

MICROTUS PENNSYLVANICUS
(RODENTIA: MURIDAE) IN FLORIDA:
A PLEISTOCENE RELICT IN A COASTAL SALTMARSH

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ABSTRACT: *Microtus pennsylvanicus* exists as a disjunct relictual population in a tidal salt marsh located on Waccasassa Bay on the Florida Gulf coast. This form, described as a new subspecies, inhabits *Distichlis* flats and other areas of low vegetation in the salt marsh, while *Oryzomys* is more common in areas of *Juncus*. The saltmarsh vole was less abundant than *Oryzomys* during the study period. In comparison with other forms of *Microtus pennsylvanicus*, the saltmarsh vole is larger in body size, darker in coloration, and has a larger hind foot. The current distribution of the new subspecies of *Microtus* appears to be relictual from a more widespread range in the Gulf Coastal Plain during the last 10,000 years. The range of the vole presumably was restricted by changes in vegetation and rising sea levels during the last 8000 years. The vole is in a grassland habitat isolated by unsuitable forest habitat and is 500 km south of the nearest population of *M. p. pennsylvanicus* in Georgia. Analysis of blood proteins indicates a lack of genetic diversity, a condition that prevails in other insular populations of *Microtus pennsylvanicus*. The saltmarsh vole survives in low numbers under very harsh ecological conditions and is vulnerable to extirpation by natural disasters associated with wind and water.

SUMARIO: *Microtus pennsylvanicus* existe como una población relictica disgregada en el pantano salino de marea ubicado en la Bahía de Waccasassa, en la costa del Golfo de Florida. Esta forma, descrita como una nueva subespecie, habita pastizales de *Distichlis* y otras áreas de vegetación baja en el pantano salino, mientras que *Oryzomys* es más común en áreas de *Juncus*. El ratón del pantano salino fue menos abundante que *Oryzomys* durante el periodo de estudio. En comparación a otras formas de *Microtus pennsylvanicus*, el ratón del pantano salino es de cuerpo más grande, coloración más oscura y pata posterior más grande. La presente distribución de la nueva subespecie de *Microtus* parece ser el relictico de una población de ratones distribuida en área más amplia en las planicies costeras del Golfo durante los últimos 10,000 años. El área de distribución de éste ratón presumiblemente ha sido restringida por cambios en la vegetación y niveles ascendentes del mar durante los últimos 8,000 años. Este ratón se encuentra en un habitat de pastizal aislado por bosque no apropiado como habitat y situado a 500 km. al Sur de la población más cercana de *M. p. pennsylvanicus* en Georgia. El análisis de proteínas de la sangre indica la falta de diversidad genética, condición que prevalece en otras poblaciones insulares de *Microtus pennsylvanicus*. El ratón del pantano salino sobrevive en limitados números bajo condiciones ecológicas muy desfavorables y es vulnerable a ser eliminado por desastres naturales asociados a vientos y agua.

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INTRODUCTION

While studying the seaside sparrow *Ammodramus maritima* in a coastal salt marsh on the west coast of Florida, we discovered the presence of *Microtus pennsylvanicus*, a small mammal previously unrecorded as an extant form in Florida. The current known range of the meadow vole in eastern North America extends as far south as Newton County in the mid-Piedmont area of Georgia, where the subspecies *M. p. pennsylvanicus* is found in wet meadows (the preferred habitat) and dry upland fields (Odum 1948, Golley 1962). Along the Atlantic coastal plain it occurs as far south as Charleston, South Carolina (Hall 1981). The Florida population of *Microtus* is 500 km south of both the above populations in the eastern United States. Recent analyses of the mammals of the lower coastal plain (Okefenokee Swamp) of Georgia did not reveal the presence of *Microtus pennsylvanicus* (Laerm et al. 1980), and the species has not been reported in Florida in recent times in spite of a long history of mammal surveys beginning in the late nineteenth century. The meadow vole is known to occur in coastal saltmarsh habitats in several parts of its range (Hall 1981, Strickland, pers. comm., Wetzel, pers. comm.) It is more frequently found in Hudsonian, Canadian, and Upper Austral life zones (Martin 1968). Near the southern limits of its range the meadow vole appears to be restricted to the lower Austral zone in Georgia and the upper Austral zone as a disjunct western population in the state of Chihuahua, Mexico (Anderson 1961, Bradley and Cockrum 1968, Anderson and Hubbard 1971). The ecological factors that limit the southern distribution of *Microtus pennsylvanicus* are unknown; but Martin (1968) speculated that they were related to temperature.

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MATERIALS AND METHODS

Animals were trapped with Sherman live traps. Two traps were set at each station; one on the ground and one up in the vegetation. To determine the comparative number of rodents on the study area in 1980 we operated 297 traps during a six-night period (March 5, 6, 9, 16, 17, 24). To make the trap array conform to the shape of a peninsula, the grid was distorted so that the traps on the E-W grid lines were at 12.5 m intervals, while on the N-S lines they were placed at 25 m intervals. The size of the trapping area was 3.75 ha. Traps were prebaited for three days and thereafter were set at twilight and checked at dawn. Subsequent trapping periods in the area were carried out in April, May, July, September, and November, 1980, and January, February, and April, 1981. For estimates of small mammal densities from mark-recapture data we employed Jolly's stochastic model (Jolly 1965).

Vegetation samples were taken following the methods of Wiens (1969). For habitat analysis we randomly placed a 1 m² quadrant along 18 randomly located transects, each 71 m long. The corners of this square served as subpoints at which we vertically positioned a thin metal rod. We tallied the number of contacts that vegetation made with the rod. From this information we were able to determine the numerically dominant vegetation at each random subpoint. In addition, we determined the dominant cover type at each trapping station by the same method.

Microtus were tagged with ear tags, sexed, weighed, and released. Six adult specimens were collected for systematic analysis and are now in the collections of the Florida State Museum. Because of the apparent small size of the population, only six specimens were collected in an effort to insure that a breeding population survived in the area.

For blood protein analysis, blood was collected in the field from the suborbital canthal sinus of 14 individuals that were subsequently released. Hemolysate and serum samples were prepared according to the methods of Selander et al. (1971). Horizontal starch gel electrophoresis was used to fractionate samples employing a 13% concentration of hydrolyzed starch (Sigma Chemical Company). Buffer systems were those described by Selander et al. (1971) with one exception, that used to fractionate albumins described by Jensen and Rasmussen (1971, 1972). Enzymes and nonenzymatic proteins were identified by the stains described by Selander et al. (1971).

For chromosomal studies voles were injected intraperitoneally with a 0.004% Velban (Eli Lilly and Company) solution. A cell suspension was obtained from the bone marrow of the hind limbs and processed according to the technique outlined by Lee (1969). A karyogram of mitotic chromosomes was constructed from a photomicrograph.

The specimens collected on the site were made into standard museum study skins and complete skeletons. For taxonomic analysis standard field measurements and ten additional measurements were taken following the format in Snyder (1954). In the analysis, only adult

animals were compared (Snyder's age groups 10-12). Males and females of the Florida population were grouped together in the analysis because of the small sample size. The Florida population was compared with 14 known adult specimens of *M. p. pennsylvanicus* from Georgia (sexes combined), which were borrowed from the Museum of Natural History, University of Georgia. A survey of major museums in the United States indicated that no other specimens of *Microtus* from Georgia were known. The Florida population was also compared with 14 specimens (sexes combined) of *M. p. nigrans* from a tidal salt marsh in Maryland, 20 specimens (sexes combined) of *M. p. pennsylvanicus* from western Connecticut, and 20 specimens (sexes combined) of *M. p. pennsylvanicus* from a tidal salt marsh in eastern Connecticut.

Other comparisons in the analysis were based on published measurements of other forms of *Microtus pennsylvanicus*. In the case of *M. p. pennsylvanicus* from Pennsylvania (Snyder 1954), only data on males were available for comparison. In this case statistical comparisons are significant only for characters shown by Snyder to be independent of sex. It was not possible to control for the influence of the season of collection on the means of the samples. Snyder (1954), however, demonstrated that in the populations of *M. p. pennsylvanicus* he studied there was no clear-cut relationship between the means and the date of the collection.

Dental variation was evaluated through the use of camera lucida drawings of tooth rows. These drawings were traced onto semi-transparent mylar sheets and superimposed for comparisons of symmetry and form. Patterns were then transferred into tabular form which enabled calculation of the normal pattern for a population as well as percent variation from the norm.

STUDY AREA

The study site is on Waccasassa Bay, an extension of the Gulf of Mexico, in Gulf Hammock, Levy County, Florida (Fig. 1). The marsh is bounded on the southwest by a creek, on the south by Waccasassa Bay, and inland by the extensive lowland hardwood forest characteristic of the upper west coast of Florida. The shoreline is gradual, dotted with numerous oyster bars and small islands and cut by many tidal creeks. The topography of the study site is flat, except for creeks up to 1 m deep. In our measurements, tides averaged 0.8 m and salinity 19.03 ± 1.09 (32 stations on 24 April). At low tide extensive mud banks, riddled with burrows of crabs (*Uca* and *Sesarma*), are exposed. Vegetation covers 94.1% of the study area, and tidal creeks cover 5.9%. Figure 2 is a photograph of the main study site at low tide. Vascular plant species, in order of percent relative cover, are: smooth cordgrass (*Spartina alterniflora*) 37.8%, black rush (*Juncus roemerianus*) 26.3%, seashore saltgrass (*Distichlis spicata*) 23.2%, perennial glasswort (*Salicornia virginica*) 8.1%, saltwort (*Batis maritima*) 3.2%, sea oxeye (*Borrhchia frutescens*) 1%, Virginia dropseed (*Sporobolus virginicus*) 1%, sea lavender (*Limonium carolinianum*) 1%, Christmas berry (*Lycium carolinianum*) 1%; key grass (*Monanthochloe littoralis*) 1%, saltmarsh aster (*Aster tenuifolius*) 1%, and wrack deposits 1%. The relative elevation of the major plant communities is indicated by water depths (cm) during spring flood tides, where greater water depths signify lower elevations: *S. alterniflora* (N = 11) 25.6 ± 7.2 , *J. roemerianus* (N = 11) 20.9 ± 5.3 , *B. maritima* (N = 3) 16.5 , *D. spicata* (N = 31) 15.3 ± 3.3 , and *S. virginica* (N = 6) 13.8 ± 1.2 .

Because the area is so low, flooding is a major factor on the study site. Extreme tides occur approximately twice a month and inundate the entire area. Unpredictable high water levels occur on the study site when a spring tide coincides with high southerly or westerly winds or rain. In the study area two such unpredictable floods occurred in 1979 and one in 1980. The effects of hurricanes are also of potential major importance. The National Oceanic and Atmospheric Administration (Fernald 1981) lists 21 major hurricanes in Florida between 1900 and 1975. Hurricane Alma in May 1970 passed directly over Levy County as it came ashore from the Gulf, and other hurricanes passed nearby in the Gulf of Mexico in 1966, 1972, and 1979 (Fernald 1981).

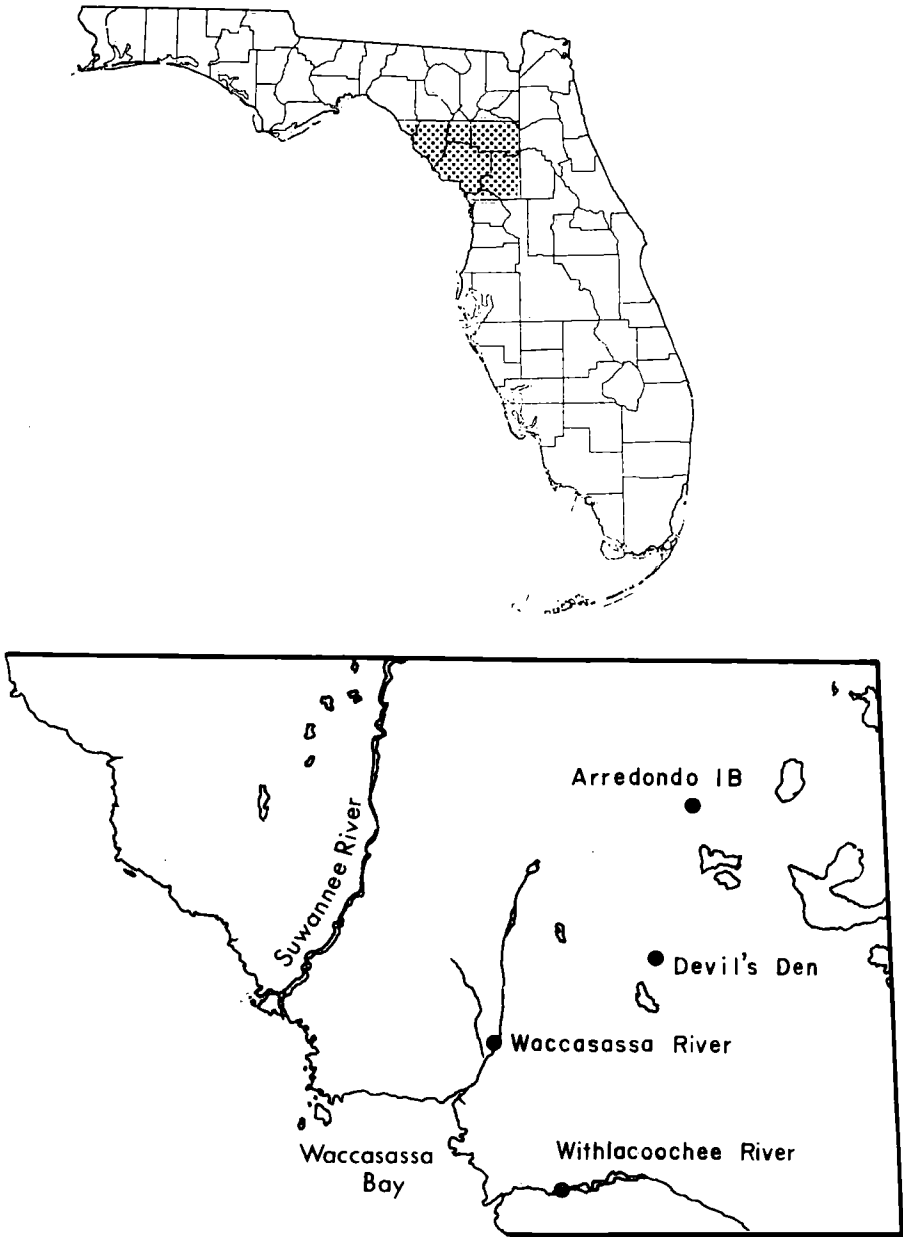


FIGURE 1. — Distribution of fossil localities of *Microtus pennsylvanicus* in Florida.



FIGURE 2.—Photograph taken on 5 September 1980 of the eastern site at low tide. In the foreground is suitable *Microtus* habitat containing *Spartina* and *Distichlis*. In the background is a band of *Juncus*. The inland coastal forest is on the horizon.

RESULTS

ECOLOGICAL OBSERVATIONS

Ecological data were collected in the Waccasassa Bay area between 22 and 26 June 1979 on a site (hereinafter referred to as the "western site") within 25 m of a maritime live oak forest. The site was abandoned because of disturbances by raccoons. Between 21 February and 15 June 1980 ecological data were collected on a nearby site farther into the marsh, which will be referred to as the "eastern site." In the combined areas of the western and eastern sites we trapped four species of rodents. In order of abundance these were *Oryzomys palustris*, *Microtus pennsylvanicus*, *Sigmodon hispidus*, and *Peromyscus gossypinus* (Table 1). The two brief study periods produced very different results, and these differences continued in the long-term general study on the western site. The western site was closer to drier areas, such as the scrub fringe and forest, and also contained more *Juncus* (black rush). In transect studies from the forest to the sea the scrub fringe was most frequented by *Sigmodon* and the forest by

TABLE 1. — Summary of small mammal trapping — Waccasassa Bay area.

	1979 ¹		1980 ²	
	New	All Captures	New	All Captures
<i>Oryzomys palustris</i>	55	69	53	211
<i>Sigmodon hispidus</i>	10	29	2	7
<i>Peromyscus gossypinus</i>	4	5	0	0
<i>Microtus pennsylvanicus</i>	0	0	9	36

¹Three days' trapping: 22, 24, 26 June

²Six days' trapping: 5, 6, 9, 16, 17, 24 March

Peromyscus. *Oryzomys* was more common in *Juncus* than in other areas of the salt marsh.

Table 2 summarizes the trapping success on both areas for all species and microhabitats. Our results differ markedly from data collected by Harris (1953) on the abundance of small mammals in a tidal salt marsh in Dorchester County, Maryland, where 121 *Microtus* were trapped in contrast to 78 *Oryzomys*. An analysis of the percentage of small mammals preyed upon by predators in the Maryland marshes yielded similar proportions: fox scats had 50% *Microtus*, 5% *Oryzomys*; barn owl pellets 72% *Microtus*, 27% *Oryzomys*; and marsh hawk pellets 73% *Microtus*, 15% *Oryzomys* (Harris 1953). Our analysis of seven marsh hawk pellets from the eastern site yielded 1 *Microtus*, 1 *Oryzomys*, and 5 passerines.

In our study in Florida the main plant associations sampled for mammals were *Juncus* (27% of trap placements) and *Distichlis* (52%). The location of these two microhabitats differs (Fig. 3; Post 1981). *Juncus* occupies slightly lower, but usually more landward sections of the marsh. The *Distichlis* flats are at higher elevations but closer to the bay. The average depth of spring tide floodwater in *Juncus* was 21 cm vs 15 cm in *Distichlis*. Comparing the number of *Oryzomys* captures in these two vegetation types (Table 3,) shows that significantly more *Oryzomys* were caught in *Juncus* than in *Distichlis* (X^2 corr., 1 df = 223; P .001). Because of limited data, no such comparison is possible for *Microtus*, but a comparison of the overall distribution of *Oryzomys* and *Microtus* in the four vegetation types shows that they differed significantly (Table 4). Proportionately more *Microtus* than *Oryzomys* were captured on the *Distichlis* flats. *Microtus*, unlike *Oryzomys*, avoids areas dominated by *S. alterniflora*. The *Microtus* were also caught less frequently in *Juncus* than were *Oryzomys*. That no *Microtus* were trapped in 1979 on the western site may be related to the dominance of *Juncus* and absence of *Distichlis* in that area.

In New York salt marshes, *Microtus* is more often associated with shorter grass (*Spartina patens*, *Distichlis spicata*) than with taller grass (*Phragmites*, *S. alterniflora*) (Post and Greenlaw, unpubl. data). In Mary-

Table 2. — Small mammal habitat selection and trapping success.

	1979 — Western Site				1980 — Eastern Site				Total				
	Traps Available	S. <i>hispidus</i>	P. <i>gossypinus</i>	O. <i>palustris</i>	Traps Available	S. <i>hispidus</i>	M. <i>pennsylvanicus</i>	O. <i>palustris</i>	Traps Available	S. <i>hispidus</i>	P. <i>gossypinus</i>	M. <i>pennsylvanicus</i>	O. <i>palustris</i>
<i>Juncus</i>	165	12	3	46	452	0	7	79	617	12	3	7	125
<i>S. alterniflora</i>	47	3	0	10	189	0	0	33	236	2	0	7	43
<i>Distichlis</i>	0				876	2	21	74	876	2	5	21	74
<i>Salicornia</i>	61	3	0	14	136	5	6	12	117	8	0	6	26
Wrack	0				46	0	2	3	46	0	0	2	3
Scrub edge	16	11	2	0					16	11	2	0	0
Unknown	8	1	0	0					8	1	0	0	0
TOTAL	297	29	5	70	1699	7	36	211	1996	36	5	36	271

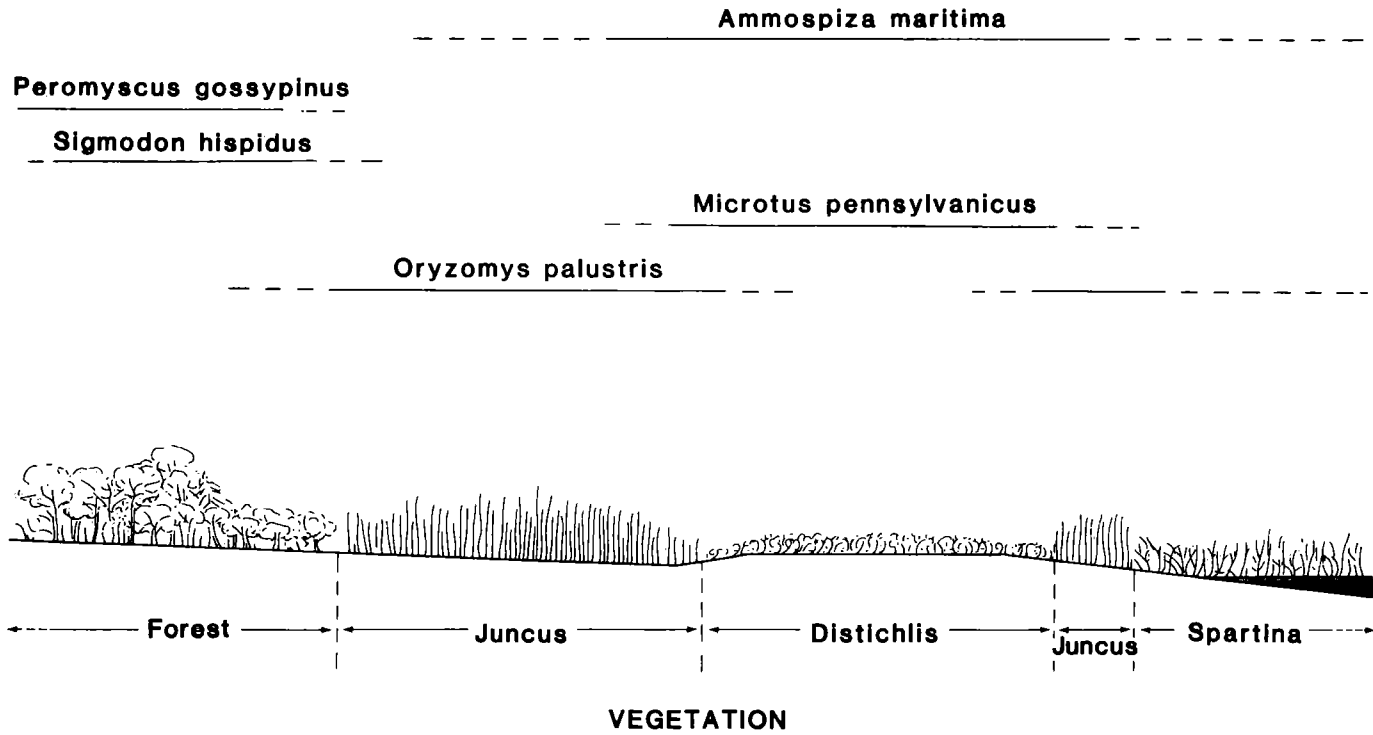


FIGURE 3. — Vegetation zones in a salt marsh in Waccasassa Bay, Levy County, Florida.

TABLE 3. — Comparative numbers of *Oryzomys palustris* captured in different microhabitats.

	Microhabitat		Total
	<i>Juncus</i>	<i>Distichlis</i>	
No. of Traps with <i>Oryzomys</i>	79	74	153
No. of traps empty ¹	366	779	1145
Total traps	445	853	1298

¹Traps containing other animals or improperly set, were not included in this category.

TABLE 4. — Comparison of number of *Oryzomys palustris* and *Microtus pennsylvanicus* caught in different microhabitats.

Microhabitat ¹	Number of:		Total
	<i>O. palustris</i>	<i>M. pennsylvanicus</i>	
<i>Juncus</i>	79	7	86
<i>S. alterniflora</i>	33	0	33
<i>Distichlis</i>	74	21	95
<i>Salicornia</i>	15	8	23
Total	201	36	237

¹The overall distribution of the two species in the various microhabitats is significantly different ($X^2 = 26.22; P .001$).

land marshes characterized by salt grasses, *S. patens*, *S. alterniflora*, and *D. spicata*, *Microtus* was more abundant than *Oryzomys* (Harris 1953). *Microtus* may avoid *Juncus* because its stems are more coarse and taller and may be less attractive as food. The more arboreal *Oryzomys* would be better adapted to use the tall, smooth stems of *Juncus* while foraging.

No estimates of *Oryzomys* density in salt marshes are published, but in some other habitats density reaches 19/ha (Smith and Vrieze 1979). No population estimate can be made for the western site because of raccoon disturbances. Comparative numbers of rodents captured on this site are: 55 *Oryzomys*, 10 *Sigmodon*, and 4 *Peromyscus* (Table 1). The latter two species were captured within 25 m of the forest. *Oryzomys* was the sole occupant of the lower elevations of the salt marsh on the western site. On the eastern site population density was estimated at 8/ha (95% confidence interval: 7/ha-10/ha). Too few of the other species were captured to estimate their populations, but in comparison with 53 *Oryzomys* captured during the period 5-24 March on the eastern site we captured 9 *Microtus* and 2 *Sigmodon*.

Getz (1961) calculated that the densities of *M. pennsylvanicus* in a freshwater marsh in Michigan varied between 16/ha in late February and 64/ha in July. It is clear from our results that densities of *Microtus* on the study plot at the time of our study were far below those observed by Getz.

Our data are too few to allow estimation of home range sizes, but

distances between successive captures allow some comparisons between sexes and species (Table 5). The average distance between captures for *Oryzomys* was 66 m, while the same value for *Microtus* was 32 m. One adult male *Oryzomys* moved 251 m. In another case a subadult male crossed a 60 m tidal inlet to reach an island 175 m from his original capture point. These data correspond to the estimates made by Negus et al. (1961) for home ranges of *Oryzomys* in coastal scrub: 0.33 ha for males and 0.21 ha for females. If these areas are considered circular, the diameter of the male's home range is 69 m, and the female's is 52 m, which agrees closely with our average intercapture distances of 71 m for males and 60 m for females.

Our data on the average distance between captures for Florida *Microtus* can be compared with other published data. Harris (1953) calculated the average maximum distance between capture points for *M. p. nigrans* in a Maryland salt marsh to be 38.5 m. This is similar to our figure of 32 m. If we transcribe these figures into the area of a circle to get a generalized average home range, then it is possible to make a comparison with other published data. For the Maryland population the generalized home range will be 1164 m², and for our Florida data it will be 804 m². Getz (1961) calculated a maximum home range size for both males and females from a freshwater marsh in Michigan to be approximately 800 m². He found that the home range size for male *M. pennsylvanicus* in the marsh was significantly larger than for females, and that home range size for both sexes was inversely proportional to population density. The population density of both male and female *Microtus* at maximum home range size was approximately 16 individuals/ha. In a study of *M. pennsylvanicus* from an old field in Virginia, Madison (1980) used radiotelemetry to demonstrate daily ranges for male voles of 192 m² (69 m² for females) at an average density of 155 individuals/ha.

From 21 February to 24 March 1980, an equal proportion of male and female *Oryzomys* were captured: 46 males and 44 females. In the same period we caught 5 male and 9 female *Microtus*.

For *Oryzomys* we noted signs of breeding activity in early March, when we first captured females with perforated vaginas and males with scrotal testes. The appearance of smaller *Oryzomys* in the population also indicated recruitment of young. The proportion of juveniles (animals weighing less than 30 g) in the population was 4% in February, 11% in March, and 21% in June. We found three litters of *Oryzomys*, each with three young. These data (Table 6) indicate that reproductive activity in *Oryzomys* increases between February and June and reaches a highpoint in June. In contrast, *Microtus* were sexually active in late February when trapping began. A specimen (UF 12136) collected on 27 February 1980 had six embryos, as did another (UF 12001) collected on 9 March 1980. A

TABLE 5. — Movements of rodents, 1980.

Species Sex	Individuals (Captures)	Distances between successive captures					
		X	SD	SE	Var.	Range	95% CI
<i>Oryzomys palustris</i>							
males	14 (48)	71.5	66.83	9.65	4466	12-263	
females	13 (38)	60.03	48.81	7.92	2382	0-251	
both	26 (86)	66.43	59.49	6.42	3539	0-263	53.67-79.19
<i>Microtus pennsylvanicus</i>							
males	3 (10)	38.8	25.66	(8.11)	658	0-80	
females	6 (13)	26.0	17.7	(4.92)	314	0-56	
both	9 (23)	31.6	21.97	4.58	483	0-80	22.12-41.08

subadult weighing 30 g was captured on 29 May 1980. In *Microtus* reproductive activity appears to extend throughout the study period, but is most active in February and March. These data are consistent with Harris' (1953) study of a saltmarsh community in Maryland. He found the peak of reproductive activity for *Microtus* in March with a lesser peak in June, while no *Oryzomys* were reproductively active in March but 100% were in June and July.

Of the two rodents occupying lower marsh elevations, *Oryzomys* weighed significantly less than *Microtus* (Table 7). *Sigmodon*, which only occupied patches of *Borrchia*, in the highest marsh elevations, weighed 74.4 g. The variability of *Oryzomys* weights increased from February to June, reflecting the addition of juveniles to the population.

TAXONOMIC STATUS

Our examination of the dental morphology of the small vole population from Florida indicates that while the pattern of the enamel reentrant folds was extremely variable, a consistent feature was the presence of a fifth rounded posterior loop on M² characteristic of *Microtus pennsylvanicus* (Hall 1981). Chromosomal analysis of a single female *Microtus* (UF 12136) from the Florida population revealed a diploid number of 46. The karyotype (Fig. 4) consists of 4 pairs of biarmed chromosomes and 19 pairs of acrocentric chromosomes. This pattern is identical to that reported in *M. pennsylvanicus* by Matthey (1952) and Hsu and Benirschke (1967). The chromosomal pattern is clearly different from that of other southeastern microtines, such as *M. ochrogaster* with 2n = 54 (Matthey 1955) and *M. pinetorum* with 2n = 62 (Matthey 1955, Beck and Mahan 1978).

Blood proteins (Table 8) from 14 *Microtus* from the Florida population encoded by nine structural loci were analyzed by horizontal starch gel electrophoresis (Selander et al. 1971). This population demonstrated a mean coefficient of genetic identity of 0.943 with northern populations (Vermont, Pennsylvania) of *M. pennsylvanicus* and 0.556 with *M. ochro-*

TABLE 6. — Indications of breeding activity among rodents trapped at Cedar Keys, 1980.

Date	<i>Oryzomys palustris</i>				<i>Microtus pennsylvanicus</i>			
	No. Examined	: No. Scrotal	: No. Perforate	Total (%)	No. Examined	: No. Scrotal	: No. Perforate	Total (%)
24 Feb	31	0	0	0	5	0	2	2 (40)
5 Mar	18	0	0	0	3	1	1	2 (66)
6 Mar	28	1	2	3 (10)	6	1	4	5 (83)
9 Mar	28	1	0	1 (3)	3	1	1	2 (66)
16 Mar	19	2	3	5 (26)	3	1	0	1 (33)
17 Mar	27	5	4	9 (33)	7	2	4	6 (85)
24 Mar	22	3	2	5 (22)	5	3	0	3 (60)
29 May	23	2	5	7 (30)	7	0	0	0
15 Jun	55	13	16	29 (52)	7	1	3	4 (57)

TABLE 7. — Weights (g) of small mammals captured in salt marsh on Waccasassa Bay (\pm SD).

Date	<i>Oryzomys palustris</i>			<i>Microtus pennsylvanicus</i>		
	Males N (\bar{x})	Females N (\bar{x})	Both Sexes N (\bar{x})	Males N (\bar{x})	Females N (\bar{x})	Both Sexes N (\bar{x})
February	27 (52.4 \pm 2.5)	22 (38.3 \pm 1.7)	49 (46.1 \pm 1.9)			
March	62 (48.5 \pm 1.7)	52 (37.4 \pm 1.2)	114 (43.4 \pm 1.2)			
February- March				13 (56.9 \pm 4.3)	17 (56.9 \pm 2.4)	30 (56.9 \pm 2.3)
May	10 (59.4 \pm 6.1)	12 (54.1 \pm 4.6)	22 (56.5 \pm 3.7)			
June	25 (52.6 \pm 4.4)	29 (46.1 \pm 2.9)	54 (49.1 \pm 2.6)			
May-June				9 (55.7 \pm 6.3)	6 (63.2 \pm 3.0)	15 (58.7 \pm 4.0)
Total, 1980			100 (46.5 \pm 1.8)			45 (57.5 \pm 2.9)

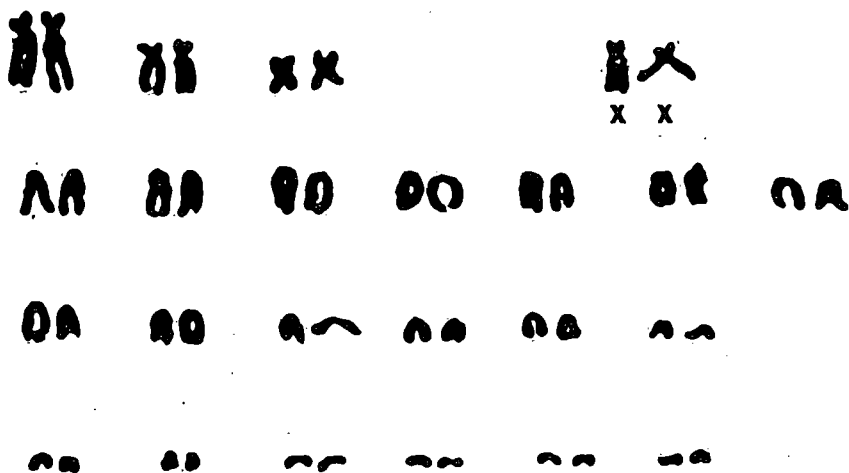


FIGURE 4. — Karyotype of female *Microtus pennsylvanicus* (UF 12136) from a salt marsh in Waccasassa Bay, Levy County, Florida.

gaster. Electrophoretic analysis of blood proteins strongly indicate that the affinities of the Florida population of *Microtus* are with *M. pennsylvanicus*. The chromosomal and electrophoretic data therefore confirm the conclusion based on morphological evidence that the Florida population is a new subspecies of *M. pennsylvanicus*.

Microtus pennsylvanicus dukecampbelli NEW SUBSPECIES

HOLOTYPE. — Male, adult, skin and skeleton; UF 12005; collected 28 April 1980 by C. A. Woods.

TYPE LOCALITY. — Island Field Marsh in Waccasassa Bay, Levy County, Florida. Because of the apparent extreme rarity of this form, the precise type locality will not be published, but is available as part of the permanent records of the Florida State Museum, University of Florida.

PARATYPES. — UF 12001 ♀, 12136 ♀, 12202 ♂, 15087 ♀, all skins with complete skeletons. Other referred material includes UF 10910, the complete skeleton of an adult ♀, and UF 15242, fur, teeth, and skeletal fragments from a marsh hawk pellet.

DISTRIBUTION. — Known only from the type locality.

DIAGNOSIS. — Entire animal and skull large; ears short, hind foot long; color dark black-brown on the back grading to dark gray on the belly.

COMPARISONS (TABLE 9). — From *M. p. pennsylvanicus*, the subspecies to the north at the southern extent of its range in Georgia (Newton, Gwinnett, Clark, and Union counties), *M. p. dukecampbelli* differs in being significantly (two-tailed *t*-test at 95% level) larger in total length, tail

TABLE 8. — Allelic frequency and genetic variability of representative populations of *Microtus*. Alleles are designated according to proportional electrophoretic mobility relative to the fast migrating allele. Frequencies of alleles at polymorphic loci are given in parentheses; all other loci are monomorphic.

Allele	<i>Microtus pennsylvanicus</i> populations			<i>Microtus ochrogaster</i>
	Florida n = 14	Pennsylvania n = 20	Vermont n = 12	
Hemoglobin				
Alpha ¹⁰⁰	1.00	1.00	1.00	1.00
Beta ¹⁰⁰	—	.25	.27	—
Beta ⁸⁷	1.00	.75	.73	1.00
Albumin ¹⁰⁰	1.00	1.00	1.00	—
Albumin ⁸⁸	—	—	—	1.00
6-Phosphogluconate dehydrogenase ¹⁰⁰	1.00	1.00	1.00	1.00
Lactate dehydrogenase-2 ¹⁰⁰	1.00	1.00	1.00	1.00
Esterase-1 ¹⁰⁰	—	.53	.25	—
Esterase-1 ⁹⁵	—	.08	—	—
Esterase-1 ⁹⁰	1.00	.38	.75	1.00
Esterase-1 ⁸⁸	—	.01	—	—
Esterase-5 ¹⁰⁰	—	.23	.25	—
Esterase-5 ⁹⁵	1.00	.77	.75	—
Esterase-5 ⁰	—	—	—	1.00
Esterase-8 ¹⁰⁰	—	—	—	1.00
Esterase-8 ⁷⁵	1.00	1.00	1.00	—
Esterase-9 ¹⁰⁰	—	—	—	1.00
Esterase-9 ⁸⁵	1.00	1.00	1.00	—

length, hind foot length, greatest length of skull, condylozygomatic length, length of incisive foramen, length of diastema, cranial breadth, and zygomatic breadth. It also differs in having a shorter rostrum and is much darker in coloration. *M. p. dukecampbelli* differs from *M. p. pennsylvanicus* at the mid-range area in Pennsylvania (Goin 1943, Snyder 1954) in all the above characters, except that tail length is not significantly different and rostrum is longer rather than shorter (i.e. the rostrum in Pennsylvania mice is exceptionally short while it is exceptionally long in Georgia mice). In addition, *M. p. dukecampbelli* has smaller ears, is heavier in body weight, has longer nasals, and a higher cranium. Compared with *M. p. nigrans*, the saltmarsh-dwelling form from coastal Maryland (Somerset County), *M. p. dukecampbelli* is larger in all characters measured except total length, tail length, hind foot length (which is larger, but not significantly so), and in the lengths of the ear, rostrum, and interorbital breadth. In *M. p. dukecampbelli* the ear and length of the rostrum are shorter (i.e. the Maryland form has a long rostrum). *M. p. dukecampbelli* is darker in coloration than *M. p. nigrans*.

TABLE 9.—External body and skull measurements (in mm) and weights (in g) of *Microtus pennsylvanicus dukecampbelli*, *M. p. pennsylvanicus* (known Georgia specimens), *M. p. pennsylvanicus* (from Pennsylvania after Snyder 1954) and *M. p. nigrans* (from Maryland)

	Total length	Tail length	Hind foot	Ear	Weight	Greatest length Skull	Condylo-Zygomatic length	Nasal length	Incisive foramen length	Diastema length	Rostrum length	Cranial breadth	Inter-orbital breadth	Zygomatic breadth	Cranial height
<i>M. p. dukecampbelli</i> (♂ ♀)															
N	5	5	5	5	5	6	6	6	6	6	6	6	6	6	6
\bar{X}	186.10	48.80	23.36	13.00	61.20	31.17	24.65	8.28	5.69	9.22	6.52	11.71	3.60	16.89	11.66
S	7.65	4.27	1.07	1.87	14.66	0.52	0.28	0.16	0.18	0.22	0.29	0.15	0.09	0.37	0.23
S ²	46.84	14.56	0.92	2.80	171.85	0.22	0.07	0.02	0.03	0.04	0.07	0.02	0.01	0.11	0.04
Range	178-198	43-55	22-25	11-16	43-80	30.7-32.0	24.3-25.1	8.1-8.5	5.5-6.0	9.0-9.6	6.2-7.0	11.6-12.0	3.5-4.0	16.5-17.3	11.2-11.8
<i>M. p. pennsylvanicus</i> (Georgia, ♂ ♀)															
N	14	14	14	7	14	4	4	6	8	8	4	3	8	5	0
\bar{X}	153.79	35.57	20.71	14.14	48.32	28.50	21.34	8.02	4.72	8.37	7.16	10.98	3.66	15.36	-
S	10.38	4.42	1.82	1.95	13.52	1.72	1.43	0.54	0.23	0.50	0.36	0.47	0.23	0.69	-
S ²	100.03	18.10	3.06	3.27	169.70	2.23	1.53	0.25	0.04	0.22	0.10	0.15	0.05	0.38	-
Range	128-173	27-43	18-25	12-18	29-75	26.8-30.5	19.8-23.1	7.4-8.7	4.4-5.1	7.7-9.3	6.8-7.5	10.5-11.3	3.4-4.1	14.4-16.1	-
<i>M. p. pennsylvanicus</i> (Pennsylvania, ♂ ♂)															
N	38	38	60	38	22	34	34	30	37	37	34	52	58	33	23
\bar{X}	167.40	44.40	20.60	14.00	44.19	27.35	21.31	7.70	5.21	8.34	6.04	11.03	3.66	15.23	10.07
S	7.40	5.70	0.80	1.00	6.29	0.63	0.52	0.42	0.28	0.27	0.23	0.29	0.12	0.47	0.27
S ²	54.76	32.49	0.64	1.00	39.16	0.40	0.27	0.18	0.08	0.07	0.05	0.08	0.01	0.22	0.07
Range	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>M. p. nigrans</i> (Maryland, ♂ ♀)															
N	13	13	13	13	13	13	13	13	13	13	13	13	13	13	12
\bar{X}	174.92	44.46	22.31	14.62	50.73	29.42	22.22	7.62	5.30	8.76	7.20	11.20	3.70	16.22	11.10
S	17.54	6.04	1.18	0.77	8.18	0.77	0.61	0.34	0.42	0.31	0.44	0.24	0.16	0.40	0.43
S ²	284.07	33.63	1.29	0.54	61.75	0.55	0.34	0.11	0.16	0.09	0.17	0.05	0.02	0.15	0.17
Range	146-203	33-56	21-25	13-16	37-62	28.4-30.9	21.7-23.3	7.2-8.3	4.5-6.1	8.2-9.3	6.6-7.8	10.8-11.6	3.4-4.0	15.7-17.0	10.4-11.7

REMARKS. — A comparison of *M. p. dukecampbelli* with other forms of *Microtus pennsylvanicus* from a variety of locations, habitats, and subspecies indicates that it is most distinct from the Georgia population. Even though the populations of mice from Georgia are considered part of the same subspecies (*M. p. pennsylvanicus*) as the Pennsylvania forms examined by Snyder (1954), the length of the rostrum in the two forms differs dramatically (see Comparisons above and Table 9). This raises the possibility that the Georgia forms are also a distinct subpopulation (subspecies) from the more typical *M. p. pennsylvanicus* to the north. The criteria for using subspecies and populations are discussed by Snyder (1954) and Anderson (1959). The known specimens from Georgia are in poor condition and limited in number. Therefore the documentation of morphological and geographical variability of *Microtus pennsylvanicus* in Georgia requires additional specimens.

Comparisons with *M. p. pennsylvanicus* from both Georgia and Pennsylvania show that the Florida form differs in most characters and is distinct from both no matter what their relations to each other might be. The Florida form is most similar in morphology to *M. p. nigrans*, which also inhabits coastal salt marshes (Handley and Patten 1947, Gordon Kirkland, pers. comm.). These similarities include large body size, long hind feet, and dark coloration. The Florida form is also similar to insular forms such as *M. p. copelandi* from Grand Manan Island, New Brunswick, and *M. p. magdalenensis* from Magdalen Island, Quebec (Youngman 1967). It shares with insular forms large body size, as well as cranial characters such as long nasals and broad braincase.

ETYMOLOGY. — Named in memory of zoologist Howard W. "Duke" Campbell, Jr., of Gainesville, Florida, who died 10 December 1981.

DISCUSSION

LATE PLEISTOCENE AND HOLOCENE DISTRIBUTION

The first report of *Microtus pennsylvanicus* from Florida was by Arata (1961), who described and illustrated the dentitions of two specimens (UF 3917, 3918) from the late Pleistocene Devil's Den fauna (near Williston, Levy County). The specimens were collected in a richly stratified bone bed approximately 9 m under water in a collapsed sinkhole. Additional Pleistocene records from Florida have been reported by Martin (1968) and Martin and Webb (1974) from Devil's Den (UF 12816), as well as from: Arredondo IA (UF 3586), a limestone chimney 10 km SW Gainesville (Alachua County), and Withlacoochee River 7A (UF 13090), a limestone pocket on the bank of the Withlacoochee River 13 km W Dunnellon (Citrus County). Other Florida specimens of *M. pennsylvanicus* in the

Florida State Museum collections are from Waccasassa River 2B (UF 16333) from near Gulf Hammock (Levy County), as well as additional specimens from Devil's Den (UF 12818) and the Withlacoochee River (UF 28000).

The locations of these four fossil sites are plotted in Figure 1. The ages of these deposits are not well known in all cases. Arredondo IA, for example, may be Illinoian, Sangamonian, or Wisconsinan (see Martin 1968). The Withlacoochee River 7A site is considered to be between 11,000 and 30,000 years old. The Devil's Den fauna is known to date around 8000 years before present (B.P.) (Martin and Webb 1974).

The small mammal fauna in southeastern North America from 10,000 B.P. to the present is not well known and the nature of the climate during the Holocene is controversial. The method of deducing the climate of an area from the presence or absence of key faunal elements, such as "steppe" species and "boreal" species, can also be hazardous because species frequently respond to different factors in different environments (Whittaker 1967). The Devil's Den fauna in Florida, for example, includes several species that are considered by Martin and Webb (1974) as "northern" forms, such as *Microtus pennsylvanicus*, the gray bat *Myotis grisescens*, and the muskrat *Ondatra zibethicus*. Whether these forms were in Florida because the climate was cool, or for some other reason, is difficult to deduce from faunal evidence alone. Other possible reasons are increased precipitation, the "Accordian Effect" (Dansereau 1957, Blair 1958), or a general reduction of environmental gradients that allowed for more diverse faunas and floras (Graham 1976).

Graham (1976) demonstrated that microtine rodent species diversity (number of vole species present per local fauna) was greater during the late Wisconsinan than it is at the present time in the same areas. This may indicate a more "equable" climate during late glacial and early post-glacial times, when temperature and moisture gradients were present but reduced. In Florida and southern Georgia, Watts (1971, 1980) contended that strong southwest winds further modified the climate and resulted in warm dry conditions. He based his conclusions on evidence from pollen samples gathered at Lake Louise on the Georgia-Florida border, approximately 180 km north of the Devil's Den site and from Sheelar and Mud Lakes near Gainesville, Florida. These data on climate and vegetation are from areas that are geographically close to the known range of *Microtus pennsylvanicus* and from approximately the same time—5000-10,000 B.P. Watts (1980) estimated that 8510 B.P. in central and northern Florida there was an oak savanna habitat with broad patches of bluestem prairie characterized by various grasses, as well as *Ambrosia*, *Iva*, and *Artemisia*. Such a climate and habitat would be suitable for voles, and it is probable that *Microtus pennsylvanicus* was broadly distributed along

water courses and wet areas in patches of bluestem prairie and savanna in northern and central Florida that existed until approximately 5000 B.P. Between 6710 and 5000 B.P. areas of pine expanded and eliminated the prairie plants. Black gum, sweet gum, ironwood, and other trees and vines became established by 5000 B.P., eliminating suitable upland habitat for grassland voles (Watts 1980).

Sea levels were much lower 10,000 years B.P., and suitable lowland savanna and prairie habitats extended far to the west into what is now the Gulf of Mexico. Blackwelder et al. (1979) estimated that at 10,000 B.P. sea levels were approximately 25 m lower than present levels in the Gulf coast area, which would extend suitable terrestrial habitats 100 km to the west of the present coastline along Waccasassa Bay and expose a broad area to the west along the Gulf coast. The area of expanded habitat would be most extensive between Clearwater and the mouth of the Appalachicola River to the north (Fernald 1981). Waccasassa Bay is in the center of this once extensive area that has been inundated in the last 10,000 years and is consistent with the location of the relict population of *Microtus*. The importance of this exposed area of habitat along the Gulf coast on Florida mammals was discussed by Webb (1977), who referred to it as the Gulf Coast Savanna Corridor.

M. pennsylvanicus is also known from the late Wisconsinan of Louisiana, where a molar was reported from Kimball Creek in West Feliciana Parish (Martin 1968). These spotty records indicate that *M. pennsylvanicus* probably had an extensive range in the Gulf coast area during the late Pleistocene. Although the current distribution of *M. pennsylvanicus* (Hall 1981) indicates that the closest population of meadow voles is far to the north, it is not clear that the Florida saltmarsh vole is necessarily a relict of northern populations. Frey et al. (1975) did not find any *M. pennsylvanicus* in their samples of late Pleistocene mammals in Georgia estuaries. Therefore *M. p. dukecampbelli* may be a relict of the more westerly distributed population of *M. pennsylvanicus* in the Gulf Coast Savanna and adjacent patches of bluestem prairie in northcentral Florida. The distribution of the vole would have been severely restricted by rising waters to the west and the expanding pine forest inland.

Archaeological evidence indicates that *M. pennsylvanicus* was not widely distributed in Florida after 5000 B.P., and that the ranges of other forms, such as *Myotis grisescens* and *Ondatra zibethicus*, were also becoming restricted. The muskrat remained in north Florida until approximately 3150 B.P. (Bullen 1958). Together with the data on sea levels and vegetation, this information indicates that the vole must have had a severely limited range for the last several thousand years. Dalquest et al. (1969) and Graham (1976) indicated that in Edwards County, Texas (Schulze Cave), the modern faunal composition was reached by 3800 B.P.

That date closely agrees with the conclusions of Bryson et al. (1970) and Webb and Bryson (1972) for the time modern faunal assemblages became established in other parts of the eastern United States. Therefore, *M. p. dukecampbelli* probably was disjunct from *M. pennsylvanicus* to the north and west for at least 5000 years, and probably longer if Watts (1980) is correct about the late Quaternary vegetative history of the southeastern United States.

The presence of a disjunct relictual population of *Microtus pennsylvanicus* in Levy County therefore is not a surprise when one examines the late Pleistocene distribution of this form (Fig. 1; Martin 1968). The small relict population from Florida is analogous to the relict populations of *M. ochrogaster ludovicianus* in the Gulf coast area of Texas and Louisiana (now probably extinct), *M. montanus arizonensis* in Arizona and New Mexico, and *M. pennsylvanicus chihuahuensis* in northern Mexico. These forms are undoubtedly relicts of populations more widely distributed during the Wisconsinan glacial period of the Pleistocene. Anderson and Hubbard (1971) noted that *M. p. chihuahuensis*, the relict population from Chihuahua, Mexico (Bradley and Cockrum 1968), is larger and darker in coloration than is *M. p. modestus* to the north. They also noted that certain southern, relict, marsh-dwelling, and small isolated populations of *M. montanus* are characterized by large size and dark pelage. Anderson (1959) stated that in *M. montanus* the largest and blackest individuals are in the southwestern part of the geographic range, while in the northern part of the range the mice are smaller and grayer.

In all of the southern relictual populations discussed here the populations are similar to *M. p. dukecampbelli* in morphology and habitat. Their disjunct status is certainly the result of changing climates after the Wisconsinan glacial event. In the case of *M. p. chihuahuensis* there are known fossil sites containing *M. pennsylvanicus* in southern New Mexico (Harris et al. 1973), as well as other isolated relict populations between Chihuahua and the current range of *M. p. modestus* in New Mexico (Anderson 1961, Anderson and Hubbard 1971). In both Florida and the southwest known dates for the fossils are between 8000 and 11,000 B.P. (Harris et al. 1973, Martin and Webb 1974). In both areas the mice probably existed in considerably broader distributions well into the Holocene, and the true influence of the unique habitat on the morphology of the populations did not become a major factor until the last 4000 years (Bullen 1958, Guilday, pers. comm.). The degree of morphological distinctiveness of *M. p. dukecampbelli* from *M. p. pennsylvanicus* is similar to that achieved by *M. p. breweri* (Muskeget Island, Massachusetts), *M. p. rufidorsum* (Martha's Vineyard Island), and *M. nesophilus* (Gull Island, Suffolk County, New York). Martha's Vineyard and Nantucket islands were separated from Cape Cod less than 5000 years ago,

and Muskeget Island became isolated from Nantucket as recently as 2000 to 3000 years ago (Youngman 1967).

MORPHOLOGICAL TRENDS

The morphological differences between *M. p. dukecampbelli* and *M. p. pennsylvanicus* to the north are difficult to explain. The large size alone could be the result of an "island effect," (Case 1978). The disjunct distribution of *M. p. dukecampbelli* in the narrow band of coastal salt marsh between the Gulf and lowland forest is, in effect, insular. It has been well demonstrated that *Microtus* gets larger when isolated on islands (Youngman 1967). However, the influence of the salt marsh (semi-aquatic habitat) also must be taken into consideration. While *M. p. dukecampbelli* is significantly distinct in most characters from *M. p. nigrans*, which is restricted to a similar coastal salt marsh in Maryland, it shares with *M. p. nigrans* similarities in body size, tail length, hind foot length, and coloration.

Von Bloeker (1932) demonstrated that saltmarsh-dwelling races of three small mammals in California were characterized by dark coloration. Grinnell (1913) noted a direct relationship between saltmarsh inhabitation and the quantity of pigmentation in the peltage of small mammals. The blackest forms occur in marshes with the least salt (von Bloeker 1932, Grinnell 1932), however, and so the dark pigmentation must be related to something other than salt alone. Most salt- and freshwater-marsh soils are dark in coloration, suggesting a relationship between extremely dark marsh soils and the dark peltage of the small mammals inhabiting the marshes.

To identify trends that might be associated with the saltmarsh habitat, we compared a population *M. p. pennsylvanicus* from interior Connecticut (Mansfield Depot, Tolland County) with one from a coastal marsh habitat (Hammonasset State Park, New Haven County). Measurements (in mm) of 20 individuals from each population were compared: *inland*—total length 152.6, tail length 41.8, hind foot length 21.7, ear length 13.9; *salt marsh*—total length 156.7, tail length 41.7, hind foot length 20.3, ear length 13.5. There was no significant difference between these two populations in coloration, total length, tail length, or ear length. The hind foot length was significantly (two-tailed *t*-test at 99% level) smaller in the saltmarsh population, the opposite trend found in *M. p. nigrans* and *M. p. dukecampbelli*. Therefore, in *Microtus pennsylvanicus* trends in coloration, body size, and hind foot length discussed above do not appear to be linked in a simple fashion to the saltmarsh environment alone.

As discussed earlier, other forms of *Microtus* that are disjunct relictual populations to the south of the main distribution of the taxon are also

large and dark. The relictual population of *M. p. chihuahuensis* is located 7.5 km SE Galeana, Ojo de los Reyes, in an area of Chihuahua, Mexico, that is currently extremely dry and unsuitable for voles. The specific area of distribution, however, is characterized by numerous spring runs, and the *Microtus* live in sedge mats along the spring run (Bradley and Cockrum 1968, Guilday, pers. comm.). As most other populations found in southern refugia are also living in pockets of moist vegetation surrounded by otherwise unsuitable habitat, they all share a similar environment. Natural selection associated with this environment may have resulted in a significant amount of parallelism in such morphological characteristics as coloration, body size, and the size of the hind foot. This "environment" includes the evolutionary factors associated with "insular effect" as well as "aquatic effect" in influencing the final morphology of the relict population.

The serum proteins of the Florida saltmarsh vole have been examined for nine loci. Northern mainland populations of *M. pennsylvanicus* have a mean heterozygosity for these nine loci of 0.17 (=17%), while the Florida vole has no polymorphism (=0%) at any loci examined. The absence of genetic variation within this population is consistent with the reduction of genetic variability observed among insular populations of mammals (Kilpatrick 1981), and has been specifically demonstrated for *M. pennsylvanicus* and *M. breweri* (Fivush et al. 1975, Kilpatrick 1981). The lack of genetic and chromosomal differentiation is also consistent with data on isolated populations of *Sigmodon hispidus* of the Colorado River Valley (McClenaghan 1980).

Even though *M. p. dukecampbelli* lacks genetic variation, as measured by variation in serum proteins, it does exhibit dental variability. Variation in the pattern of reentrant folds in *Microtus* has been noted by many authors (Miller 1896, Goin 1943, Guilday and Bender 1960, Guthrie 1965, Corbet 1975). One frequently observed anomaly is the presence of six triangles instead of five on the first lower molar. Miller (1896) found this anomaly in 4 (8.3%) of the 285 specimens of *M. pennsylvanicus* he examined. We found the variant in 4 (28.6%) of the 14 specimens of *M. p. pennsylvanicus* from Georgia and 2 (14%) of the 14 specimens from Maryland. In two specimens from Georgia one side had six triangles while the other side had five. All specimens of *M. p. dukecampbelli* examined had six triangles on the first lower molar. However, one specimen (UF 12001) had six triangles on one side and seven on the other. Other features in the pattern of reentrant folds of the remaining molar teeth were extremely variable. Therefore, it must be kept in mind that the pattern of reentrant folds in *Microtus*, especially of the first lower molars, is normally variable.

Although all the *M. p. dukecampbelli* examined had at least six

triangles on the first lower molar, we are hesitant to consider this character diagnostic of the subspecies. The small sample size of our population, as well as normal dental variation that is characteristic of *Microtus*, cause us to doubt the stability of this character. In addition, Corbet (1975) found that a similar dental characteristic in a disjunct population of *Clethrionomys glareolus* was ephemeral. When Corbet reexamined the population he described 15 years earlier, he found that the dental variant he discussed had returned to the normal condition. The high percentage of six triangles on the first lower molar of *M. p. dukecampbelli* could be the result of "bottleneck effect" as a consequence of periodic reductions in population size to a few individuals. An alternative explanation is that small population size results in inbreeding, increasing the frequency of a polygenic character. We favor the latter hypothesis in the light of the finding of Nei et al. (1975) of the inability of an evolutionary bottleneck to significantly alter the genetic structure of populations.

Guthrie's (1965, 1971) theory that the high level of variation observed in the dental morphology of *Microtus pennsylvanicus* is the result of rapid evolution may be applicable to *M. p. dukecampbelli*, for it has diverged in morphology from standard populations of *M. p. pennsylvanicus* and may be subjected to strong selective pressures. The continued high level of dental variation in spite of an apparent reduction in genetic variability in *M. p. dukecampbelli* would be a result of the breakdown of balanced heterozygous linkage groups if this vole is part of a rapidly evolving population (Guthrie 1965). Corbet (1963) showed that two populations of *Clethrionomys glareolus* living in adjacent habitats having different vegetation types differed greatly in tooth complexity. Guthrie (1971) concluded that dental morphology is directly tied up with the demands of the diet, and teeth are sensitive indicators of dietary shifts. Therefore, the combination of increased tooth complexity and a high level of dental variability could be the result of intense natural selection related to the diet of *M. p. dukecampbelli* in a salt marsh characterized by abrasive plant materials.

The lack of genetic variability in association with the observed dental variability is difficult to explain, however, and raises the probability that some dental variability could result from mechanical factors such as tooth-wear. Guthrie (1971) was not able to demonstrate a high level of heritability in the pattern of reentrant folds in the areas of molar teeth that are most variable. Great care should be taken in using subtle differences in dental patterns as taxonomic characters.

SURVIVAL IN A TIDAL SALTMARSH ENVIRONMENT

The means by which the Florida saltmarsh vole survives tidal flooding are unknown. Tides at the study site frequently cover the marsh with up

to 25 cm of water, and occasional natural disasters have flooded the area with wind-driven water. Harris (1953) posed a similar question for *M. p. nigrans* living in tidal marshes in Maryland. One significant difference between Maryland and Florida is the presence of large populations of muskrats (*Ondatra zibethicus macrodon*) in Maryland marshes. Harris (1953) demonstrated that *Microtus* frequently use *Ondatra* "houses" (feeding shelters, abandoned houses, as well as occupied houses). The usage became especially frequent at times of high water. After the marsh had been covered by 5 cm of water for several days, vole sign was found at 25 percent of muskrat houses, whereas when the marsh was covered with 30 cm of water sign was recorded at 72 percent of 60 muskrat houses examined. Muskrat houses therefore are important in the survival of *Microtus* in Maryland and may partially explain why *Microtus* is more common in tidal marshes in Maryland than it is in Waccasassa Bay.

The habitat of the California vole, *Microtus californicus*, is subjected to daily tidal submergence during the winter months, and that species therefore faces the same problem of survival faced by voles in Florida. Fisler (1961) investigated how small mammals survive under these extreme conditions and observed that *Microtus californicus* climbs into vegetation and remains well concealed just above the rising water level. The voles sit in a humped-back position with their tails tucked under their bodies, and for the most part are completely dry. He also observed mice sitting on boards and under the bark of floating logs. When the water became higher than the vegetation itself, the mice were able to swim. Fisler observed that even when forced to swim, the animals stayed within their home ranges. They are able to do this even under difficult conditions, and Fisler reported examples of *Microtus* swimming through rough water and against strong tidal currents. He reported observing one *Microtus* swim a 12.3 m slough, diving to a depth of more than 1.3 m and swimming a distance of about 6.8 m under water. Therefore, in spite of a high mortality rate that occurs when the occasional high tide inundates all the marsh vegetation, *Microtus californicus* were capable of remaining on their home ranges through the winter high tides and successfully maintained the adult population in the marshes during this critical period (Fisler 1961).

In Florida, survival during high tides and at times of extreme inundation from wind-driven water off the shallow Gulf might be accomplished in several ways: (1) voles might move to high land adjacent to the marshes or onto the occasional islands in the marshes; (2) they might climb up into the tops of vegetation to stay above the water level; (3) they might have an unusual ability to withstand becoming watersoaked and surviving long periods under these conditions while swimming about; and (4) they might have an extensive distribution throughout the saltmarsh area

and depend on frequent recolonization of marginal habitats most severely affected by tides and storms. All of these factors must be at least partially true. Harris (1953) found vole sign on nearby islands in Maryland and also found voles clinging to branches of the high tide bush (*Iva frutescens*). In addition, *Microtus pennsylvanicus* is well known for its ability to withstand adverse conditions related to water and cold. The total distribution of *Microtus* in the area of Waccasassa Bay is unknown at this time because of the extreme difficulty of trapping in the area and because the vole is (or was for the trapping period) so rare. During the entire study period, 31 separate *Microtus* were tagged. However the study area is in a suitable position to be sheltered from wind-driven levels of high water, and may represent a refugium from which *Microtus* spreads out into the more exposed areas of marsh. Unlike the situation in Maryland, however, where the distribution of *Microtus* includes areas of suitable habitat in interior sections which also could serve as sources of recolonization following natural disasters, the Florida saltmarsh vole seems to be totally restricted to the vulnerable saltmarsh habitat.

It is clear from the above discussion that *Microtus pennsylvanicus* survives in Florida salt marshes under much more severe conditions and restrictions than it does in Maryland and faces many of the same problems as *Microtus californicus*. It must survive by a variety of mechanisms, but the two most likely conditions are its ability to climb the saltmarsh vegetation to get above high water levels (even swimming from plant to plant when the need arises) and the unique, somewhat sheltered position of the study site in Waccasassa Bay. However the population is extremely vulnerable to the effects of tides and weather. The very existence and continued survival of *M. p. dukecampbelli* as a relict population under such conditions for such a long period of time is an evolutionary and ecological paradox.

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