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A ZOOGEOGRAPHIC ANALYSIS OF VARIATION IN RECENT *GEOMYS PINETIS* (GEOMYIDAE) IN FLORIDA

KENNETH T. WILKINS

UNIVERSITY OF FLORIDA GAINESVILLE

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ZOOGEOGRAPHIC ANALYSIS OF VARIATION IN RECENT *GEOMYS PINETIS* (GEOMYIDAE) IN FLORIDA

KENNETH T. WILKINS[1]

ABSTRACT: Cranial characters were used to assess phenetic relationships of *Geomys pinetis* populations in Florida. The observed pattern of geographic variation is examined in light of rivers and patchy distribution of suitable habitats that influence dispersal of pocket gophers and the effects of sealevel changes on isolation of populations. Phenetic breaks in the pattern of geographic variation correspond to the Apalachicola and, to a lesser extent, the Suwannee rivers. Several features of these river corridors explain their relative effectiveness as barriers: (1) potential for gene flow around river headwaters, (2) effective width of the river corridors, and (3) various streamflow parameters. The barrier effects of the Apalachicola and Suwannee rivers on other vertebrate and invertebrate taxa are discussed.

RESUMEN: Características craniales de *Geomys pinetis* fueron utilizadas para establecer relaciones fenéticas en poblaciones de esta especie en Florida. Los patrones observados de variación geográfica fueron examinados en base a ríos y distribución fragmentada ("en parche") de hábitats favorables que influencian la dispersión de las tuzas de bolsillo, así como los efectos de cambios del nivel del mar sobre sislamiento de poblaciones. Rupturas fenéticas en los patrones de variación geográfica corresponden al río Apalachicola y, en menor grado, al río Suwannee. Varias características de estos corredores de ríos explican su relativa eficacia como barreras: (1) potencial para flujo de genes alrededor de cabeceras de ríos; (2) ancho efectivo de corredores, y (3) parámetros de flujo de corriente. Se discute también los efectos de barrera de los ríos Apalachicola y Suwannee sobre otros taxones de vertebrados e invertebrados.

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[1] The author is Assistant Professor of Biology, Baylor University, Waco, Texas 76798 (formerly a Postdoctoral Research Associate of the Florida State Museum, Gainesville, Florida, 32611).

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INTRODUCTION

Geographic isolation is a key component in many speciation models (Wiley 1981). Fragmentation of populations is important in the differentiation process because it may serve to reduce the amount of gene flow between populations (Wright 1943). The degree of divergence between populations may depend on many factors including distance between populations, duration of isolation, effective population sizes, vagility of the organism, and others (Patton and Feder 1981). Because of their fossorial lifestyle, low vagility, skewed sex ratio of breeding adults, and low effective population sizes, pocket gophers (Rodentia: Geomyidae) exemplify the effects of geographic isolation in terms of recognizable morphological and chromosomal variability. For example, over 200 subspecies of *Thomomys bottae* have been recognized (Hall and Kelson 1959).

Like many pocket gopher species, the southeastern pocket gopher (*Geomys pinetis*) is patchily distributed because of its restriction to soils of suitable friability and moisture content. Hubbell and Goff (1939:131) recognized the discontinuous distribution of pocket gophers in Florida as the result of the patchy occurrence of deep, well-drained soils elevated slightly above surrounding wetter habitats which are unsuitable and impassable to pocket gophers. They (1939:134) stated that "it would not be surprising . . . to find that specific or racial differentiation corresponding to the degree of isolation had occurred" in *Geomys pinetis*. This study utilizes craniometric data from over 800 specimens to examine geographic variation in Recent *Geomys pinetis* in Florida. The pattern of variation found is interpreted in the light of both the relative roles of river valleys as dispersal barriers and the effects of past sealevel changes on isolation of pocket gophers during the Quaternary Period.

ACKNOWLEDGEMENTS

This paper represents part of a doctoral dissertation in the Department of Zoology, University of Florida. I thank S. David Webb and Charles A. Woods for their guidance throughout the study. I sincerely thank curators from the museums and collections listed in the Appendix for permission to examine specimens. S. D. Webb, B. J. MacFadden, A. Berta, J. W. Hermanson, and G. S. Morgan critically read earlier drafts of this manuscript. This paper further benefited from comments made by J. L. Patton. Grants from National Geographic Society, Southern Regional Education Board, and Sigma Xi supported this work. Northeast Regional Data Center (University of Florida) provided computer facilities for data analyses and text editing.

DISTRIBUTION AND HABITATS

Geomys pinetis occurs along the Atlantic and Gulf coastal plains of Alabama, Florida, and Georgia (Hall 1981:505). Figure 1 shows the detailed distribution of *G. pinetis* in Florida. Specimens are known from all

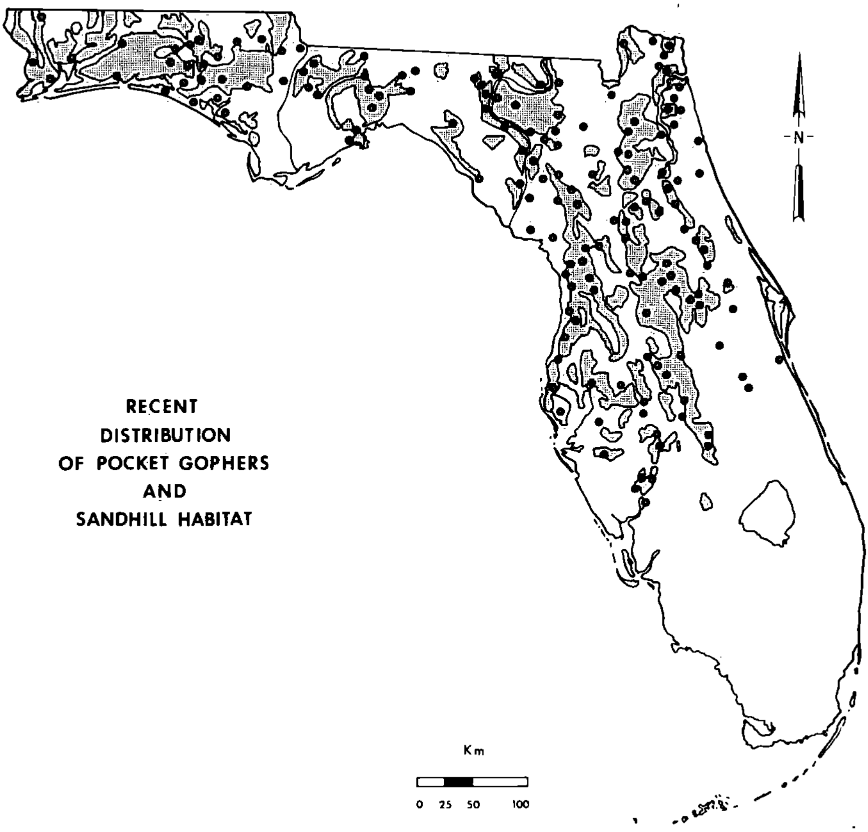

Figure 1.—Recent distribution of *Geomys pinetis* (dots) overlaid by general distribution of sandhill habitat (outlined stippled areas) in Florida. The Apalachicola (central panhandle) and Suwannee (eastern panhandle) rivers are indicated by darkened lines.

panhandle counties except Gulf County. The range extends through the northern two-thirds of the peninsula to a southern tier of counties (Manatee, DeSoto, Highlands, Osceola, and Brevard). Thus, the occurrence of *G. pinetis* in Florida is much more extensive than depicted in Hall (1981:505) or in Hamilton and Whitaker (1979:173), but less extensive than indicated by Williams and Genoways (1980). The latter extension of its range into St. Lucie County probably originated as an error in geographic terminology. Pocket gophers do not occur in St. Lucie County as cited by Williams and Genoways (1980). Walton (St. Lucie Co.) is about 90 km south of the southernmost record of living *Geomys* along the Atlantic coast (Melbourne, Brevard Co.). Rather, these specimens are probably from Ft. Walton (Okaloosa Co.) in the Florida panhandle.

The occurrence of pocket gophers in Florida is controlled by geomorphological and habitat features. Prime pocket gopher habitat is the sandhill ecosystem characterized by two codominant tree species, longleaf pine (*Pinus palustris*) and turkey oak (*Quercus laevis*). *Geomys* selects its diet from the grasses, forbs, and sedges that comprise the fire-perpetuated ground cover. Terrain in the sandhill ecosystem is rolling and the soils are well-drained (Monk 1968). A second habitat occupied by *G. pinetis* is the xeric hammock ecosystem that commonly occurs in association with the sandhill community. Xeric hammocks are dominated by live oaks (*Q. virginiana*) and other hardwood species; soils are slightly moister and contain more organic material than soils of the sandhill (Monk 1968). *Geomys pinetis* occurs less commonly in longleaf pine flatwoods and sand pine scrub habitats.

A close correspondence exists between museum specimen localities and the distribution of suitable habitat. In Figure 1, known locality records of pocket gophers are superimposed on the distribution of the sandhill ecosystem as mapped by Davis (1980). Over 125 of the more than 150 plotted localities coincide with (or are at the edges of) parcels of sandhill habitat. Most of the remaining localities do in fact correspond to patches of sandhill habitats that were too small to be included on the large-scale map, although a few populations do occupy other habitats such as sand scrub or longleaf pine flatwoods. Hence, Florida pocket gopher populations occur in a mosaic of islands of suitable habitats within a sea of unsuitable habitats, primarily the excessively moist pine flatwoods. The opportunity for allopatric differentiation exists for pocket gophers in Florida despite what appears to be fairly uniform topography.

The correspondence of pocket gopher occurrence with geomorphology is particularly evident towards range limits in the southern peninsula. Suitable habitats predominate along such higher-elevation features as the Polk Upland, DeSoto Plain, and Lake Wales Ridge (see White 1970). At the escarpment of the DeSoto Plain, habitats abruptly change to pine flatwoods, cypress swamps, and others too moist for pocket gophers. For example, pocket gophers range to the DeSoto Plain escarpment in Manatee County, but are unknown in adjacent lowland Sarasota County.

HISTORICAL PERSPECTIVE

Geomys pocket gophers are first known in Florida from the early Irvingtonian (earliest Pleistocene) Inglis IA site dated at about 1.8 million years before present (mybp; Webb 1974). Fossil evidence suggests a continuous occupation of the Florida peninsula since then with probable *in situ* evolution of the Inglis IA *Geomys propinetis* into *G. pinetis* by about 1 mybp (Wilkins 1984). It is of interest to note here that previous morphological and genic studies show *G. pinetis* and *G. bursarius* to have diverged from a common ancestor about 300,000 ybp during the early Rancholabrean (Russell 1968, Penney and Zimmerman 1976). While agreeing that the *G. pinetis* and *G. bursarius* complexes are distantly related, Heaney and Timm (1983, citing Kurten and Anderson 1980) reported origination of these two species groups as "no later than the late Irvingtonian." My own morphological studies of Quaternary Florida *Geomys*, wherein pocket gophers statistically indistinguishable from modern *Geomys pinetis* extend back to the late Irvingtonian Coleman IIA deposit, corroborates the latter opinion (Wilkins 1984).

Because of Florida's low and gentle topographic relief (maximum elevation of 105 m), sealevel changes during the last several million years have drastically altered the configuration of the emergent Florida land mass (Healy 1975). During the high sea stands of earlier interglacials (i.e. the Miocene and Pliocene Coharie, Okefenokee, and Wicomico shorelines; see Alt and Brooks 1965) seas covered much of the present state, leaving only an archipelago of islands to represent the present-day peninsula. The body of water separating the mainland from the peninsular archipelago was the Suwannee Straits. Pleistocene transgressions, though less severe than those previous, undoubtedly affected pocket gopher biogeography. Approximately 22 glacial-interglacial cycles (rather than the traditional four cycles) characterized the last 870,000 years of the two million year long Pleistocene epoch (Shackleton and Opdyke 1973).

A scenario by which sealevel changes influence the pattern of geographic variation among populations of pocket gophers may be developed in accordance with the allopatric model of speciation. This model holds that gene flow occurring between populations will lead to homogeneity of these populations; conversely, restriction of gene flow leads to inbreeding within isolated populations and resultant divergence of populations via differential selection regimes, founder effect, or genetic drift. Pocket gopher populations, if present on such islands at these times, were isolated from other insular populations and from the mainland, and thereby were afforded opportunities to differentiate. During ensuing glacials, however, sealevel fell well below the present level (by 100 m or more), thereby reconnecting islands with each other. With sea barriers removed, islands and suitable parcels of pocket gopher habitat tended to regain contact. Concomitantly, formerly restricted pocket gopher populations expanded and probably established breeding connections between populations throughout the peninsula. During such intervals, pocket gopher populations would have been characterized by their greatest phenotypic homogeneity, with any differentiation achieved during former isolation (if not already secured by reproductive isolation) being obliterated through panmixia.

The preceding direct-inundation mechanism of population isolation is accompanied by a second mechanism: Levels of water tables in inland areas of the Florida peninsula tend to track changes in sealevel. Effects of water table variation can affect pocket gophers directly through soil regimes unsuitably wet or dry. Changes in soil moisture conditions also determine which plant communities can occupy given tracts of land. Because pocket gopher distribution is closely linked with that of suitable habitats, it is apparent that changes in soil moisture conditions affect *Geomys* distribution.

According to this scenario, the current pattern of geographic variation presumably reflects the influence of the most recent glacial-interglacial cycle. The Pamlico Shoreline (about 9 m above present mean sealevel) apparently was formed by the latest high sea stand about 125,000 years before present during the late Sangamonian interglacial.

MacNeil (1950) mapped the shorelines of Florida resulting from ocean transgressions in the Pleistocene (including Pamlico) and earlier in the late Tertiary. The emergent peninsular landmass during Pamlico times consisted of a more-or-less connected spine of uplands in the central peninsula, numerous islands east of the present St. Johns River, and a few isolated uplands in present day south Florida and in the Tampa region. Sangamonian fossil sites abound along this central peninsular spine: *Geomys pinetis* is known from Arredondo, Sabretooth Cave, Reddick, several Haile sites, and several others (Wilkins 1984). No Sangamonian sites have as yet been found in the coastward Pamlico emergent islands. Yet, during earlier and later glacial times, *Geomys* occurred in similar areas which are now at (e.g. early Irvingtonian Inglis IA, Citrus Co.) or below present sealevel (e.g. late Wisconsinan vertebrate fauna in the Atlantic Ocean about 100 m offshore from Ft. Pierce, St. Lucie Co.). The fact that *Geomys* distributions have changed drastically through nearly two million years by tracking sealevel changes is well-documented (Wilkins 1984). Although the Pamlico transgression did not isolate the peninsula from the mainland, it almost certainly increased the degree of fragmentation of pocket gopher populations. But any divergence that might have been achieved between these populations during late Sangamonian fractioning of ranges could well have been swamped during the subsequent range re-extensions that accompanied the late Wisconsinan return to lower sealevels. At the height of the late Wisconsinan (about 19,000 ybp), seas fell to about 90 m to 130 m below present (Bloom et al. 1974, Harmon et al. 1978). Since then, glaciers have been melting and the sea continuously rising towards its present level. During the last 19,000 years, therefore, the degree of isolation between *Geomys* populations in peninsular Florida presumably has again increased with increasing sea and ground water levels.

However, it should be noted here that, in light of recent research, the scenario proposed above may not be tenable. Study of genetic structure of pocket gopher (*Thomomys bottae*) populations in California has demonstrated that, despite moderate rates of gene flow, differentiation attained during isolation is maintained via non-random breeding and drift (Patton and Feder 1981). Hence, enhanced gene flow accompanying reunion of once-separated areas need not lead to genetic homogeneity over geography for animals of low vagility.

MATERIALS AND METHODS

Locality data from 1123 skin and skull specimens of Florida *Geomys pinetis* were used to construct the distribution map (Fig. 1). The Appendix lists specimens examined. Craniometric analysis was restricted to the 854 adult specimens which were divided into two age classes on the basis of three osteological features: (1) degree of fusion of the basisphenoid and basioccipital bones, (2) development of the temporal ridges, and (3) degree of porosity of the palatine bone and of the maxillary process of the zygoma. In younger adults (age class 1) the basisphenoid-basioccipital suture is closed with no intervening gap, but yet is not obliterated by accumulated bone as in old adults (age class 2). The temporal ridges in old adults (especially males) are highly rugose and usually meet to form the sagittal ridge. Rarely, if ever, is such a sagittal ridge found in females, although (as in males) the distance between temporal ridges decreases and their degree of development increases with age. In both sexes, porosity in the palatine and maxillary bones decreases with age.

Twenty cranial characters were measured to the nearest 0.1 mm with Helios dial calipers for all adults. Descriptions and abbreviations of these characters follow: greatest length of skull (GLS), from exoccipital to anterior surface of incisors; greatest zygomatic width (ZYGO); width across mastoid processes (WMAST); depth of cranium (DCRAN), dorsoventral distance from top of cranium to ventral surface of auditory bullae; depth of rostrum (DROST), least dorsoventral distance from dorsal surface of nasals to ventral surface of premaxillae; width of rostrum (WROST), greatest width across rostrum usually at level of premaxillary-maxillary suture; least interorbital constriction (IOC); least distance between temporal ridges (TEMP), generally at or anterior to the anterior width of interparietal; anterior width of interparietal (AWINT); posterior width of interparietal (PWINT): length of interparietal (LINT), taken along midsagittal axis; least width across nasals (LWNAS); greatest width across nasals (GWNAS); length of premaxillary extensions (PMEXT), distance that premaxillaries extend posterior to posterior tip of nasals; length of upper diastema (LUDIAST); alveolar length of maxillary toothrow (LMXTR); width of upper incisor (WUINC); length of lower diastema (LLDIAST); alveolar length of mandibular toothrow (LMNDTR); width of lower incisor (WLINC). *Geomys pinetis* crania are illustrated in Merriam (1895), Pembleton and Williams (1978), and Hall (1981).

In order to analyze geographic variation it was necessary to combine specimens from adjacent localities into larger samples. The state was divided into 13 partial to multicounty natural regions delimited by rivers (Fig. 2). The intent was to define objectively geographic units containing populations that might be morphometrically distinguishable because of their histories of isolation. Because rivers are known to influence movements of pocket gophers (Udvardy 1969, Lowery 1974), care was taken not to group into the same samples specimens from opposite sides of boundary rivers. Further details defining these natural regions are available in Wilkins (1982).

Additionally, three geographic areas were recognized to permit assessment of the roles

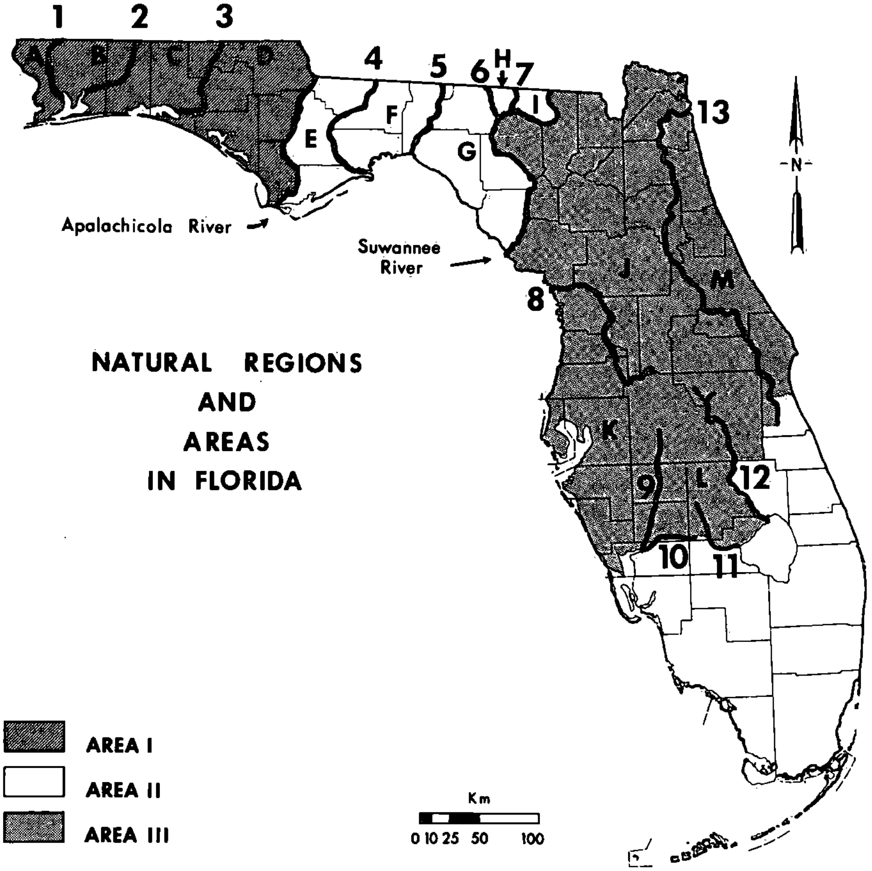

Figure 2.—Areas (I-III) and component natural regions (A-M) of Florida divided by rivers (heavy black lines). The unshaded portion of the southern peninsula lies outside the range of *Geomys pinetis*. Codes for inter-region boundary waterways are: (1) Escambia R., (2) Yellow R., (3) Choctawhatchee R., (4) Ocklockonee R., (5) Aucilla R., (6) Withlacoochee R., (7) Alapaha R., (8) Withlacoochee R., (9) Peace R., (10) Prairie Creek, (11) Fisheating Creek, (12) Kissimmee R., and (13) St. Johns R.

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of Florida's two largest rivers (Apalachicola and Suwannee, respectively) in pocket gopher zoogeography (Fig. 2). Area I includes regions (A, B, C, and D) west of the Apalachicola River. Regions E, F, G, H, and I between the Apalachicola and Suwannee rivers comprise area II. The peninsular regions J, K, L, and M of area III are separated from area II by the Suwannee River.

ANALYSES CONDUCTED.—Intrapopulation variation was examined for *Geomys pinetis* from Gainesville (Alachua Co.), the largest available local sample (n = 209). The MEANS and TEST procedures of the Statistical Analysis System (SAS, Helwig and Council 1979) evaluated sex, age, and individual character variation in each sex/age category.

Multivariate analyses were used first to explore phenetic relationships among regional samples (cluster analyses) and then to test for differences among regional or area samples (multivariate analyses of variance and canonical analyses). All multivariate analyses were conducted separately for each of the four sex/age categories. For cluster analyses, input data were the standardized regional mean character values for each of 16 cranial characters. Regions represented by one or no specimens were omitted from multivariate analyses. Data sets standardized to zero mean and unit standard deviation were submitted to the Ward's method algorithm (Ward 1963) of the CLUSTAN multivariate statistical package (Wishart 1975). Multivariate analyses of variance (MANOVA's) were used to test the null hypotheses of no significant differences (1) among all regional samples and (2) among area samples. Using character measurements of individual specimens as input, MANOVA's were computed by the GLM procedure of SAS. MANOVA results are graphically presented in canonical variates projections. Character loadings and other details pertaining to MANOVA's are available in Wilkins (1982).

RESULTS

NON-GEOGRAPHIC VARIATION

Coefficient of variation (CV) values were used to assess within-sample variation in the 20 cranial characters. Because of extremely large CV values (Table 1), four characters (TEMP, AWINT, PWINT, LINT) were omitted from further analyses. Others with relatively large CV values were retained because of their previous usage in systematic studies of southeastern United States pocket gophers. Variation in character means due to sex and age was evaluated using *t*-tests. For age class 1, males were larger than females in all of the remaining 16 characters; LWNAS was the only character for which the sexes were not different ($P>0.05$). For the older adults (age 2), females were slightly, but not significantly, larger than males only in GWNAS. The sexes were similar in size for IOC, LWNAS, and PMEXT. Males were significantly larger than females in the remaining measurements.

The means for male *Geomys pinetis* of both age categories were similar in four characters: IOC, LWNAS, GWNAS, and PMEXT. Old adult males were significantly larger than younger adult males in all other features examined. For females, mean values for IOC in both age groups were equal. In the remaining characters, older adult females were larger than younger adult females; these differences were significant for all features except LWNAS, GWNAS, and PMEXT. Because the Gainesville sample of *Geomys pinetis* demonstrated such marked sex and age variation, subsequent analyses of geographic variation entailed comparisons of subsamples of like sex and age. The four subsamples recognized are (1) males of age class 1, (2) males, age 2, (3) females, age 1, and (4) females, age 2.

Table 1—Non-geographic variation in 20 cranial characters for Recent *Geomys pinetis* from Gainesville, Alachua County, Florida. Univariate statistics presented for each of four sex/age categories. Each entry contains the mean and standard deviation (first line) and extreme values and coefficient of variation (second line). Measurements are in millimeters; coefficient of variation is expressed as a percentage.

	Male (N = 87)		Female (N = 122)	
Character	Age 1 (N = 53)	Age 2 (N = 34)	Age 1 (N = 84)	Age 2 (N = 38)
Skull Length (GLS)	49.6, 2.53 44.2–54.8, 5.1	52.5, 1.69 48.4–55.7, 3.2	44.6, 1.77 40.0–50.7, 4.0	46.3, 2.75 40.1–55.1, 5.9
Zygomatic Width (ZYGO)	29.6, 1.74 26.0–33.6, 5.9	32.1, 1.33 29.7–35.6, 4.1	26.3, 1.33 23.5–30.3, 5.1	28.0, 1.68 25.1–34.3, 6.0
Mastoid Width (WMAST)	25.5, 2.98 20.1–28.8, 11.7	27.1, 1.56 20.1–28.9, 5.7	23.6, 1.47 14.5–28.9, 6.3	24.9, 1.30 22.5–28.9, 5.2
Depth of Cranium (DCRAN)	14.9, 0.59 13.8–16.4, 4.0	15.2, 0.51 14.2–16.1, 3.4	14.0, 0.47 12.8–15.5, 3.4	14.4, 0.49 13.4–16.2, 3.4
Depth of Rostrum (DROST)	7.4, 0.51 6.2–9.0, 6.9	7.7, 0.44 6.9–8.6, 5.7	6.6, 0.40 5.7–7.8, 6.1	7.0, 0.49 6.1–8.2, 7.0
Width of Rostrum (WROST)	10.5, 0.58 9.1–11.8, 5.6	11.0, 0.50 9.9–12.1, 4.6	9.6, 0.51 8.2–10.9, 5.4	10.0, 0.49 9.3–11.4, 5.0
Interorbital Constriction (IOC)	7.0, 0.33 6.3–7.7, 4.7	6.9, 0.45 6.0–7.8, 6.4	6.9, 0.33 6.1–7.7, 4.8	6.9, 0.30 6.4–7.7, 4.4
Distance between Temporal Ridges (TEMP)	4.0, 1.25 1.7–7.7, 30.9	2.5, 1.62 0.7–7.6, 63.3	5.8, 1.43 1.9–12.4, 24.7	4.7, 1.64 2.5–7.8, 30.9
Anterior Width of Interparietal (AWINT)	2.2, 1.14 0.1–6.1, 51.3	1.4, 0.79 0.2–3.2, 55.9	3.65, 1.15 0.9–8.6,31.6	3.1, 1.09 1.4–6.3, 35.2
Posterior Width of Interparietal (PWINT)	5.7, 1.13 2.0–8.0, 19.7	5.6, 0.92 3.5–7.6, 16.4	6.2, 0.66 4.0–8.2, 10.6	5.7, 0.87 3.3–7.4, 15.3
Length of Interparietal (LINT)	4.7, 0.84 3.5–7.2, 17.7	4.8, 0.65 3.6–6.6, 13.3	4.5, 0.64 3.0–6.7, 14.2	4.3, 0.52 3.3–5.7, 12.2

Least Width of Nasals (LWNAS)	2.2, 0.32 1.3–3.0, 14.3	2.2, 0.39 1.4–3.2, 17.5	2.1, 0.26 1.5–2.8, 12.3	2.2, 0.86 1.6–7.2, 37.7
Greatest Width of Nasals (GWNAS)	2.8, 0.34 2.1–3.6, 12.3	2.7, 0.38 1.9–3.4, 14.0	2.6, 0.28 2.0–3.3, 10.8	2.8, 0.84 2.2–7.6, 29.9
Maxillary Extension beyond Nasals (PMEXT)	3.1, 0.74 1.5–4.4, 23.9	2.9, 0.65 1.4–4.6, 22.0	2.7, 0.65 1.2–4.2, 24.1	2.9, 0.62 1.2–4.6, 21.5
Length of Upper Diastema (LUDIAST)	19.5, 1.50 16.2–22.7, 7.7	21.2, 1.01 18.9–23.0, 4.8	16.4, 1.25 10.2–20.1, 7.6	17.8, 1.45 15.3–23.2, 8.2
Length Maxillary Toothrow (LMXTR)	10.1, 0.51 9.1–11.6, 5.1	10.5, 0.60 9.3–11.7, 5.7	9.7, 0.70 5.2–11.6, 7.3	10.0, 0.46 9.3–11.6, 4.6
Width of Upper Incisor (WUINC)	2.3, 0.23 1.9–3.0, 10.0	2.4, 0.15 2.2–2.7, 6.2	2.1, 0.14 1.8–2.6, 6.7	2.2, 0.16 1.8–2.6, 7.2
Length of Lower Diastema (LLDIAST)	12.0, 1.33 7.2–14.9, 11.1	13.1, 1.00 11.7–16.1, 7.6	10.2, 0.81 8.5–13.2, 7.9	11.1, 1.02 9.2–14.5, 9.2
Length Mandibular Toothrow (LMNDTR)	8.7, 0.43 7.6–9.7, 4.9	9.1, 0.42 7.9–10.0, 4.6	8.3, 0.47 6.1–9.3, 5.7	8.6, 0.39 7.8–9.6, 4.6
Width of Lower Incisor (WLINC)	2.2, 0.22 1.7–2.9, 10.2	2.3, 0.13 2.1–2.6, 5.7	1.9, 0.12 1.7–2.3, 6.3	2.0, 0.18 1.6–2.6, 8.9

GEOGRAPHIC VARIATION

CLUSTER ANALYSES

In this study phenetic similarities between samples of like sex and age are assumed to reflect the degree of past or present gene flow between populations in adjacent regions (*sensu* Pounds and Jackson 1981). An alternative argument for high phenetic resemblances between populations is that of highly similar selection regimes operating in populations not experiencing gene flow (Ehrlich and Raven 1969). Cluster composition in the following analyses addresses the relative importance of the various boundaries (principally rivers) in inhibiting pocket gopher dispersal (Fig. 3).

MALES, AGE 1.—In the dendrogram depicting similarities between samples of young adult males, the four peninsular regions (area III) cluster tightly with each other, yet distantly from all other area I and II regions (Fig. 3). The only two area I regions (C and D) represented in this comparison comprise a discrete cluster. Regions G and F (area II) form two single-member branches.

MALES, AGE 2.—The separation of samples by area is less clear in this comparison due to positioning of the area II regions F and H (Fig. 3). G bears little resemblance to any region, whereas F is included with area III. The two regions from area I (C and D) form a distinct cluster. Three of the four peninsular regions comprise another highly similar group; the fourth peninsular region (L) occurs in the same major cluster as regions J, K, and M.

FEMALES, AGE 1.—Two primary clusters are evident in the dendrogram generated for females of age class 1 (Fig. 3). One of these clusters contains all four peninsular regions (J, K, L, and M). The remaining regions, all west of the Suwannee River, are split into three groups. One group contains only panhandle forms (B, C, and D) from west of the Apalachicola River (area I). Of the three area II regions included in this analysis, two (F and G) are closely united in one cluster. Region H, however, is distant from both area I and II clusters.

FEMALES, AGE 2.—The dendrogram for age class 2 females resembles that for old age males (Fig. 3). Regions A, C, and D form a discrete cluster containing regions from no other areas. A second major cluster includes regions J, K, and M (all peninsular) plus region F (area II); these same four regions formed a group in the age 2 male comparison. The remaining two regions (E and L) in this analysis are similar to each other but different from all other regions.

In each of the four cluster analyses, all area I regions were consistently and exclusively grouped together. In the two age 1 dendrograms the four

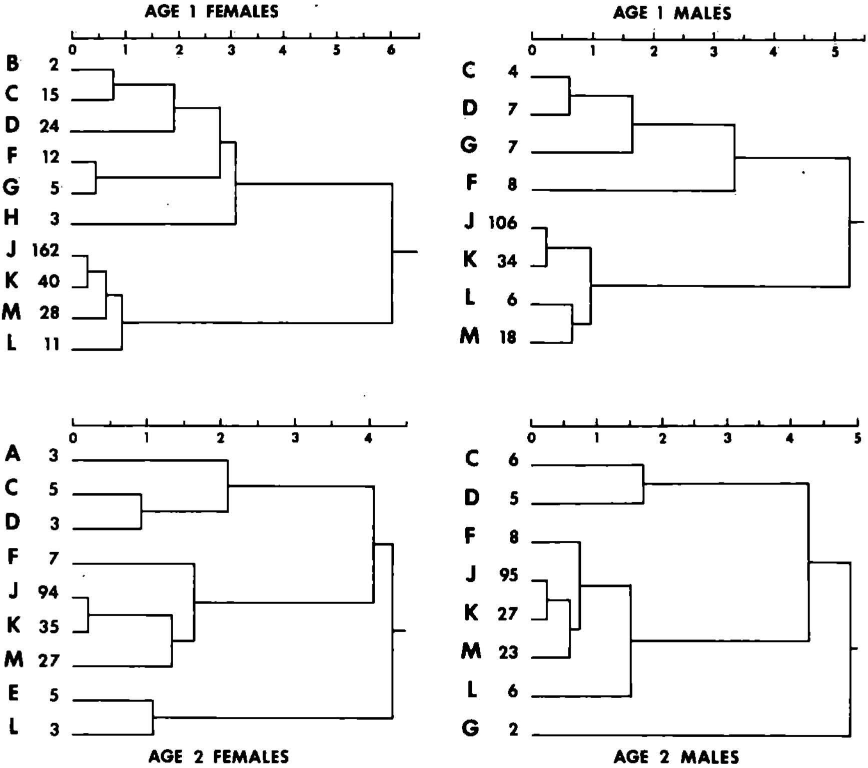

Figure 3.—Results of cluster analyses of the four sex/age categories of Recent *Geomys pinetis* in Florida. Dendrograms were computed from distance matrices using Ward's method. Letters identify natural regions; associated numbers indicate sample size. Horizontal scales are a dissimilarity measure.

peninsular regions formed exclusive, highly similar clusters, while in the age 2 dendrograms three peninsular regions grouped with an area II region. In all four comparisons, area II regions were placed either alone, or with another area II region, or with peninsular regions. These data support the hypothesis that both the Apalachicola and Suwannee rivers are barriers to gene flow in pocket gophers, with the Apalachicola being the more effective of the two rivers.

MULTIVARIATE ANALYSES OF VARIANCE: VARIATION AMONG REGIONS

The occurrence of statistically significant morphometric differences ($P<0.0002$) among samples characterizing different natural regions was demonstrated for each sex/age category (Table 2).

MALES, AGE 1.—For age 1 males, the first three canonical variates

Table 2—Results of multivariate analyses of variance for differences among regional samples and among area samples of Recent *Geomys pinetis* from Florida. Included are statistics for three tests for significant differences between samples plus Roy's test for significance of the first canonical vector. Presented separately for each sex/age category.

	Males		Females	
Statistics	Age 1	Age 2	Age 1	Age 2
	Variation Among Regions			
Hotelling-Lawley Trace	1.7571	2.3766	1.8625	1.9108
F	1.74	2.36	2.86	1.78
d.f.	160,1582	144,1289	176,2972	160,1492
Prob≥*F*	0.0001	0.0001	0.0001	0.0001
Pillai's Trace	1.3032	1.5997	1.2528	1.2951
F	1.58	2.07	2.27	1.49
d.f.	160,1690	144,1377	176,3102	160,1600
Prob≥*F*	0.0001	0.0001	0.0001	0.0002
Wilk's Criterion	0.2224	0.1456	0.2230	0.2130
F	1.67	2.23	2.54	1.62
d.f.	160,1385	144,1161	176,2504	160,1308
Prob≥*F*	0.0001	0.0001	0.0001	0.0001
Roy's Maximum Root Criterion	0.5326	0.7899	0.9610	0.9553
F	9.32	14.04	25.07	15.86
d.f.	10,175	9,160	11,287	10,166
	Variation Among Areas			
Hotelling-Lawley Trace	0.7324	0.9282	0.9651	0.4744
F	3.82	4.38	8.54	2.34
d.f.	32,334	32,302	32,566	32,316
Prob≥*F*	0.0001	0.0001	0.0001	0.0001
Pillai's Trace	0.5257	0.5874	0.5808	0.3676
F	3.77	3.98	7.29	2.25
d.f.	32,338	32,306	32,570	32,320
Prob≥*F*	0.0001	0.0001	0.0001	0.0002
Wilk's Criterion	0.5396	0.4824	0.4786	0.6597
F	3.79	4.18	7.91	2.30
d.f.	32,336	32,304	32,568	32,318
Prob≥*F*	0.0001	0.0001	0.0001	0.0002
Roy's Maximum Root Criterion	0.4810	0.7300	0.8123	0.3590
F	44.01	60.95	121.43	31.24
d.f.	2,183	2,167	2,299	2,174

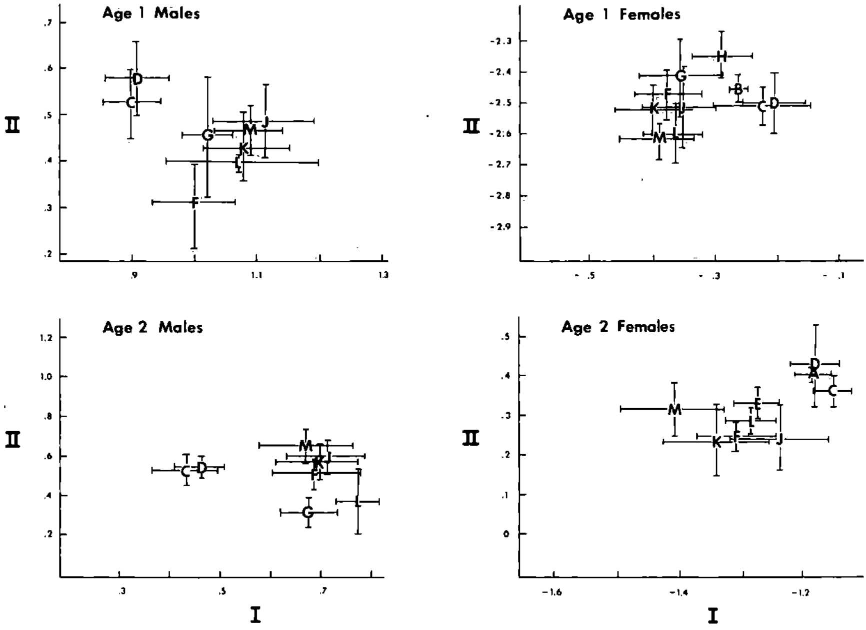

Figure 4.—Canonical variates projections showing relationships among regional samples separately for the four sex/age categories of Florida *Geomys pinetis*. Bars represent one standard deviation to either side of sample means (indicated by position of letters). Sample sizes indicated in text.

represent 30.31%, 25.87%, and 19.94% of the variation, respectively; the other vectors each entail less than 8% of the total variation. GLS (18.14%) and LMXTR (16.23%) contributed most to separation of samples along variate I; the only other characters on variate I with more than 8% influence were IOC and DROST. Over 70% of the dispersion along variate II stemmed from five characters: WMAST, LUDIAST, IOC, LMXTR, and DCRAN. GLS, WMAST, and LMNDTR were the most important discriminators for variate III.

The plot of sample centroids and corresponding 1 standard deviation bars on axes I vs II shows two sample clusters where regions C and D (area I) form one group and regions from areas II and III collectively form the other (Fig. 4). In this plot, regions C and D broadly overlap each other but do not overlap other samples. Area II samples (F and G) are intermediate between those of areas I and III and broadly overlap various of the area III regions. Regional sample sizes are as follows: A, 1; C, 4; D, 7; E, 1; F, 8; G, 4; I, 1; J, 104; K, 34; L, 6; and M, 17.

MALES, AGE 2.—Variates I, II, and III individually represent 33.24%, 25.69%, and 17.65% of the inter-sample variation, collectively explaining

76.58%. Less than 10% of the variation accompanies each of the remaining axes. The five most influential variables for variate I (LMXTR, GLS, IOC, LUDIAST, and DROST) individually explained greater than 9% (and collectively the majority) of the observed variability. Three-quarters of the dispersion along axis II was attributable to five characters: WROST, GLS, DROST, WMAST, and DCRAN. Along variate III five characters (LUDIAST, WMAST, GLS, ZYGO, and DCRAN) accounted for more than 56% of the variation.

Two distinct sample clusters are evident in the scatter plot of regional sample centroids along variates I and II (Fig. 4). Samples C and D (area I) variously overlap, but are widely separated from the cluster composed of area II and III samples. Overlap of confidence bars of region F (area II) with those of J, K, L, and M (area III) is extensive. Regional sample sizes are as follows: B, 1; C, 6; D, 5; E, 1; F, 8; G, 2; J, 95; K, 26; L, 6; and M, 24.

FEMALES, AGE 1.—Over 78% of the variation between regional samples corresponds to the first three canonical variates which individually entail 51.60%, 16.56%, and 10.26% of the variation, respectively. Eight other roots each account for less than 8% of the variation. Along variate I, about 60% of the dispersion occurred through five characters, each with greater than 9% influence: IOC, DCRAN, LUDIAST, ZYGO, and WMAST. Over 57% of the dispersion along variate II is shared between ZYGO, LMNDTR, IOC, WMAST, and DCRAN. The five most important characters along variate III were DROST, ZYGO, LMNDTR, WUINC, and IOC; the first two of these together exert nearly 50% of the discriminating ability of this vector. In the plot of regional sample centroids on axes I and II (Fig. 4), area I samples (B, C, and D) group closely together and are separate from area II and III samples. Regional sample sizes are as follows: A, 1; B, 2; C, 15; D, 23; E, 1; F, 12; G, 5; H, 3; J, 161; K, 39; L, 9; and M, 27.

FEMALES, AGE 2.—Variates I, II, and III entail 49.99%, 16.86%, and 10.38% of the overall variation, respectively, and 77.23% collectively. Less than 8% of the variation is explained by each of the remaining vectors. The five most influential characters along variate I (LMNDTR, LUDIAST, DCRAN, GWNAS, and LMXTR) accounted for 49% of its dispersion. WMAST, GLS, IOC, LMNDTR, and DROST were the five most important characters along variate II. Three attributes (LMXTR, WMAST, and ZYGO) on variate III explained 61% of the variation. The canonical variates plot on axes I and II shows area I regions A, C, and D to form an overlapping cluster separate from the area II and III regions (Fig. 4). Regional sample sizes are as follows: A, 3; B, 1; C, 5; D, 3; E, 5; F, 7; G, 1; J, 93; K, 34; L, 5; and M, 27.

MULTIVARIATE ANALYSES OF VARIANCE: VARIATION AMONG AREAS

The preceding MANOVAs and canonical variates plots suggest a pattern of variation wherein phenetic breaks among regional samples correspond to the three geographic areas defined by the Apalachicola and Suwannee rivers. A final series of MANOVAs tested the null hypothesis of no differences among joint means of samples representing areas I, II, and III. For each of the four sex/age categories, the hypothesis of equal means was rejected for all test statistics at $P<0.0002$ (Table 2). Hence, *Geomys pinetis* from the three areas of Florida differ significantly in cranial dimensions. Plots of centroid means ± 1 standard deviation (Fig. 5) as developed from plots of individual specimens show the same pattern of overlap as in Figure 4. In all cases area I is distinct from areas II and III; areas II and III overlap variously with each other.

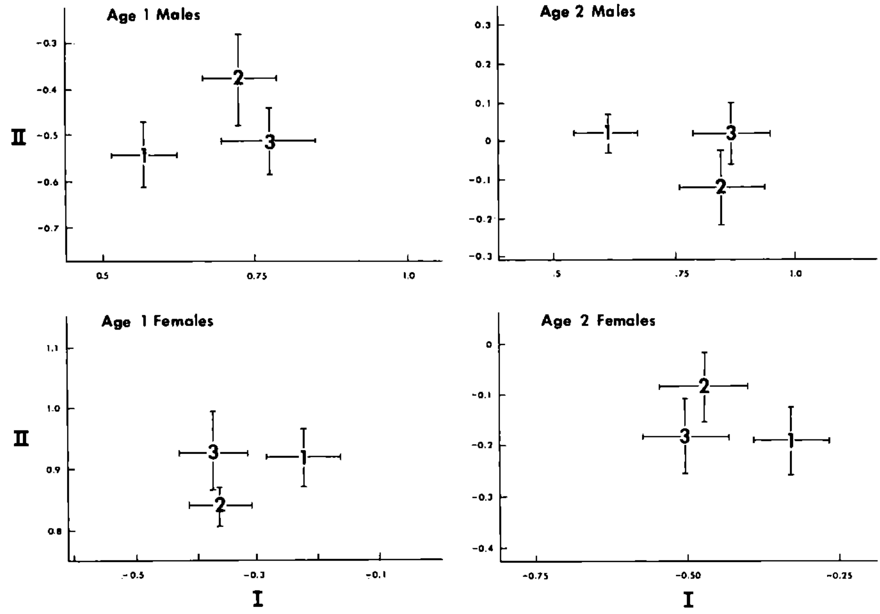

Figure 5.—Canonical variates projections showing relationships among areas separately for the four sex/age categories of Florida *Geomys pinetis*. Bars represent one standard deviation to either side of sample means (indicated by position of letters).

DISCUSSION

Pocket gophers in Florida occur in two major zoogeographic units: the panhandle west of the Apalachicola River (area I), and the remainder of the state, which may be further subdivided. The areas east of the Apalachicola River are separated by the Suwannee River into the eastern panhandle (area II) and the peninsula (area III). MANOVA and canonical variate analyses show slight to extensive overlap of samples from the peninsula and eastern panhandle, but no overlap of these with the western panhandle samples. Hence, the Apalachicola River apparently comprises a more effective barrier to pocket gopher dispersal and gene flow than the Suwannee River.

This study clearly indicates that interruption of gene flow to varying degrees by rivers of different magnitudes is manifest in the pattern of geographic variation in cranial characters of *Geomys pinetis* in Florida. Study of southeastern United States fence lizards (*Sceloporus undulatus*) demonstrating direct correlation between river size and amount of differentiation of populations on opposite sides of such rivers is highly supportive of results of this pocket gopher investigation (Pounds and Jackson 1981). The findings of both of these studies contradict Ehrlich and Raven's (1969) contention that populations lacking gene flow will remain undifferentiated when similar selection regimes are acting on both populations. It is hard to imagine that different selective forces operate on *G. pinetis* populations in seemingly identical habitats separated by as little as a few hundred meters on opposite banks of the Suwannee River or by a few kilometers on opposite sides of the Apalachicola River. Rather, phenetic divergence seems dependent on degree of gene flow across these rivers.

Avise et al. (1979) studied genetic variation of the entire *Geomys pinetis* complex using mitochondrial DNA and electrophoretic techniques and demonstrated a similar pattern of geographic variation corresponding to these rivers. They acknowledged a significant role for the Apalachicola-Chattahoochee-Flint river system in separating eastern and western "forms" of *Geomys pinetis*. Further, geographic distribution of electromorph frequencies of 6-phosphogluconate dehydrogenase (PGD) hints that the Suwannee River might separate peninsular populations from mainland populations (Avise et al. 1979:6697).

In the latest published revision of *Geomys pinetis*, Williams and Genoways (1980) found no subspecific breaks in Florida *Geomys pinetis* nor did they recognize any barriers to gene flow in Florida. They viewed the complex as one species with two subspecies: *G. p. pinetis* representing the entire species range except for the isolated colony of *G. p. fontanelus* (formerly *G. fontanelus*) near Savannah, Georgia. Evaluation of the importance of the Suwannee River was precluded by their method of grouping samples because their samples 14 and 20 each included specimens from both sides of the Suwannee River (Williams and Genoways 1980:406–408).

RIVERINE BARRIER MECHANISMS

It is of some interest to consider why the Apalachicola appears to serve (or have served) as a more important barrier to pocket gopher gene flow than has the Suwannee. Three different features are evaluated in this analysis of the effectiveness of these river valleys as barriers to animal dispersal.

POTENTIAL FOR COMMUNICATION AROUND HEADWATERS.—For genes to flow between populations on opposite sides of a river, individuals need not actually cross the waterway. An alternative is for genes to be exchanged with adjacent colonies thereby facilitating flow up one side of the river, around the headwaters, and then down the opposite side of the river. For this mechanism to function, pocket gopher populations must be appropriately distributed. The entire Suwannee River watershed is contained within the range of *Geomys pinetis*. Therefore, populations on opposite sides of the Suwannee River are potentially in genetic communication, albeit indirectly. However, this scheme of gene flow is not presently possible for Apalachicola-Chattahoochee-Flint river basin populations because these rivers originate in the Appalachian Mountains far beyond the northernmost extent of the range of *Geomys pinetis*.

EFFECTIVE WIDTH OF RIVER CORRIDOR.—The Apalachicola and Suwannee rivers also differ importantly in their effective widths. Effective width includes width of the watercourse and the distance between suitable habitats on opposite sides of the rivers. Actual width of the Suwannee in most places can be measured in a few tens of meters. Suitable sandhill and xeric hammock habitats extend to river's edge along much of the Suwannee River (Davis 1980). In many places (e.g. in Suwannee-Lafayette and Columbia-Hamilton counties) active pocket gopher colonies occur on opposite sides of the Suwannee within a few hundred meters of each other (pers. obs.).

The effective width of the Apalachicola River is much greater—on the order of several kilometers. Actual width of this river approaches (and near the mouth exceeds) 100 m. Unlike the Suwannee, the Apalachicola has cut a deep valley occupied by habitats (e.g. swamp hardwood floodplain forests) excessively wet for *Geomys*. These forests are very broad (several km) in Gulf and Franklin counties (along the Gulf coast) and in southern parts of Calhoun and Liberty counties. Sandhill habitat suitable for pocket gophers approaches the river to within as little as 2 or 3 km only in northwestern Liberty and western Gadsden counties (pers. obs.)

STREAMFLOW PARAMETERS.—Various streamflow measurements also demonstrate the larger size of the Apalachicola River (Heath and Wimberly 1971:466, 531). Average discharge of the Suwannee at Branford (Suwannee Co.) is 192 cubic meters per second (cms) in contrast to 709 cms for the Apalachicola at Blountstown (Calhoun Co.). Recorded maximum and minimum discharges (and associated water gage heights) for the Suwannee are 2374 cms (10.38 m) and 43 cms (0.60 m); those values for the Apalachicola are 2773 cms (6.77 m) and 152 cms (0.73 m).

Because both rivers are subject to vast fluctuations in water height and discharge, the possibility exists that pocket gophers could swim or conceivably even walk across the waterway during drought periods. Barrington (1940) experimentally showed *G. pinetis* capable of swimming in quiet water a distance of 23 m in 8 min. For this to be effective, however, pocket gophers must be in residence in the immediate vicinity. Because of the greater proximity of colonies and suitable habitat to the Suwannee than to the Apalachicola, this mode of interchange appears feasible only for the Suwannee. For the same reason, rivercourse changes and oxbowing could enhance cross-channel gene flow only for the Suwannee River populations.

BIOGEOGRAPHIC CONSIDERATIONS.—The pattern of geographic variation in modern Florida pocket gophers can be examined with respect to two opposing biogeographic hypotheses. A vicariant explanation involves a widespread population that is later dissected by the Apalachicola and Suwannee rivers. Conversely, the dispersalist view has pocket gophers invading a Florida theater already having these rivers and associated riparian corridors well-entrenched. Both the Apalachicola and, as noted above, Suwannee rivers have geological histories antedating the earliest documented (early Irvingtonian) and the earliest conceivable (Blancan) arrival of *Geomys* in Florida (White 1970). The means and timing of movements of *Geomys* from the western to eastern sides of the Apalachicola remain an enigma, although meandering and oxbowing when sandy soils of delta regions were exposed during lowered sealevels seem to be plausible mechanisms.

Whereas the Apalachicola has probably always been a continuously flowing surficial stream (because its bed is of rock types generally impervious to water flow), the Suwannee River has a highly intermittent history because it (and most other peninsular Florida streams) flows through a region of karst limestone. During moister interglacial periods, piezometric surfaces were high and peninsular rivers flowed at the ground surface. Crossing the Suwannee at such times would involve swimming of shallow waters during seasonal dry periods or even travel across dry river beds during extreme droughts. During the drier glacial intervals, however, water table levels dropped substantially, and surficial river beds were abandoned in favor of subterranean flow through karst limestone. A surficial Suwannee River was, at least along portions of its course, nonexistent during certain glacial intervals, and movement across deserted river corridors was surely unimpeded. It is apparent, then, that the dispersalist hypothesis applies to the Apalachicola River and that dispersalist and vicariance hypotheses alternatively apply to the Suwannee River.

RIVERINE BARRIER EFFECTS ON OTHER TAXA

APALACHICOLA RIVER.—The effect of the Apalachicola River as a zoogeographic barrier has been widely recognized in many animal groups in addition to *Sceloporus undulatus* fence lizards as noted above (Pounds and Jackson 1981). Two genera (*Mycotrupes* and *Gronocarus*) of beetles (Scarabaeidae: Geotrupinae) occur on opposite sides of the Apalachicola River system (Hubbell 1954, Howden 1963). Neill (1957) noted that the Apalachicola and other rivers of the panhandle mark the eastern distributional limits of many western fishes and the western limits of eastern forms.

The mutually exclusive distributions of two species of pocket gopher lice (Mallophaga: Trichodectidae) bear directly on *Geomys pinetis* zoogeography (Price 1975). *Geomydoecus mobilensis* has been found only on southeastern pocket gophers collected from west of the Apalachicola River. A closely related species (*Geomydoecus scleritus*) fills this ectoparasitic niche in *Geomys* populations east of Apalachicola River. The existence of this variation pattern in species so closely connected to pocket gophers supports the interpretation that the Apalachicola River has influenced gene flow between Florida *Geomys* populations.

Not all mammalian species, however, are significantly restricted by the Apalachicola River. Hall (1981:505) figured this river as the division between a western subspecies and two eastern subspecies of *Geomys pinetis*. Survey of range maps in Hall (1981) of all mammal species occurring in Florida reveals *Neotoma floridana* to be the only other mammal with subspecies boundaries coinciding with the Apalachicola River. The entire range of *Neofiber alleni* lies east of Apalachicola River. Of the approximately 70 species of native land mammals in Florida (Stevenson 1976), the distributions of about 48 species span the Apalachicola River. Hence, this river seems to pose a barrier of some recognizable magnitude to only about 6% of the more widely distributed Florida mammal species. Similarly, Christman (1980) found that geographic variation patterns in none of 15 species of Florida snakes corresponded with the Apalachicola River.

SUWANNEE RIVER.—The Suwannee Straits, the former salt water channels between the United States mainland and peninsular Florida that existed to various extents during the Neogene interglacials, occupied that area now drained by the Suwannee and St. Marys rivers and their tributaries (Neill 1957:188). During these interglacials, the Suwannee Straits apparently barred movement of many species between the mainland and the "peninsula." The effectiveness of these straits as a barrier is evidenced by the lengthy list of subspecies and species of vertebrates and invertebrates presently restricted to peninsular Florida (Neill 1957:189–194). The ranges of several mainland species of mollusks do not extend south or east of the Suwannee River (Dall 1890–1903, Clench and Turner 1956). Additionally cyprinid, sucker, and darter fishes, groups which occur abundantly in the southeastern United States, are very poorly represented in the Florida peninsula (Neill 1957:193). One of the most important patterns of geographic variation observed in 15 species of Florida snakes, the Suwannee Straits pattern, demonstrates the zoogeographic effect of the Suwannee River (Christman 1980). Review of species and subspecies boundaries of the approximately 48 species of Florida mammals with distributions spanning the Suwannee River reveals five species (*Sciurus niger, Oryzomys palustris, Neofiber alleni, Mustela vison,* and *Spilogale putorius*), or about 10%, that have subspecies limits approximating the Suwannee River. No Florida mammals have species boundaries coinciding with this river.

A further probable reason that the phenetic break in *Geomys* corresponding to the Suwannee River is of lesser significance pertains to the antiquity and persistence of the Suwannee Straits as compared to the Apalachicola as a barrier to *Geomys* gene flow in the Florida peninsula. The Suwannee Straits existed intermittently during the Miocene and Pliocene, an interval spanning from about 25 mybp to 5 mybp. The Straits' last occurrence corresponds to the 30 m to 52 m marine shorelines: Sunderland shoreline (Cooke 1945) and Okefenokee shoreline (MacNeil 1950). Alt and Brooks (1965) and most subsequent researchers recognize Miocene and Pliocene ages for these and earlier (higher) shorelines. Later transgressions produced lower shorelines (Wicomico, 21 m to 30 m; Penholoway, 13 m to 21 m; Talbot, 8 m to 13 m; and Pamlico, 3 m to 8 m; see Healy 1975), none of which were of sufficient elevation to isolate the peninsula from the mainland. These lower shorelines are of Pliocene and Pleistocene age (Alt and Brooks 1965).

The first appearance of the genus *Geomys* in the fossil record was in the mid-Pliocene at the beginning of the Blancan Land Mammal Age, some 3.5 mybp (Lindsay et al. 1975). The earliest known occurrence of geomyids in Florida is from the early Irvingtonian Inglis IA deposit (Citrus Co.), an early Pleistocene site about 1.8 million years old (Wilkins 1984). The actual time of arrival of geomyids in Florida is as yet uncertain, but could have been during the Blancan. The Pleistocene is generally regarded as beginning about 2 million years ago. Therefore, the historic importance of the Suwannee Straits seemingly has no bearing on pocket gopher distribution because geomyids could not have entered Florida until after the mid-Pliocene. Hence, the Suwannee River valley as a terrestrial feature has played a role in occluding gene flow in pocket gophers in Florida only during the Quaternary.

This study underscores the role that river valleys can serve as dispersal barriers to various taxa. It may be noted, however, that under other circumstances pocket gophers may not find river systems to be barriers. An example includes *Geomys arenarius* in the Rio Grande valley (Williams and Genoways 1978). In such semiarid to arid settings the only friable soils and suitable vegetation occur within the riparian corridor. Smith and Patton (1980) demonstrated that gene flow in *Thomomys bottae* occurs across the lower Colorado River between the Palo Verde and Cibola valleys and between the Imperial and Yuma valleys, but that barriers to north-south gene flow along both river banks exist. Pocket gophers presumably crossed these rivers on occasions when water flow had diminished or ceased altogether, thus maintaining gene flow along both sides of the river.

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APPENDIX

Specimens Examined

The 1123 specimens of *Geomy pinetis* examined in this study are listed below by region. The number of specimens and the museum in which they are deposited for each locality are enclosed in parentheses. Collection acronyms are as follows: American Museum of Natural History (AMNH); Carnegie Museum of Natural History (CMNH); Delaware Museum of Natural History (DMNH); Field Museum of Natural History (FMNH); University of Florida, Florida State Museum (UF); University of South Florida (USF); Florida State University (FSU); University of Georgia (UGA); Harvard University, Museum of Comparative Zoology (MCZ); University of Illinois, Museum of Natural History (UIMNH); University of Kansas, Museum of Natural History (KU); Michigan State University, The Museum (MSU); University of Michigan, Museum of Zoology (UMMZ); Albert Schwartz private collection (AS); Shippensburg State College, Vertebrate Museum (SSC); Tall Timbers Research Station (TTRS); Texas Tech University, The Museum (TTU); and United States National Museum of Natural History (USNM).

REGION A (10 *specimens*).—*Escambia Co.*: Century (1, AMNH); Gonzales (3, AMNH); 7 mi N, 2 mi W Gonzales (1, AMNH); Pensacola (1, UF; 1, MCZ; 3, USNM).

REGION B (12 *specimens*).—*Santa Rosa Co.*: Milton (12, USNM).

REGION C (44 *specimens*).—*Holmes Co.*: Ponce de Leon (1, AMNH; 1, USNM); Westville (1, USNM). *Okaloosa Co.*: Crestview (7, AMNH; 4, USNM); 4.5 mi N, 1 mi W Fort Walton (1, AMNH); 5 mi N, 0.5 mi E Fort Walton (1, AMNH); Shalimar (2, AMNH); 0.5 mi W Co. line, Hwy 90 (2, TTU). *Walton Co.*: Argyle (1, AMNH; 1, USNM); 3 mi E Bruce (3, USNM); 1 mi W Bruce (1, USNM); 20 mi E Crestview (2, USNM); 6.5 mi SE DeFuniak Springs (2, USNM); 5 mi NW DeFuniak Springs (2, UF); 10.6 mi W DeFuniak Springs (1, AS; 3, USNM); 1.2 mi N Freeport, Rt. 331 (2, UGA); 1.3 mi N Freeport, Rt. 331 (1, UGA); Rockhill (5, USNM).

REGION D (55 *specimens*).—*Bay Co.*: Highland Park (1, USNM); 5 mi E Inlet Beach (1, USNM); 5 mi E Saunders (1, USNM); Saunders (Park) (3, USNM); Southport (1, AMNH); 5 mi S Youngstown (1, USNM); 1.4 mi S Rt. 79 on Rt. 98 (1, UGA); 1.6 mi N Rt. 98 on

Rt. 79 (1, UGA). *Calhoun Co.*: Blountstown (4, AMNH; 1, USMN); 1 mi W Blountstown (1, UF); 1.4 mi W Blountstown (1, UF); 3.5 mi W Blountstown (1, UF). *Jackson Co.*: 0.7 mi S Butler (1, UF); Cypress (1, USNM); Marianna (1, UF; 3, USNM); Sneads (2, USNM); 4 mi N Snead (2, UF); 7 mi N Snead (1, UF). *Walton Co.*: Grayton Beach (1, USNM); 1.2 mi E Point Washington (2, USNM); 2.5 mi E Point Washington (1, USNM); 4 mi E Point Washington, Rt. 98 (1, USNM); Seagrove Beach, Rt. 395 (1, UF; 3, USNM); Rt. 30A near Seagrove Beach (1, UF); Rt. 30A between (Hwy.) 98 and Seagrove Beach (3, UF); 6.2 mi E Rt. 395 on US 98 (1, UGA); 6.6 mi E Rt. 395 on US 98 (1, UGA); 8.3 mi E Rt. 395 on US 98 (2, UGA). *Washington Co.*: Chipley (1, UF); 2 mi E Chipley (1, USNM); Crystal Lake (1, AMNH); Redbay (1, AMNH); Vernon (2, AMNH); 2 mi N Vernon (1, USNM); 4 mi N Vernon (1, USNM); 10 mi SW Vernon, Miller's Ferry (1, USNM).

REGION E (11 *specimens*).—*Franklin Co.*: St. James Island (1, UF). *Gadsen Co.*: Chattahoochee (2, USNM); E of Concord, 1 mi W Ochlockonee River along Hwy. 12 (2, TTRS; 2, USNM); 5 mi W, 2 mi N Havana (=0.2 mi W Ochlockonee River on Hwy. 12) (2, UGA). *Liberty Co.*: Hosford (1, UF); Rock Bluff (1, TTRS).

REGION F (51 *specimens*).—*Jefferson Co.*: 3 mi S Lloyd (1, UF); Monticello (1, USNM); 2.8 mi W Monticello (1, UF); Waukeenah (1, UF); 2 mi N Waukeena (1, UF). *Leon Co.*: Tallahassee, West Campus (1, FSU); FSU Dairy Farm Pasture (Tallahassee) (7, FSU); 3 mi E Tallahassee (1, UF); 1/4 mi N Hwy. 371, 1 mi W on 371A (1, FSU); 2 1/2 mi N Tallahassee (2, FSU); 10 mi S Tallahassee, on Adams St. (1, FSU); 10.2 mi S, 4.3 mi E Tallahassee (1, FSU); 7.4 mi SW Tallahassee (1, AS); 7.8 mi SW Tallahassee (2, AS); 5 mi WSW Tallahassee (1, FSU); 1.5 mi N Wakulla, Rt. 363 (1, UGA); 5 mi W Wakulla (1, UF); 1 mi N Wakulla Co. line, Hwy. 61 (1, UF); 6 mi E Wakulla Springs Hwy. 61 (1, FSU); Woodville (4, UF); 4 mi E Woodville (1, AMNH); 2.5 mi E Woodville on Natural Bridge Rd. (4, UF). *Wakulla Co.*: Crawfordsville (1, UF); Panacea (1, UIMNH); 1.7 mi N Wakulla (=0.9 mi S Co. line) (1, UGA); 1 mi S Wakulla Gate (2, FSU); near Wakulla Springs (1, FSU); 0.5 mi S Wakulla Springs (4, FSU); 2 mi S Leon Co. line, Rt. 61 (1, FSU); 3.5 mi S Leon Co. line (2, FSU); US 319 and SR 61 (1, FSU); Unknown (1, FSU).

REGION G (24 *specimens*).—*Dixie Co.*: Jena (2, UF); Old Town (4, UF; 3, USNM). *Lafayette Co.*: 4 mi E Alton (1, UF); 3 mi W Branford (1, UF); 1 mi W Suwannee River, SH 27, near Branford (1, UF); 0.5 mi S jct. Hwys. 250 and 251, near Day (1, UF). *Madison Co.*: Lee (2, USNM); Madison (2, USMN); 2 mi W Madison (2, AS). *Taylor Co.*: 3 mi E Perry (1, UF); 4 mi NNW Perry (2, AMNH); 5 mi SSE Perry (1, UF); 3.5 mi SW Perry (1, AMNH).

REGION H (3 *specimens*).—*Hamilton Co.*: 1 mi E Blue Spring (2, UF); 3 mi E Blue Spring (1, UF).

REGION I (1 *specimen*).—*Hamilton Co.*: White Springs (1, UF).

REGION J (588 *specimens*).—*Alachua Co.*: Archer (6, UF); 4.7 mi E Archer (1, UF); Gainesville (12, AMNH: 201, UF; 1, MCZ; 1, UMMZ; 4, USNM); 5 mi SW Gainesville (2, UF); 8 mi SW Gainesville (2, UF); Kanapaha (2, UF); 6 mi E LaCrosse (1, UF); 3 mi E Newberry (1, UF); 1 mi W Newnan's Lake (3, UF); Payne's Prairie (1, UF); San Felasco (1, USNM); Unknown (9, UF). *Baker Co.*: Glen St. Mary (1, USNM). *Bradford Co.*: 0.1 mi S Keystone Heights SR 21 (1, UGA); 2.1 mi S Keystone Heights, SR 21 (2, UGA); 2.2 mi S Keystone Heights, SR 21 (1, UGA); 1.9 mi N Co. line, SR 21 (1, UGA); 3.2 mi N Co. line, SR 21 (1, UGA). *Clay Co.*: 6 mi NE Camp Blanding (1, UF); Green Cove Springs (2, UF); 0.7 mi N Keystone Heights (1, UF); 5.8 mi N Keystone Heights, SR 21 (1, UGA); 2.2 mi NE Keystone Heights (1, UF); 1 mi NW Keystone Heights (1, UF); 2 mi NW Keystone Heights (1, UF); 2.5 mi NW Keystone Heights (1, UF); 1 mi W Keystone Heights (1, UF); Kingsley Lake (6, UF); 3 mi SW Middleburg (1, UF). *Columbia Co.*: Ellisville (1, UF); 0.9 mi E Fort White (1, UGA); 1.0 mi E Fort White, SR 18 (1, UGA); 1.1 mi E Fort White, SR 18 (1, UGA); 4 mi NW Fort White (1, UF); 14 mi N Lake City (1, UF);

16 mi N Lake City, US 441 (15, UGA); 5 mi S Lake City (1, UF); 4.7 mi N Santa Fe River US 41 (1, UF); 1 mi N Co. line, US 27 (1, UGA); 2.3 mi N Co. line, US 27 (1, UGA); 3.5 mi N Co. line, US 41 (1, UGA). *Duval Co*.: Jacksonville (3, FMNH); Jacksonville, N along US Rt. 17 (6, USNM); New Berlin (27, MCZ); Oceanway, US 17 (8, USNM); 0.6 mi N firetower, US Rt. 17 (Tisonia) (1, USNM); 13 mi S, 2 mi W Yulee, I–95 (3, UGA). *Gilchrist Co*.: 1 mi S Bell (1, UF); Trenton (1, UF). *Lake Co*.: Leesburg (27, UF); Mascotte (2, UF); Mt Dora (1, UMMZ); 1 mi W Okahumpka (1, UGA); Tavares (10, UF); 3.1 mi S Tavares (2, AS); 2 mi W Tavares (6, UF); 2 mi NW Lake Yale (Umatilla) (4, UF). *Levy Co*.: Bronson (2, UF); 2.2 mi NE Bronson (1, UF); 9 mi S Chiefland (2, UF); Lebanon Station (1, UF); 18 mi SW Otter Creek, Rt. 24 (1, UF); Sumner (9, UF); 2 mi NE Williston (1, UF); Wylly (2, UF); 6 mi SW Wylly (1, UF). *Marion Co*.: Camp Roosevelt, Ocala National Forest (3, UF); 1.5 mi E Dunnellon (2, UF); 1.6 mi E Dunnellon (1, UF); 4.4 mi E Dunnellon (1, UF); 4.5 mi E Dunnellon (1, UF); 4.6 mi E Dunnellon (2, UF); 4.9 mi E Dunnellon (2, UF); 5 mi E Dunnellon (1, UF); 5.3 mi E Dunnellon (2, UF); 5.7 mi E Dunnellon (1, UF); 9.3 mi E Dunnellon (3, UF); Lake Bryant Ranger Sta., Ocala Natonal Forest (18, USNM); 1.3 mi W Lynne (3, AS); 3 mi W Orange Springs, Hwy. 318 (3, UF); 7 mi W Salt Springs (1, UF); 7 mi E Silver Springs (1, UF); E of Withlacoochee River (3, UF). *Nassau Co*.: Chester (1, USNM); Crandall (11, USNM); 6 mi NW Hilliard (1, UF); Raser's Bluff (7, AMNH); Reed's Bluff (1, AMNH); Rose Bluff, St. Mary's River (2, MCZ); 1.6 mi S St. Mary's River, US 1 (2, UF); Yulee (1, UF); 1.0 mi E Yulee, Rt. 200A (1, USNM); 1.8 mi E Yulee, Rt. A1A (1, USNM); 1.2 mi E Yulee, Rt. 200A (1, USNM); 2 mi E Yulee (2, UGA); 2.4 mi E Yulee, Rt. 200A (1, USNM); 2.5 mi E Yulee, Rt. 200A (1, USNM); 3 mi E Yulee (1, UGA); 3.6 mi E Yulee (1, UGA); Yulee, 1.35 mi NE A1A, C220A (2, UGA); Yulee, 1.4 mi NE A1A, C220A (1, UGA); 2 mi S Yulee (4, AS). *Orange Co*.: 1 mi N Fort Christmas (1, UF); Lockhart (1, UF); 1.5 mi NE Lockhart (1, UF); 1.5 mi SE Lockhart (1, UF); Orlando (2, MCZ; 1, USNM); Tangerine (2, UF); Winter Park (1, UF); Zellwood, Bay Ridge Blvd. (2, MSU). *Osceola Co*.: 5 mi N Kenansville (2, AMNH); 7 mi N Kenansville (2, AMNH; 2, UF); 9 mi N Kenansville (2, UF); 11 mi N Kenansville (2, UF); Nittaw (1, UF); St. Cloud (2, UF). *Putnam Co*.: 5 mi NE Hawthorne (1, UF); W side Levy Prairie (1, UF); 2.5 mi S Melrose (1, UF); Palatka (2, UF; 1, MCZ); 5 mi W Palatka (1, UF). *Seminole Co*.: Fern Park (1, UF); Forest City (1, UF); Geneva (2, USNM). *Sumter Co*.: Wildwood (14, AMNH; 1, UMMZ); 9 mi S Wildwood (1, UGA); SR 470, 3.5 mi W US 301 (1, UGA); SR 470, 4 mi W US 301 (1,UGA); SR 470, between SR 33 and US 301 (2, UGA). *Suwannee Co*.: 0.4 mi E Suwannee River, SH 27 (near Branford) (1, UF); 0.8 mi E Suwannee River, SH 27 (near Branford) (2, UF); Falmouth (5.7 mi E Suwannee RR Sta., Rt. US 90) (1, UF); Live Oak (1, UF); 12 mi W Live Oak, US 90 (1, UGA); 2.5 mi W co. line, US 90 (1, UGA); 24 mi W co. line, US 90 (2, UGA); 25 mi W co. line, US 90 (4, UGA). *Union Co*.: E Lake Butler (3, UF); 3 mi E Lake Butler (1, UF); 0.9 mi N co. line, SR 100 (2, UGA).

REGION K (165 *specimens*).—*Citrus Co*.: Citronelle (2, MCZ); 3.4 mi E Dunnellon (2, UF); 5 mi E Dunnellon (1, UF); 1.4 mi SE Dunnellon (1, UF); 1.7 mi SE Dunnellon (1, UF); 2 mi SE Dunnellon (1, UF); 2.2 mi SE Dunnellon (1, UF); 2.3 mi SE Dunnellon (1, UF); 2.6 mi SE Dunnellon (2, UF); 4.2 mi SE Dunnellon (2, UF); 5.2 mi SE Dunnellon (1, UF); 5.3 mi SE Dunnellon (1, UF); 9 mi SW Dunnellon (1, UF); 6 mi W Dunnellon, SR 488 (2, UGA); 7 mi W Dunnellon, SR 488 (1, UGA); Inverness (1, USNM); 7 mi S Inverness (1, UF); Trenton (1, UF); S of Withlacoochee River (1, UF). *DeSoto Co*.: 4 mi NW Arcadia (1, AS); 8 mi NW Arcadia (1, AS). *Hardee Co*.: Wauchula (2, AMNH; 1, UF). *Hernando Co*.: Bayport (1, UF); Coogler's Camp (1, UF); Weekiwachee Springs (2, AMNH); 1.4 mi W US 19 and Fla. 50 (1, UF). *Hillsborough Co*.: Dug Creek (1, UF); Plant City (3, UF); Tampa, Univ. of South Florida Campus (5, UF; 26, USF); 19.5 mi N Tampa, SR 587 (5, UGA); Wimauma (4, AMNH). *Manatee Co*.: Sullivan's Bridge (1, UF); Jct. Hwys. 64

and 675, N side Manatee River (1, UF); Unknown (1, UF). *Pasco Co*.: New Port Richey (5, AMNH); 5 mi E New Port Richey (9, USNM); SW corner of co. (3, UF). *Pinellas Co*.: Bellaire (5, UF; 2, MCZ); Clearwater (8, UF); 9 mi N Clearwater, Wall Springs (1, UF); 1 mi N Davis Causeway (3, UF); Dunedin (2, UF; 1 UMMZ); Safety Harbor (2, UF); St. Petersburg (4, MCZ; 1, USMN); Tarpon Springs (4, AMNH; 1, UMMZ; 12, USNM); Tarpon Springs Golf Course (2, AS); 1/2 mi N, 1 mi E Tarpon Springs (1, AMNH); 2 mi N, 1 mi E Tarpon Springs (1, AMNH); Unknown (1, UF). *Polk Co*.: Auburndale (1, UF; 7, USNM); 3.2 mi N Bartow (2, UGA); 1 mi NE Davenport (8, AMNH); 1.5 mi NE Davenport (12, AMNH); Along Hwy. 27, 0.6 mi N jct. Rd. 547, near Davenport (1, UF); Along Hwy. 27, 0.6 mi S jct. Rd. 547, near Davenport (1, UF); Along Rd. 547, 0.3 mi E jct Hwy 27, near Davenport (1, UF); Along Rd. 547, 0.6 mi W jct. Hwy. 27 near Davenport (1, UF); Fort Meade (1, AMNH); Frostproof (3, UF); Lake Juliana (1, USNM); 2 mi S Lake Wales, US 27 (1, UGA); 1 mi S Polk City (1, UF); 5 mi S Winter Haven (1, UF).

REGION L (37 *specimens*).—*DeSoto Co*.: Arcadia (3, USNM); N of Arcadia (1, UF); Fort Ogden (1, UF). *Hardee Co*.: S Zolfo Springs (1, UF); 5.4 mi W co. line, Hwy. 66, E of Zolfo Springs (3, UF); 5.5 mi W co. line (5, UGA). *Highlands Co*.: DeSoto City (13, AMNH); 7 mi N Lake Placid (1/4 mi N Josephine Creek) (2, UF); Sebring (5, CMNH); 1 mi N Sebring (1, SSC); SE corner (T34S, R29E, Sec 20) (2, SSC).

REGION M (122 *specimens*).—*Brevard Co*.: Eau Gallie (5, AMNH; 1, DMNH; 4, UF; 1, KU; 12, MCZ; 2, AS). *Duval Co*.: 4 mi W Atlantic Beach (1, UF); 1 mi NW Bayard, Hwy. 1 (3, TTU); 2 mi W Bayard (1, UF); 6 mi SE Jacksonville (1, UF); Mandarin (1, UF); 1/2 mi N St. Johns-Duval Co. line (= 1 mi E Mandarin) (1, UF). *Flagler Co*.: 0.3 mi S St. Johns Co. line, US 1 (1, UF); 0.5 mi S St. Johns Co. line, US 1 (1, UF). *Putnam Co*.: S of Crescent City, US 17 (2, UGA); 13 mi S Palatka, US 17 (2, UGA); Pomona (Park?) (4, USNM); San Mateo (8, UF); 2 mi E San Mateo (1, USNM); 5 mi NE San Mateo (5, USNM); Satsuma (6, UF); 8 mi S Satsuma (1, UGA); Silver Lake (2, AS; 2, UMMZ); Welaka (7, UF); Welaka, Univ. Conservation Reserve (2, UF). *St. Johns Co*.: 13 mi N Bunnell (2, AMNH); 14 mi N Bunnell (1, AMNH); Carterville (21, MCZ); St. Augustine (3, UF); 4 mi S St. Augustine (1, UF); 6 mi S St. Augustine (1, UF); Switzerland (1, UF); 1 mi N Flagler Co. line (1, UF); 1.75 mi N Flagler Co. line (1, UF). *Volusia Co*.: Barberville (1, AMNH; 1, UF); DeLand (1, UF); DeLeon Springs (3, AMNH); Enterprise (1, AMNH); New Smryna (1, DMNH); Pierson city limits, US 17 (4, UGA); S of Seville, US 17 (1, UGA).

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