0	0.04	2.81
19	37	1.93	1.8–2.3	0.04	5.71
6	98	1.93	1.8–2.1	0.02	3.99
12	4	1.92	1.9–2.0	0.05	2.60
17	8	1.91	1.8–2.0	0.05	3.35
9	11	1.91	1.8–2.1	0.06	5.47
16	49	1.91	1.7–2.0	0.02	3.98
11	14	1.90	1.8–2.0	0.05	4.62
14	8	1.89	1.8–2.0	0.07	5.25
10	5	1.86	1.8–1.9	0.05	2.94

Oklahoma; however, scores of geographically adjacent southeastern and southwestern samples were discriminated clearly.

Four routines of MANOVA were employed to test the hypothesis that there is no significant morphometric difference among samples. The results of all four tests—Hotelling-Lawley's Trace (F = 18.05); Pillai's Trace (F = 4.43); Wilk's Criterion (F = 7.77); and Roy's Maximum Root Criterion (F = 149.57)—were significant at $P < 0.0001$. The variance-covariance matrix gave nine canonical variates among the nine characters for all 19 samples. The first canonical variate expressed 89.56% of the phenetic variation; the second, 3.00; and the third, 2.29. Two-dimensional plots of the first two canonical variates (showing the mean and one standard deviation on each side of the mean for each sample) are illustrated in Fig. 3. The samples are arranged into two groups—samples 1–5, 7, 8, 13, and 18 in the upper left of the figure, and samples 6, 9–12, 14–17, and 19 in the lower right.

DISCUSSION

Univariate and multivariate analyses of southern short-tailed shrews indicate that southwestern and southeastern populations constitute distinct phena. Reference samples of these two phena were separated by discriminant analysis. Overlap between discriminant scores of a

Table 2.—*Discriminant multipliers resulting from a discriminant function analysis comparing* Blarina *from western Kansas (sample 1) with* Blarina *from Alabama, Georgia, Mississippi, South Carolina, and Tennessee (sample 8). Measurements are explained in text.*

Measurement	Discriminant multiplier
OPLEN	−2.297952
PMLEN	0.7744092
CRNBR	0.2387917
ZYPBR	0.1793111
MAXBR	−3.685247
INOBR	1.080935
LENMA	0.9018796
HEMAN	−1.026482
ARTBR	1.072587
Constant	52.46786

few specimens from northeastern Arkansas and northeastern Texas and those of specimens from southern Oklahoma and northwestern Louisiana reflects geographic variation within both southwestern and southeastern plena of *Blarina*. Univariate statistics and the canonical analysis revealed a clinal decrease in size from Kansas to Oklahoma and Louisiana in the larger, southwestern phenon, and from northeastern Arkansas to Louisiana and from northeastern Texas to southeastern Texas in the smaller, southeastern phenon. The smallest southwestern specimens from Oklahoma and northwestern Louisiana thus overlap with the largest southeastern specimens from Arkansas and Texas when analyzed with discriminant functions. With one exception (discussed below), this overlap is between specimens from noncontiguous populations and apparently is not indicative of mensural intergradation.

Karyotypes from northern Florida, northern Louisiana, South Carolina, western Tennessee, and eastern Texas (George et al., 1982) exhibit a fundamental number of 44 and diploid numbers ranging from 37 to 46 (probably the result of Robertsonian events). Divergence between these karyotypes and those (FN = 62, 61, or 60; 2N = 52) from Oklahoma and Kansas therefore is appreciable, and the probability that the two taxa intergrade is low. Morphometric data from this study support this conclusion and indicate that southeastern and southwestern phena of *Blarina* almost certainly represent two distinct species. The name *Blarina carolinensis* should be restricted to populations of short-tailed shrews in the southeastern United States, whereas the name *Blarina hylophaga* is available for populations of short-tailed shrews in the southwestern region of the range of the genus.

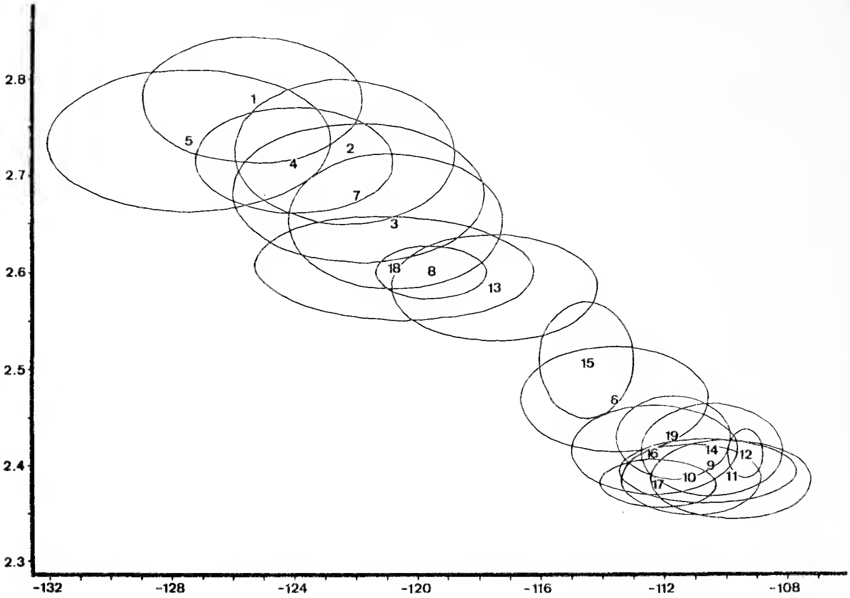

Fig. 3.—Plot of the mean and one standard deviation of the first two canonical variates for 19 samples of *Blarina*. Numbers refer to samples described in text.

Blarina hylophaga hylophaga Elliot

Blarina brevicauda hulophaga [sic] Elliot, Field Columbian Mus., Zool. Ser., 1:287, 1899; Blair, Amer. Midland Nat., 22:99, 1939; Hall and Kelson, The mammals of North America, 1:54, 1959.

Blarina brevicauda hylophaga Elliot, Field Columbian Mus., Zool. Ser., 6:461, 1905 (correction of previous error in spelling or transliteration).

Blarina brevicauda carolinensis: Blair, Amer. Midland Nat., 22:99, 1939; Cockrum, Univ. Kansas Publ., Mus. Nat. Hist., 7:43, 1952; Hall and Kelson, The mammals of North America, 1:53, 1959; Jones and Glass, Southwestern Nat., 5:138, 1960; Jones, Univ. Kansas Publ., Mus. Nat. Hist., 16:69, 1964; Bowles, Spec. Publ. Mus., Texas Tech Univ., 9:37, 1975; Hall, The mammals of North America, 1:54, 1981.

Blarina carolinensis carolinensis: Genoways and Choate, Syst. Zool., 21:114, 1972; Ramsey, unpubl. M.S. thesis, Arkansas State University, p. 40, 1977; Schmidly and Brown, Southwestern Nat., 24:45, 1979; Selander, A guide to Arkansas mammals, p. 44, 1979.

Holotype.—Male, adult; skin and skull; FMNH 6770, Field Museum of Natural History; from Dougherty, Murray Co., Oklahoma; collected 4 April 1899 by Mr. Thaddeus Surber, original number 154. (In Elliot's original description, it is unclear which of the two specimens, a male and a female, he had at hand was to be the holotype; however, in a subsequent publication [Elliot, 1907], the male is clearly indicated as the "type" and the female as the "paratype.")

Diagnosis.—Size medium for the genus in both external and cranial measurements; 2N = 52; FN = 62, 61, or 60.

Comparisons.—*Blarina h. hylophaga* can be distinguished from *B. brevicauda* by its much smaller size, shorter winter pelage, and by its karyotype (*B. brevicauda*: 2N = 50, 49, or 48; FN = 48). *B. hylophaga* can be distinguished from *B. carolinensis* by its significantly larger size (both cranial and external), and by its karyotype (*B. carolinensis*: 2N = 46, 39, 38, or 37; FN = 44 or 45).

Range.—From southern Nebraska (Jones, 1964; Genoways and Choate, 1972), southwestern Iowa (Bowles, 1975), extending into east-central Colorado along the Republican River (Armstrong, 1972), through Kansas, Missouri (exclusive of the northeastern and extreme southeastern corners), northwestern Arkansas (Hall, 1981), central and eastern Oklahoma (exclusive of the southeastern corner), and extending into northeastern Louisiana. Specimens from northeastern Texas reported by Schmidly and Brown (1979) as *B. c. carolinensis* are considered to belong to that species and not *B. hylophaga*.

Remarks.—Specimens with complete measurements from southeastern Missouri were unavailable, and we were unable to locate the contact zone between *Blarina carolinensis* and *Blarina hylophaga* in that state. A few specimens with incomplete measurements were examined, and some suggestions about the distributional relationship between the two species can be made based on these. Two specimens from St. Louis Co., Missouri, apparently represent *B. carolinensis*. Whether these specimens represent a relict population of *B. carolinensis* isolated from the range of that species by the range of *B. hylophaga,* or whether the two species are sympatric on the Mississippi floodplain in eastern Missouri, cannot be determined until more extensive collecting is done in that region. Merriam (1895) assigned a specimen from Kimmswick, Jefferson Co., Missouri, which he regarded as an intergrade between large shrews known as *B. brevicauda brevicauda* and small shrews he referred to as *B. b. carolinensis*, to the taxon *B. b. brevicauda*. That specimen clearly pertains to *B. hylophaga,* and thus would have seemed almost intermediate in size between the much larger *brevicauda* and smaller *carolinensis*.

We were also unable to obtain specimens from southeastern Oklahoma, with the exception of one shrew from McCurtain County. This specimen had incomplete measurements, but those that it had (ZYPBR = 1.6; MAXBR = 6.6; INOBR = 5.2; LENMA = 10.4; HEMAN = 5.5; ARTBR = 1.8) indicate that it pertains to *Blarina carolinensis,* rather than *B. hylophaga*. How far *B. carolinensis* extends its range into Oklahoma cannot be determined, as the nearest specimens collected (Atoka County to the west, Pittsburg County to the north) pertain to *B. hylophaga*.

Sample 13, from the vicinity of Greenwood, Caddo Parish, Louisiana, grouped with the shrews from Kansas and Oklahoma in all tests performed, although the sample generally was the smallest in size of the species; this conformed with the north-south clinal decrease in size described above. The sample was distinct from a sample from Blanchard, Caddo Parish, Louisiana (only 10 mi. northeast of Greenwood), which grouped with the other samples from Louisiana, Arkansas, and eastern Texas. As the sample from Greenwood, Louisiana, is on the opposite side of the Red River from the samples with which it is grouped, it might represent a relict population of *Blarina hylophaga*. An alternative explanation of this distribution is that *B. hylophaga* has extended its range across the Red River, but not south of the Sabine River. The range of *B. carolinensis* extends from Louisiana across the Red and Sabine rivers into eastern Texas. Thus, the area between the Red and Sabine rivers could have acted as a corridor whereby *B. hylophaga* has moved southward and eastward and come into contact with *B. carolinensis* in Caddo Parish, Louisiana. This cannot be determined until more specimens are collected in southern Oklahoma, northeastern Texas, northwestern Louisiana, and southwestern Arkansas.

Schmidly and Brown (1979) found shrews from northeastern Texas to be significantly larger than shrews from southeastern Texas, and thus assigned the former group to the same taxon as shrews from Kansas and Oklahoma. The results of this study, however, clearly show that animals from northeastern Texas group much closer to shrews from southeastern Texas and Louisiana than to those from Oklahoma and Kansas, and thus should be included within *Blarina carolinensis*, rather than *B. hylophaga*. Specimens from northeastern Texas are larger than those to the south and the east (excluding the sample from Greenwood, Louisiana); this variation probably is clinal, but this cannot be concluded with any certainty until more animals are obtained from those areas.

In Elliot's (1899) original description of *B. b. hylophaga*, the new name was misprinted or erroneously transliterated as *hulophaga*. Article 32(a) of the International Code of Zoological Nomenclature . . . states that the original spelling of a name may be corrected if "there is in the original publication clear evidence of an inadvertent error, such as a lapsus calami, or a copyist's or printer's error . . . ." The new name, "*hulophaga*," was used only once in the original description, and was said (p. 288) to be a transliteration of "feeding in the woods." The correct transliteration should have been *hylophaga*. This error was recognized by Elliot (1905), who corrected the spelling to *hylophaga,* but his correction was overlooked by subsequent authors (for example, Bole and Moulthrop, 1942; Miller and Kellogg, 1955; Hall and Kelson, 1959). Elliot's correction constituted a "justified emendation" of an "incorrect original spelling," and the name *hulophaga* thus has no status in nomenclature (see articles 32 and 33 of the International Code of Zoological Nomenclature . . .) .

Specimens examined.—ARKANSAS. *Benton Co.:* Hickory Creek, 6½ mi. NE Springdale, 1 (UA). *Fulton Co.:* T.20N, R.5W, Sec. 16, 1 (ASUZC). *Madison Co.:* 4 mi. N Fredericktown on E Hwy., 1 (ASUZC); 5½ mi. SW Fredericktown on Hwy. 80, 1 (ASUZC). *Marion Co.:* 13.9 mi. N Summit, 1 (ASUZC). *Stone Co.:* T.15N, R.11W, Sec. 5, 1 (ASUZC); Fiftysix (T.15N, R.12W, NW ¼ Sec. 12), 1 (ASUZC); 5 mi. S Fiftysix, 1 (ASUZC). *Washington Co.:* Fayetteville, 2 (UA); Winslow, 1 (UA); 2 mi. S Winslow, 1 (UA).

KANSAS. *Allen Co.:* no particular locality, 1 (KU); Moran, 3 (KU). *Anderson Co.:* 7 mi. S Garnett, 1 (KU); 1 mi. N Welda, 1 (KU). *Atchison Co.:* 1.8 mi. N Atchison, 1 (KU); 1½ mi. S Muscotah, 7 (KU). *Bourbon Co.:* 10 mi. S, 8 mi. W Fort Scott P.O., 2 (PSK); 6 mi. SW Uniontown, 1 (PSK). *Brown Co.:* Brown County Lake, 1 (MHP); 7 mi. N, ½ mi. E Hiawatha, 1 (KU); 3 mi. N Hiawatha, 1 (KU); 1 mi. S, 7 mi. E Hiawatha, 1 (MHP); 5 mi. S Hiawatha, 1 (KU); 1 mi. N Horton, 1 (KU). *Butler Co.:* 2 mi. N, 3/10 mi. W El Dorado, 1 (MHP). *Chase Co.:* 9 mi. E Lincolnville, 1 (KU); ¼ mi. N Matfield Green, 1 (KU). *Chautauqua Co.:* 1 mi. W Wauneta, 1 (KU). *Cherokee Co.:* no particular locality, 1 (KU); 3 mi. N Columbus, 2 mi. W Jct. 7 and 96, 1 (PSK); 1½ mi. S. Galena, 1 (KU); 1 mi. N Tri-State Monument, 1 (KU). *Cheyenne Co.:* 15 mi. N, 11½ mi. W St. Francis, 2 (KU); 1 mi. W St. Francis, 2 (KU). *Cloud Co.:* 3 mi. N, 2 mi. W Clyde, 1 (MHP); 4 mi. E Glasco, 1 (KU). *Coffey Co.:* Burlington, 1 (USNM); 2½ mi. S Burlington, 1 (KU). *Cowley Co.:* 6 mi. N, 12 mi. E Arkansas City, 1 (KU); 8.1 mi. E Arkansas City, 2 (KU); 3 mi. SE Arkansas City, 5 (KU); 2 mi. N, 3 mi. E Cameron City, 1 (MHP); 2 mi. S, ½ mi. W Udall, 1 (KU). *Crawford Co.:* no particular locality, 8 (PSK); 2 mi. N, 2 mi. E Arma, 1 (PSK); 1¼ mi. E Crawford County State Lake, 1 (PSK); Frontenac, 1 (PSK); Pittsburg, 5 (4 PSK, 1 UWSP); 2½ mi. E Pittsburg, 1 (PSK); 2 mi. S, 3 mi. E Pittsburg, 1 (PSK); 2½ mi. SW Pittsburg, 1 (PSK); 5 mi. S, 1 mi. W Pittsburg, 1 (PSK). *Dickinson Co.:* ½ mi. S Chapman, 1 (MHP); 2 mi. W Herington, 6 (MHP). *Doniphan Co.:* Geary, 1 (KU); ½ mi. N, ½ mi. W Severance, 1 (KU). *Douglas Co.:* no particular locality, 18 (KU); 1¼ mi. N Baldwin City, 1 (KU); 0.5 mi. S, 5.2 mi. W Clinton, 1 (KU); ½ mi. W Eudora, 2 (KU); 7 mi. NNE Lawrence, 2 (KU); 6 mi. NNE Lawrence, 1 (KU); 5 mi. N Lawrence, 2 (KU); 4.8 mi. N, 0.7 mi. E Lawrence, 1 (KU); 2.2 mi. N, 0.8 mi. E Lawrence, 2 (KU); 2 mi. N Lawrence, 1 (KU); 2 mi. N, 2 mi. E Lawrence, 2 (KU); 1½ mi. N, 1⅕ mi. E Lawrence, 12 (KU); 1½ mi. N, 1¾ mi. E Lawrence, 7 (3 KU, 4 MHP); 1 mi. N, 4 mi. W Lawrence, 1 (KU); ½ mi. N, 1 mi. E Lawrence, 1 (KU); 2½ mi. W Lawrence, 1 (KU); 1 mi. W Lawrence, 4 (KU); Lawrence, 25 (3 AMNH, 20 KU, 2 USNM); 0.8 mi. S, 2.5 mi. W Lawrence, 1 (KU); 3.9 mi. S, 2.6 mi. E Lawrence, 1 (KU); 5¾ mi. S, ¾ mi. W Lawrence, 1 (KU); 7 mi. SW Lawrence, 4 (KU); 7½ mi. SW Lawrence, 5 (KU); ½ mi. S, ½ mi. E Pleasant Grove, 1 (KU); Rock Creek, 1 (KU); 1 mi. S, 1¼ mi. W Vinland, 1 (KU). *Ellis Co.:* 1 mi. S, 6½ mi. W Antonino, 19 (MHP); Ellis, 1 (MHP); 16 mi. N, 1 mi. W Hays, 3 (MHP); 9 mi. N, 4 mi. W Hays (T.12S, R.19W, NE ¼ Sec. 14), 2 (MHP); 8½ mi. N, 4 mi. W Hays (T.12S, R.19W, SE ¼ Sec. 14), 1 (MHP); 5 mi. N, 3.4 mi. W Hays, 1 (MHP); 4 mi. N, ¼ mi. W Hays, 1 (MHP); 3½ mi. W Hays, 1 (KU); Hays, 2 (1 MHP, 1 USNM); ¾ mi. S, 3½ mi. W Hays, 1 (KU); 1 mi. S, 6 mi. W Hays, 1 (MHP); 1 mi. S, 2 mi. W Hays, 1 (MHP);

1½ mi. W Hays (T.14S, R.18W, NE ¼ Sec. 7), 1 (MHP); 2½ mi. SW Hays, 1 (MHP). *Geary Co.:* 5 mi. S Grandview Plaza, 1 (MHP). *Graham Co.:* Antelope Lake, 1 mi. N, 14 mi. W Hill City, 2 (MHP); 2 mi. N, 2 mi. W Morland, 1 (MHP). *Greenwood Co.:* Hamilton, 34 (3 AMNH, 2 MMNH, 2 CM, 22 KU, 5 UMMZ); ½ mi. E Hamilton, 2 (KU); ¼ mi. S Hamilton, 2 (KU); ¼ mi. SE Hamilton, 1 (KU); ½ mi. SW Hamilton, 1 (AMNH); ½ mi. S Hamilton, 5 (KU); ½ mi. SE Hamilton, 2 (KU); 3.4 mi. S Hamilton, 1 (KU); 1 mi. S Hamilton, 2 (KU); 1½ mi. S Hamilton, 5 (KU); 8½ mi. SW Toronto, 1 (KU). *Harper Co.:* 1½ mi. S, 6 mi. W Anthony, 1 (MHP). *Harvey Co.:* ½ mi. N, 1 mi. E Halstead, 1 (KU); Newton, 1 (KU). *Jackson Co.:* ½ mi. N Holton, 1 (KU); Holton, 2 (1 AMNH, 1 KU); 5½ mi. E Holton, 2 (KU). *Jefferson Co.:* 5 mi. N, 2 mi. E Lawrence (*in* Douglas Co.), 1(KU); 4 mi. N, 2 mi. E Lawrence (*in* Douglas Co.), 1 (KU). *Jewell Co.:* 2 mi. N Lovewell (T.2S, R.6W, Sec. 10), 3 (MHP); 2 mi. N, 1 mi. E Lovewell (T.2S, R.6W, Sec. 11), 1 (MHP); 2 mi. N, 2 mi. E Lovewell (T.2S, R.6W, Sec. 12), 5 (MHP); 1 mi. N Lovewell (T.2S, R.6W, Sec. 15), 2 (MHP); 1 mi. S, 1 mi. W Lovewell (T.2S, R.6W, Sec. 28), 4 (MHP); 1 mi. S, 1 mi. E Lovewell (T.2S, R.6W, Sec. 26), 1 (MHP); 2 mi. S, 2 mi. W Lovewell (T.2S, R.6W, Sec. 32), 1 (MHP); 2 mi. S, 1 mi. W Lovewell (T.2S, R.6W, Sec. 33), 3 (MHP); 2 mi. S, 2 mi. E Lovewell (T.2S, R.6W, Sec. 16), 1 (MHP); 3 mi. N, 3 mi. W Mankato (T.2S, R.7W, Sec. 31), 1 (MHP); 3 mi. N, 1 mi. W Mankato (T.2S, R.7W, Sec. 33), 1 (MHP); 4 mi. N, ½ mi. W Montrose (T.2S, R.7W, Sec. 34), 3 (MHP); 2½ mi. S, 1½ mi. W North Branch (T.1S, R.10W, Sec. 25), 1 (MHP); 4 mi. N, 1 mi. E Webber (T.1S, R.6W, Sec. 5), 3 (MHP); 4 mi. N, 3 mi. E Webber (T.1S, R.6W, Sec. 3), 1 (MHP); 3 mi. N, 5 mi. E Webber (T.1S, R.6W, Sec. 12), 1 (MHP); 2 mi. N, 4 mi. W Webber (T.1S, R.7W, Sec. 16), 4 (MHP); 2 mi. N, 2 mi. E Webber (T.1S, R.6W, Sec. 16), 2 (MHP); 2 mi. N, 5 mi. E Webber (T.1S, R.6W, Sec. 13), 1 (MHP); 1 mi. N, 6 mi. W Webber (T.1S, R.7W, Sec. 19), 3 (MHP); 1 mi. N, 2 mi. W Webber (T.1S, R.7W, Sec. 23), 2 (MHP); 2 mi. E Webber (T1S, R.6W, Sec. 28), 1 (MHP); 4 mi. E Webber (T.1S, R.6W, Sec. 26), 1 (MHP); 1 mi. S, 5 mi. W Webber (T.1S, R.7W, Sec. 32), 3 (MHP); 1 mi. S, 2 mi. W Webber (T.1S, R.7W, Sec. 35), 3 (MHP); 1 mi. S, 1 mi. W Webber (T.1S, R7W, Sec. 36), 3 (MHP); 2 mi. S, 5 mi. W Webber (T.2S, R.7W, Sec. 5), 1 (MHP); 2 mi. S, 4 mi. W Webber (T.2S, R.7W, Sec. 4), 1 (MHP); 2 mi. S, 2 mi. E Webber (T.2S, R.6W, Sec. 4), 23 (MHP); 2 mi. S, 4 mi. E Webber (T.2S, R.6W, Sec. 2), 5 (MHP); 3 mi. S, 5 mi. W Webber (T.2S, R.7W, Sec. 8), 1 (MHP); 3 mi. S, 3 mi. W Webber (T.2S, R.7W, Sec. 10), 1 (MHP); 3 mi. S Webber (T.2S, R.6W, Sec. 7), 6 (MHP); 3 mi. S, 1 mi. E Webber (T.2S, R.6W, Sec. 8), 3 (MHP). *Kiowa Co.:* 6 mi. S, 2 mi. E Haviland, 9 (MHP). *Labette Co.:* Oswego, 1 (PSK); 2 mi. SW Parsons, 1 (PSK); 3 mi. S, 2 mi. E Parsons, 1 (PSK). *Leavenworth Co.:* no particular locality, 1 (KU); 1 mi. N, 4 mi. W Bonner Springs, 2 (KU). *Linn Co.:* ½ mi. N, 4 mi. W Prescott, 1 (KU). *Lyon Co.:* Emporia, 1 (UMMZ). *Marion Co.:* 1 mi. N, ½ mi. E Lincolnville, 1 (KU). *Marshall Co.:* Lake Idlewild, 1½ mi. N, ½ mi. E Waterville, 1 (KU); 2 mi. N, ½ mi. E Oketo, 5 (MHP); 1½ mi. N, ½ mi. W Oketo, 1 (MHP); 1½ mi. N Oketo, 2 (MHP); 1 mi. N Oketo, 3 (MHP); 1 mi. W Oketo, 1 (MHP); 1 mi. N Waterville, 1 (KU); ½ mi. NW Waterville, 3 (KU); 1 mi. E Waterville, 4 (KU); ½ mi. SW Waterville, 2 (KU). *McPherson Co.:* ½ mi. S, ½ mi. W Lindsborg, 1 (KU); 1 mi. S, ½ mi. W Lindsborg, 2 (KU). *Miami Co.:* 11 mi. SSE Paola, 2 (KU). *Montgomery Co.:* Coffeyville, 1 (OU); Independence, 1 (KU). *Morris Co.:* 4⅛ mi. S, 5½ mi. W Council Grove, 1 (KU). *Nemaha Co.:* 6 mi. N Sabetha, 1 (KU); 2½ mi. S Sabetha, 2 (KU); 3½ mi. S, ¾ mi. E Sabetha, 3 (KU). *Norton Co.:* 1 mi. SW Norton, 1 (KU). *Osage Co.:* 1¾ mi. S, 1$^{7}/_{10}$ mi. E Berryton, 1 (KU); 8 mi. N, 9 mi. E Osage City, 10 (MHP). *Osborne Co.:* 2½ mi. S, 6 mi. E Covert, 1 (MHP). *Phillips Co.:* 1 mi. S, 1 mi. W Agra, 1 (MHP); ¾ mi. S, ¼ mi. W Kirwin, 1 (MHP); 1 mi. S Kirwin, 1 (MHP); Catfish Cove, 3¾ mi. S, 3 mi. W Kirwin, 2 (MHP); 4½ mi. S, 3¼ mi. W Kirwin, 1 (MHP); 5 mi. S, 4 mi. W Kirwin, 1 (MHP). *Pottawatomie Co.:* Manhattan, 2 (USNM);

Onaga, 2 (USNM); 5 mi. N Westmoreland, 2 (MHP). *Pratt Co.:* 4 mi. N, ¼ mi. E Pratt, 1 (KU). *Rawlins Co.:* Atwood Lake, Atwood, 3 (KU); 2 mi. S Ludell, 1 (KU). *Republic Co.:* Rydal, 1 (KU). *Rice Co.:* 5 mi. W Sterling, 1 (MHP). *Riley Co.:* Fort Riley, 1 (USNM); Manhattan, 15 (13 AMNH, 1 KU, 1 UMMZ); 1 mi. E Manhattan, 2 (UCONN); 6 mi. E Manhattan, 1 (UCONN). *Rooks Co.:* 3 mi. S, 3 mi. W Stockton, 5 (MHP). *Rush Co.:* 1/16 mi. E LaCrosse, 2 (MHP). *Russell Co.:* 5 mi. N, 1 mi. E Dorrance (T.13S, R.11W, NE ¼ Sec. 17), 2 (MHP); 4 mi. N, 4 mi. E Dorrance (T.13S, R.11W, SW ¼ Sec. 23), 2 (MHP); 3 mi. N, 4 mi. E Dorrance (T.13S, R.11W, NE ¼ Sec. 26), 3 (MHP); 6½ mi. S, ½ mi. E Lucas (T.12S, R.11W, NE ¼ Sec. 34), 1 (MHP); 8½ mi. S, ½ mi. E Lucas (T.13S, R.11W, NE ¼ Sec. 10), 1 (MHP). *Shawnee Co.:* 1 mi. N, 3 mi. W Auburn, 5 (KU); 4½ mi. N, 3 mi. W Topeka, 1 (KU); 1.6 mi. N, 3 mi. W Wakarusa, 1 (KU). *Sheridan Co.:* 13 mi. E Hoxie, 4 (MHP); Saline River, 15 mi. S, 15 mi. E Hoxie, 17 (KU). *Smith Co.:* ½ mi. N, 1 mi. E Smith Center, 1 (MHP); 2 mi. E Smith Center, 2 (KU). *Stafford Co.:* 5½ mi. N, 8 mi. E Hudson (T.21S, R.11W, NW ¼ Sec. 34), 1 (MHP); 1 mi. S, 4 mi. E Hudson, 1 (MHP). *Sumner Co.:* ¼ mi. S, 3 mi. E Oxford, 1 (KU). *Trego Co.:* ½ mi. N, 3¼ mi. W Ellis (*in* Ellis Co.), 2 (MHP); ½ mi. N, 3 mi. W Ellis (*in* Ellis Co.), 3 (MHP); 2½ mi. W Ellis (*in* Ellis Co.), 1 (MHP); 14½ mi. S, 5½ mi. E Ogallah, 1 (MPH). *Woodson Co.:* Neosho Falls, 3 (2 KU, 1 USNM); 2½ mi. N Toronto, 1 (KU); 2 mi. S Toronto, 1 (KU).

Louisiana. *Caddo Par.:* 5 mi. NE Greenwood, 2 (LSU); 3.75 mi. N, 0.75 mi. W Greenwood, 15 (LSU).

Missouri. *Camden Co.:* Hahatonka, 2 (UMMZ). *Cape Girardeau Co.:* Cape Girardeau, 3 (MOU). *Douglas Co.:* T.27N, R.13W, Sec. 1, 1 (MOU). *Franklin Co.:* Merramec State Park, 2 (MOU); Washington, 1 (MOU). *Greene Co.:* Springfield, 4 (MOU). *Jefferson Co.:* Kimmswick, 1 (USNM). *Morgan Co.:* Gravois Mills, 1 (MOU). *St. Clair Co.:* no particular locality, 1 (MOU). *Ste. Genevieve Co.:* Sprott, 1 (MOU). *Wright Co.:* Mountain Grove, 1 (MOU).

Oklahoma. *Atoka Co.:* 20 mi. SW Atoka, 2 (OU). *Cleveland Co.:* Norman, 7 (6 KU, 1 OU); 2 mi. S, 1 mi. W Norman, 1 (OSU); 4 mi. S Norman, 1 (OU); 5 mi. S Norman, 1 (OU). *Comanche Co.:* Camp Bolder, Wichita Mts. Refuge, 1 (OSU). *Creek Co.:* Sapulpa, 3 (KU). *Garvin Co.:* 3 mi. N, 2 mi. W (by road) Davis (*in* Murray Co.) on I-35, 1 (MHP). *Kay Co.:* mouth Salt Fork River, 1 (OSU). *Logan Co.:* T.16N, R.4W, Sec. 11, 1 (OU). *McClain Co.:* 8 mi. W Norman (*in* Cleveland Co.), 2 (PSK). *Murray Co.:* 1.3 mi. S, 2.2 mi. W (by road) Davis, 4 (MHP); 5.7 mi. S, 2.3 mi. W (by road) Davis, 1 (MHP); Platt National Park, 5 (KU); Sulphur, near Travertine Creek, 1 (OSU). *Noble Co.:* 1 mi. E Jct. Hwy. 177 and Hwy. 15, 1 (OU). *Osage Co.:* Adams Ranch, 12 mi. N, 5 mi. E Shidler, 40 (MMNH); "3 mi. W Indian Hills Bridge, 3 mi. E Arkansas River Bridge at Ponca," 1 (OSU). *Ottawa Co.:* 1½ mi. S, 1½ mi. W Picher, 1 (OSU). *Payne Co.:* no particular locality, 2 (OSU); T.18N, R.2E, Sec. 2, 1 (OSU); T.19N, R.1E, SE ¼ Sec. 18, 1 (OSU); Boomer Lake, 1 mi. N Stillwater, 1 (OSU); Hwy. 177, 3 mi. N Hwy. 51, 1 (OSU); 1 mi. N Jct. Hwy. 51 and Hwy. 81, 1 (OSU); Lake Carl Blackwell, 9 mi. W Stillwater, 7 (OSU); Lake Carl Blackwell, 7 mi. W Stillwater, 1 (OSU); 6 mi. NE Stillwater, 1 (OSU); 3 mi. N, 5 mi. W Stillwater, 1 (OSU); Hwy. 177, 3 mi. N Hwy. 51 (3 mi. N Stillwater), 1 (OSU); 2 mi. N, ½ mi. E Stillwater, 1 (OSU); 1 mi. N Jct. Hwy. 51 and Hwy. 81, 1 (OSU); ⅛ mi. N, 2¼ mi. W Stillwater, 1 (OSU); 6 mi. W Stillwater, 1 (OSU); 3 mi. W Stillwater, 2 (OSU); Stillwater, 4 (OSU); 2 mi. E Stillwater, 1 (OSU); ½ mi. S, 7 mi. W Stillwater, 1 (OSU); 2 mi. S Stillwater, 1 (OSU); 2 mi. S, ½ mi. E Stillwater, 1 (OSU); 2½ mi. S Stillwater, 3 (OSU); 3 mi. S, 4 mi. W Stillwater, 1 (OSU); 3 mi. S Stillwater, 1 (OSU); 2 mi. W Yale, 1 (OSU). *Pittsburg Co.:* 9 mi. SE Eufaula, 1 (OU). *Pottawatomie Co.:* Tecumseh, 2 (KU). *Rogers Co.:* 7 mi. N Claremore, 1 (OSU). *Tulsa Co.:* Mohawk Park, 3 (UMMZ); 7 mi. S, 4 mi. E Tulsa, 1 (OU); West Rim Sequoyah Lake, 1 (OSU). *Washington Co.:* Bartlesville, 1 (OSU).

Blarina hylophaga plumbea Davis

Blarina brevicauda plumbea Davis, J. Mamm., 22:317, 1941; Hall and Kelson, The mammals of North America, 1:54, 1959; Hall, The mammals of North America, 1:56, 1981.

Blarina carolinensis plumbea Schmidly and Brown, Southwestern Nat., 24:45, 1979.

Holotype.—Female, adult; skin and skull; TCWC 1541, Texas Cooperative Wildlife Collection; from ½ mi. W Marano Mill, Aransas National Wildlife Refuge, Aransas Co., Texas; collected 31 January 1941, by J. O. Stevenson, original number X26.

Diagnosis.—This is an allopatric population, separated from other populations of *Blarina hylophaga* by an area unoccupied by short-tailed shrews, and then by populations of *Blarina carolinensis*.

Comparisons.—*Blarina hylophaga plumbea* is morphologically indistinguishable from southern populations of *B. h. hylophaga*, but is smaller than material from Kansas.

Range.—Known only from Aransas National Wildlife Refuge, Aransas Co., Texas.

Remarks.—In this study, this population is placed consistently with samples of *Blarina hylophaga* rather than with the nearer populations of *B. carolinensis*, corroborating the results of Schmidly and Brown (1979), who found this population significantly different from other populations of *Blarina* in Texas. As this population has never been karyotyped, and as it is isolated from the range of all species of *Blarina*, it should be retained provisionally as a distinct subspecies.

Specimens examined.—TEXAS. *Aransas Co.:* Aransas Wildlife Refuge, 22 mi. S Austwell (*in* Refugio Co.), 7 (TCWC).

ADDITIONAL SPECIMENS EXAMINED

Blarina carolinensis

ALABAMA. *Cullman Co.:* Ardell, 8 (USNM). *Etowah Co.:* Attalla, 1 (USNM). *Hale Co.:* Greensboro, 1 (USNM). *Russell Co.:* Seale, 1 (USNM). *Sumter Co.:* York, 2 (USNM).

ARKANSAS. *Ashley Co.:* T.19S, R.8W, SW ¼ SE ¼ Sec. 14, 1 (UAM); ½ mi. S Crossett on Hwy. 133, 1 (ASUZC); Lucas Pond near Crossett, 1 (UAM); 8 mi. NE Hamburg, 5 (UA). *Bradley Co.:* 10 mi. NW Warren, 1 (TTU); 1 mi. E Warren, 1 (ASUZC). *Clay Co.:* T.19N, R.8E, Sec. 7, 1 (ASUZC); 2 mi. E Boydsville on Hwy. 90, 1 (ASUZC); 3 mi. N Pollard, 1 (ASUZC); 3 mi. N Rector, 1 (ASUZC); ½ mi. S Rector on Hwy. 1, 1 (ASUZC); 2 mi. S Rector on Hwy. 1, 1 (ASUZC); 1 mi. S Reyno, 1 (ASUZC). *Craighead Co.:* no particular locality, 4 (ASUZC); T.12N, R.6W, Sec. 22, 1 (ASUZC); ½ mi. E Airport Road, 2 (ASUZC); Arkansas State University, 2 (ASUZC); S of Arkansas State University, 1 (ASUZC); 2 mi. SE Arkansas State University, 1 (ASUZC); Craighead Lake, 1 (ASUZC); 4 mi. N Jonesboro, 2 (ASUZC); 3 mi. NE Jonesboro, 1 (ASUZC); 3 mi. N Jonesboro, 1 (ASUZC); 2 mi. NE Jonesboro, 1 (ASUZC); 2 mi. N Jonesboro off Hwy. 141, 1 (ASUZC); 1 mi. N Jonesboro, 1 (ASUZC); Jonesboro, 5 (ASUZC); Jonesboro Airport, 5 (ASUZC); Lake City, 3 (USNM); 2 mi.

S Otwell, 1 (ASUZC); S of TV 8 Tower, 15 (ASUZC). *Crittendon Co.:* 1 mi. N Stavy on Hwy. 61, 1 (ASUZC). *Cross Co.:* 3 mi. S Birdeye on Hwy. 163, 4 (ASUZC); Cherry Valley, 33 (ASUZC); Village Creek State Park, 9 (ASUZC). *Drew Co.:* T.12S, R.7W, SW ¼ NE ¼ Sec. 35, 1 (UAM); T.12S, R.7W, Sec. 35, 2 (UAM); T.13S, R.7W, Sec. 2, 2 (UAM); T.13S, R.7W, Sec. 11, 1 (UAM); T.14S, R.6W, NW ¼ Sec. 4, 1 (UAM); Arkansas A&M, 2 (TTU); 2½ mi. S, 1¾ mi. W Monticello, University of Arkansas at Monticello campus, 5 (UAM); "3.3 mi. on Old Hamburg Road," 1 (TTU); Wilson Saw Mill, ¼ mi. E Harman, 1 (TTU). *Garland Co.:* no particular locality, 2 (USNM). *Greene Co.:* no particular locality, 1 (ASUZC); ASU Fishponds, Walcott, 25 (ASUZC); across from Beech Grove Cemetery, on Hwy. 141, 1 (ASUZC); 5 mi. N Paragould on Hwy. 135, 1 (ASUZC); 4.5 mi. N Paragould on Hwy. 135, 1 (ASUZC); 3.5 mi. W Rector, 1 (ASUZC). *Howard Co.:* 1.5 mi. S, 9 mi. W Umpire, 2 (UA). *Independence Co.:* T.12N, R.4W, Sec. 3, 1 (ASUZC); T.12N, R.4W, Sec. 4, 1 (ASUZC); T.13N, R.6W, Sec. 8, 1 (ASUZC). *Jackson Co.:* no particular locality, 1 (ASUZC); ½ mi. N mouth of Village Creek, 1 (ASUZC); Village Creek, SE of Swifton, 1 (ASUZC). *Jefferson Co.:* Pine Bluff, 9 (UWSP); 1.5 mi. NW Whitehall, 1 (UALR). *Lawrence Co.:* 5.4 mi. E Hoxie on Hwy. 63, 2 (ASUZC); 4 mi. W Lawrence, Craighead Co. line on Hwy. 230, 2 (ASUZC); ⅛ mi. E Portia on Hwy. 63, 1 (ASUZC); ⅕ mi. SE Portia on Hwy. 63, 1 (ASUZC). *Lee Co.:* 2.5 mi. N Felton on Hwy. 1, 1 (ASUZC). *Little River Co.:* Millwood State Park, 1 (UALR). *Mississippi Co.:* 3 mi. N, 2 mi. E Dell, 1 (ASUZC); ½ mi. S Manila on Hwy. 18, 1 (ASUZC); 3 mi. W Manila on Hwy. 18, 22 (ASUZC); 3 mi. W Manila on Hwy. 39, 1 (ASUZC); 3 mi. W Manila, 4 (ASUZC). *Pike Co.:* Delight, 1 (USNM). *Poinsett Co.:* T.12N, R.3E, Sec. 36, 1 (ASUZC); ½ mi. S Craighead Co. line on Hwy. 39, 1 (ASUZC); S Craighead Co. on Hwy. 39, 1 (ASUZC); Harrisburg, 2 (ASUZC); 6 mi. N Weiner on Hwy. 39, 1 (ASUZC). *Polk Co.:* Rock Creek, 3½ mi. W Mena, 2 (UA). *Prairie Co.:* 4 mi. E Des Arc, 1 (ASUZC); 8 mi. S Des Arc, 1 (UALR); ⅕ mi. W Little Dixie, 1 (ASUZC). *Pulaski Co.:* 1 mi. N Jacksonville, 2 (UALR); Jacksonville, 2 (UALR); 1 mi. SW Jacksonville, 1 (UALR); 1 mi. S Jacksonville, 1 (UALR); 2 mi. SW Jacksonville, 1 (UALR); 9 mi. N Little Rock, 1 (UA); 10 mi. SW Little Rock, 1 (UALR). *Randolph Co.:* 1 mi. NE Pocahontas, 1 (ASUZC); 1 mi. W Pocahontas, 1 (UA). *Saline Co.:* Col. Glen Rd., 10 mi. W I-430, 1 (UALR). *Union Co.:* Eldorado, 2 (UA). *White Co.:* Beebe, 1 (USNM). *Woodruff Co.:* 4 mi. S Fair Oaks on Hwy. 39, 1 (ASUZC).

GEORGIA. *Dodge Co.:* McRea, 3 (ISU). *Earl Co.:* 5 mi. S Blakeley, 1 (USNM). *Grady Co.:* Beachton, 4 (USNM). *Liberty Co.:* St. Catherine's Island, 2 (AMNH). *Thomas Co.:* Boston, 1 (USNM).

LOUISIANA. *Bienville Par.:* 6 mi. N Mt. Olive, Dugdemono River, 2 (LSU). *Caddo Par.:* 3 mi. S, 2 mi. W Blanchard, 8 (LSU). *Calcasieu Par.:* 7 mi. W Lake Charles, ½ mi. SW Maplewood, 1 (LSU); 2 mi. SW Sulphur, 1 (LSU). *Evangeline Par.:* 4 mi. NNW Ville Platte, Rte. 373, 1 (LSU). *Grant Par.:* 2 mi. SW Montgomery Pond on Wardlow Estate, 1 (LSU). *Lincoln Par.:* Ruston, 2 (LATU); Tech Farm, 1 mi. S Ruston, 10 (LATU). *Sabine Par.:* Bayou Nagreet River, 1 (LSU). *Vernon Par.:* ¾ mi. E Simpson, 1 (LSU). *West Baton Rouge Par.:* 6 mi. W Port Allen, on I-10, 1 (LSU); 7 mi. W Mississippi River on I-10, 1 (LSU). *Winn Par.:* 1 mi. N Winnfield, 1 (LATU).

OKLAHOMA. *McCurtain Co.:* Flat Swamp, 6 mi. SE (by road) Eagletown, 1 (OSU).

MISSISSIPPI. *Adams Co.:* Washington, 8 (USNM). *Harrison Co.:* 3 mi. N Biloxi, 2 (AMNH); Biloxi, 2 (USNM). *Marshall Co.:* Pleasant, 1 (OU); Wall Doxey State Park, 2 (KU). *Scott Co.:* 3.5 mi. E Morton Corp. Limit, 6 (KU). *Tishomingo Co.:* 2 mi. S, 2 mi. E Tishomingo, 2 (KU). *Washington Co.:* 4½ mi. W Hollandale, 1 (KU).

MISSOURI. *Butler Co.:* 3 mi. W (by Hwy. 60) Ash Hill, 1 (MHP); Poplar Bluff, 1 (MOU). *Dunklin Co.:* Kennett, 1 (MOU). *St. Louis Co.:* St. Louis, 2 (USNM). *Stoddard Co.:* Mingo National Wildlife Refuge, 1 (MOU).

SOUTH CAROLINA. *Charleston Co.:* Merrymede, St. Andrew's Parish, 1 (KU); Porcher's Bluff, 3 (ROM). *Georgetown Co.:* Georgetown, 1 (USNM); Plantersville, 2 (USNM).

Tennessee. *Decatur Co.:* Perryville, 1 (OU). *Madison Co.:* Jackson, 1 (ROM). *Shelby Co.:* 13 mi. N Memphis, 1 (KU).

Texas. *Hardin Co.:* 0.8 mi. N, 2.6 mi. E Saratoga, 12 (TCWC); Saratoga, Lance Rosien Recreational Park, 3 (TCWC); 8 mi. NE Sour Lake, 1 (USNM); 7 mi. NE Sour Lake, 1 (USNM); 1.8 mi. S, 2.9 mi. E Village Mills, 4 (TCWC); 2 mi. S, 3¼ mi. E Village Mills, 1 (TCWC). *Nacogdoches Co.:* 1 mi. E Nacogdoches, 1 (SFASU); Banita Creek, Nacogdoches, 1 (SFASU); La Nana Creek, Nacogdoches, 2 (SFASU); Nacogdoches, 2 (SFASU); 7 mi. SE Nacogdoches, 1 (SFASU); Stephen F. Austin College Farm, 1 (SFASU). *Newton Co.:* 10.5 mi. N Burkeville, 1 (TCWC); 10.4 mi. N Burkeville, 1 (TCWC); 10 mi. N Burkeville, 4 (TCWC); Burkeville, 13 (TCWC). *Polk Co.:* 1.4 mi. N, 2.2 mi. W Dallardsville (30°38′56″N, 94°40′13″W), 3 (TCWC). *San Jacinto Co.:* Shepherd, 1 (TCWC). *Tyler Co.:* 1.7 mi. N, 1.6 mi. W Spurger, 3 (TCWC); 3.1 mi. N, 2.5 mi. W Spurger, 8 (TCWC); Town Bluff Reservoir, 15 mi. E Woodville, 1 (TTU); 4.2 mi. S, 1.6 mi. W Warren, 6 (TCWC); 4.3 mi. S, 1.4 mi. W Warren, 4 (TCWC); 4.3 mi. S, 1.1 mi. W Warren, 1 (TCWC); 4.5 mi. S, 0.5 mi. W Warren, 2 (TCWC); 4.8 mi. S, 0.7 mi. W Warren, 2 (TCWC). *Walker Co.:* Huntsville, 1 (TCWC); 2 mi. E Huntsville, 1 (TCWC).

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