

SYSTEMATICS AND ZOOGEOGRAPHY OF FOSSIL  
AND RECENT POCKET GOPHERS IN FLORIDA

BY

KENNETH T. WILKINS

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Kenneth T. Wilkins

Dedicated to  
Christine Nasie Wilkins  
and  
Roy and Gwendolyn Wilkins

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Abstract of Dissertation Presented to the Graduate Council  
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By

KENNETH T. WILKINS

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Major Department: Zoology

Cranial and dental features were examined in Recent and fossil pocket gophers (Rodentia: Geomyinae) with the objective of documenting their nearly two million year zoogeographic history in Florida. Movements of these fossorial rodents is inhibited by unsuitable habitats and by water. Multivariate statistical methods were used to determine the importance of rivers as barriers between populations as exhibited by morphological differences between samples. The Apalachicola and Suwannee Rivers, respectively, were found to be the two most important barriers to Geomys movement in Florida. The relative inhibitory influence of these rivers corresponds to features including proximity of suitable habitat to the river, regional topography and soil types, width of the watercourse, and volume and rate of water flow.

The distribution of Geomys in Florida has been strongly influenced by repeated Pleistocene and Recent sealevel changes. At low sea stands Geomys has been widespread with extensive gene flow

throughout the peninsula. However, opportunity for divergence of populations has existed during transgressions when populations have been isolated in refugia of higher elevations. Studies of geographic variation between Wisconsinan (low sealevel) samples revealed no significant morphometric differences, whereas variation between present-day (higher sealevel) samples from the same peninsular areas is significant.

Chronological trends in individual characters from the early Irvingtonian to present are generally towards increasing size. A phylogenetic trend in increasing strength and efficiency of the masticatory apparatus is indicated, especially by the enlargement of the retromolar fossa. Multivariate analyses show a correspondence between geological ages of samples and their phenetic similarity.

The preferred habitat of Geomys pinetis in Florida was identified as the longleaf pine-turkey oak sandhill association. Geomys less often occurs in xeric hammocks, longleaf pine flatwoods, and sand pine scrub. Geographic and chronological distributions of Geomys in Florida are provided.

## INTRODUCTION

Isolation is one of several factors leading to genetic divergence of populations, oftentimes resulting in subspeciation or speciation. Because of their restrictions to suitable soils, many pocket gopher species (Rodentia: Geomyidae) are patchily distributed. Pocket gophers epitomize the effects of isolation in terms of recognizable geographic forms. The effects of isolation on pocket gophers are perhaps best seen in the 229 subspecies of Thomomys umbrinus, the southern pocket gopher, many of which are restricted to one or a series of mountain peaks (Hall, 1981:469-496). Although some biologists (see Anderson, 1966:189) berated the official recognition of so many forms, phenotypic divergence of populations is indeed visible. Stephen Durrant (University of Utah) could name, solely from visual inspection of a specimen, the particular mountain peak in Utah from which a pocket gopher specimen was collected.

An analogy exists between Thomomys mountaintop isolation and the mosaic distribution of Geomys pinetis, the southeastern pocket gopher, in Florida. The Florida "mountaintops" are parcels of suitable habitat slightly elevated above surrounding wetter habitats that are impassable to pocket gophers. Relict dunes and other features of former shorelines comprise much of the range inhabited by Geomys pinetis. At least as early as 1939, Hubbell and Goff (1939: 131) recognized the "discontinuous distribution" of pocket gophers

"in the state" as being "the result of the 'patchy' occurrence of areas having deep, well-drained soils, to which pocket-gophers are almost restricted in the region." They credit Harley B. Sherman with having previously recognized this relationship, and further state that "it would not be surprising . . . to find that specific or racial differentiation corresponding to the degree of isolation had occurred" in Geomys pinetis (Hubbell and Goff, 1939:134).

The main thrust of other recent studies of geographic variation in the Geomys pinetis species complex (Avisé et al., 1979; Williams and Genoways, 1980) has been towards systematic revision of the group. The present study, which relies on a similar morphometric data base, examines zoogeographic aspects of the topic. One objective of this study is to examine geographic variation in Recent Florida pocket gophers and to evaluate the effects of isolation on these populations in terms of morphological divergence. It is hypothesized that the pattern of geographic variation will correspond to the distribution of suitable habitats, and that the extent of divergence between populations will correspond to the magnitude of various physiographic features (e.g., rivers, unsuitable habitats) separating populations.

The fossil record of pocket gophers in Florida spans nearly two million years. Beginning with the early Irvingtonian land mammal age, fossil material is known in at least 37 deposits from more than 27 localities collectively representing the Irvingtonian, RanchoLabrean, and Recent ages. Fossil specimens occur primarily as dentaries and isolated teeth with fewer fragments of the anterior portion of the

cranium. Isolated postcranial elements also occur, but are not treated in this study. The material has been attributed to two species: Geomys pinetis, the only extant geomyid in Florida, and Thomomys orientalis, an extinct species representing a genus now restricted to central and western North America (Simpson, 1928). This record of Thomomys consists of but a single rostromaxillary fragment (AMNH 23441) from Sabertooth Cave (Citrus Co.). However, additional material thought to be Thomomys has been recognized in this study from the Rock Springs site (Orange Co.) and from Williston III B (Levy Co.). The present study addresses only Geomys material.

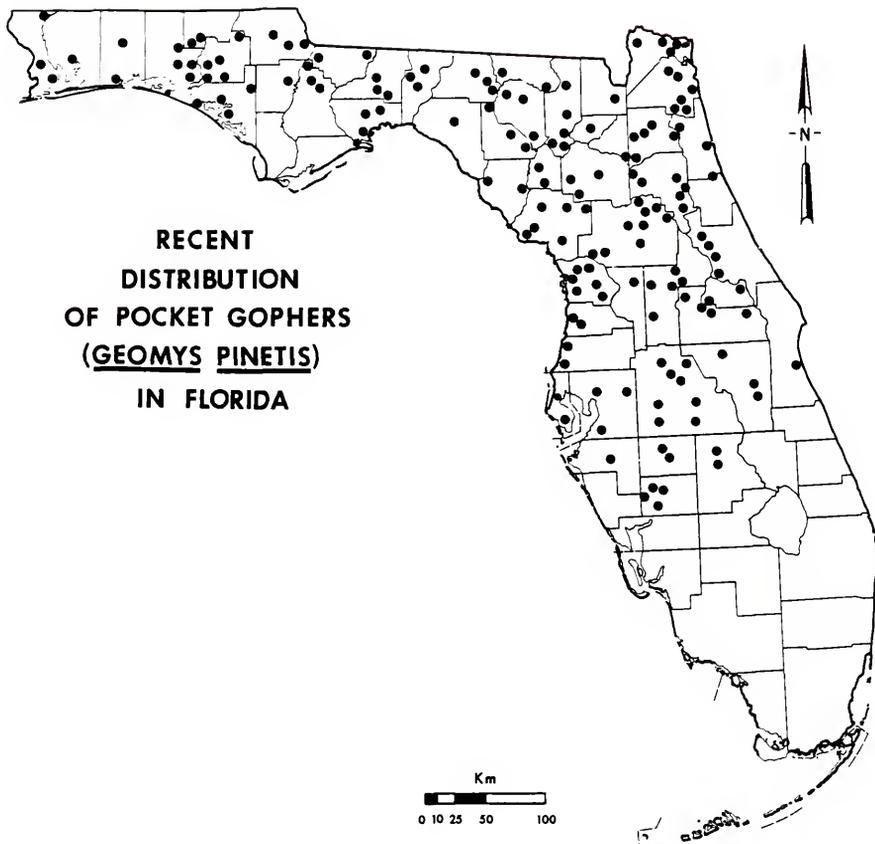
Study of Florida pocket gopher material is intriguing for at least two reasons. First, geomyid occurrence in Florida is rather well represented in the fossil record, beginning in the early Irvingtonian, thereby allowing examination of various phylogenetic trends characterizing geomyid evolution (Russell, 1968). Particular emphasis is here accorded to changes in the basitemporal (= retro-molar) fossa. Second, because Florida has experienced repeated cycles of sealevel rise and fall (in response to fluctuations of continental glaciers), the effects (i.e., morphological divergence) of isolation of central peninsular forms from peripheral peninsular forms during interglacial periods might possibly be visible in both the qualitative and the quantitative characters of teeth and dentaries. The chronological and spatial distribution of Pleistocene samples comprised of measurable dentary material is such that both geographic and temporal variation can be separately examined within the Florida peninsula.

### Distribution

Before a recent taxonomic revision of pocket gophers of the southeastern United States (Williams and Genoways, 1980), four species were recognized: the wide-ranging Geomys pinetis and the narrowly-distributed forms G. colonus, G. cumberlandius, and G. fontanelus. Williams and Genoways (1980) now consider all forms in this species complex to be G. pinetis. The general distribution of G. pinetis in the Atlantic and Gulf coastal plains of Alabama, Florida, and Georgia. A detailed distribution of the species in Florida is shown in Fig. 1. Specimens are known from all Florida panhandle counties, except Gulf Co. where diligent field efforts would probably reveal a few isolated colonies. The range extends through approximately the northern two-thirds of the peninsula to a southern tier of counties (Brevard, Osceola, Highlands, DeSoto, and Manatee). 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). I have been unable to substantiate the "records" of Geomys pinetis in St. Lucie Co. (vicinity of Ft. Walton), the southeasternmost localities reported in Williams and Genoways (1980). Although a town named "Walton" does occur in St. Lucie Co., it is more likely that these specimens were taken in Okaloosa Co. in the Florida panhandle.

The possibility exists that Geomys pinetis distribution is (or within the last century might have been) more extensive than shown on the range map (Fig. 1), which indicates only those localities documented by voucher specimens. Bangs (1898:176) noted

Fig. 1.--Recent distribution of pocket gophers (Geomys pinetis) in Florida. Dots represent localities for which museum specimens were examined.



reports of "hills" of Geomys being seen south of Micco, a mainland town on the intracoastal waterway in southeastermost Brevard Co. Micco is about 32 km south of the Melbourne-Eau Gallie area that is the type locality of G. p. goffi and comprises the southernmost documented occurrence of Geomys along the Atlantic coast.

Hubbell and Goff (1939:134) reported that in parts of southern Florida "an 'archipelago' of turkey oak and sand scrub 'islands' extends to the vicinity of Palmdale and Punta Gorda" located in Glades Co. and Charlotte Co., respectively. They further noted that "pocket gophers are present on some of these as far southwest as the latter locality" (i.e., Punta Gorda). Apparently no voucher specimens exist from any localities in Glades Co. or Charlotte Co. During March 1981, I drove many kilometers of roadway in south-central Florida in efforts to better delimit the southern extremity of occurrence of Geomys in the state. Twice we covered the route from Palmdale to Cleveland (Charlotte Co.) via Highway 74, thence northward via Highway 17 to Fort Ogden (DeSoto Co.). No evidence of Geomys in either Charlotte Co. or Glades Co. was found, although in about a dozen places both east and north of Cleveland and just south of Fort Ogden we observed lines of sandy mounds in lawns, pastures, and along roadsides. Excavation of portions of several mound systems revealed them to be the workings of moles (Scalopus aquaticus). Tunnels were either immediately beneath or within 10 cm of the surface. Tunnel diameters were less than 5 cm. Spoil piles were roughly conical and composed of plugs of earth characteristic of mole diggings. These signs of mole activity

could easily be mistaken for pocket gopher diggings. On this basis I prefer to discount "records" from these and other counties located on the periphery of the documented range of G. pinetis pending procurement of voucher specimens.

Numbered localities in Fig. 2 designate sites from which fossil geomyid material is available; site numbers correspond to numbers in Table 1. Past and present ranges of Geomys in Florida overlap broadly. The occurrence of Geomys material at Vero, Indian River Co., demonstrates that Geomys previously enjoyed wider distribution than at present. This is in contrast to Kurten and Anderson's (1980:229) statement that the Vero site is "within the modern range of the species." The one non-peninsular Florida locality yielding fossil geomyid material (a single lower premolar) is the St. Mark's River, Wakulla Co., site (Gillette, 1976).

#### Habitats Preferred

Geomys pinetis has been reported from a variety of habitats differing extensively in terms of characteristic flora but being similar in regard to the sandy, well-drained nature of the soils. References detailing such habitat information include Harper (1927: 336-342), Hubbell and Goff (1939:130-133), Quay (1949:67), Golley (1962:105), and Ehrhart (1978:6-7). My personal observations identify four primary habitats used by G. pinetis and listed here in descending order of preference: sandhill association, xeric hammocks, longleaf pine flatwoods, and sand scrub areas.

Fig. 2.--Pleistocene pocket gopher localities. Legend to site numbers included in Table 1. Dashed line approximates southern extent of modern distribution of Geomys pinetis.

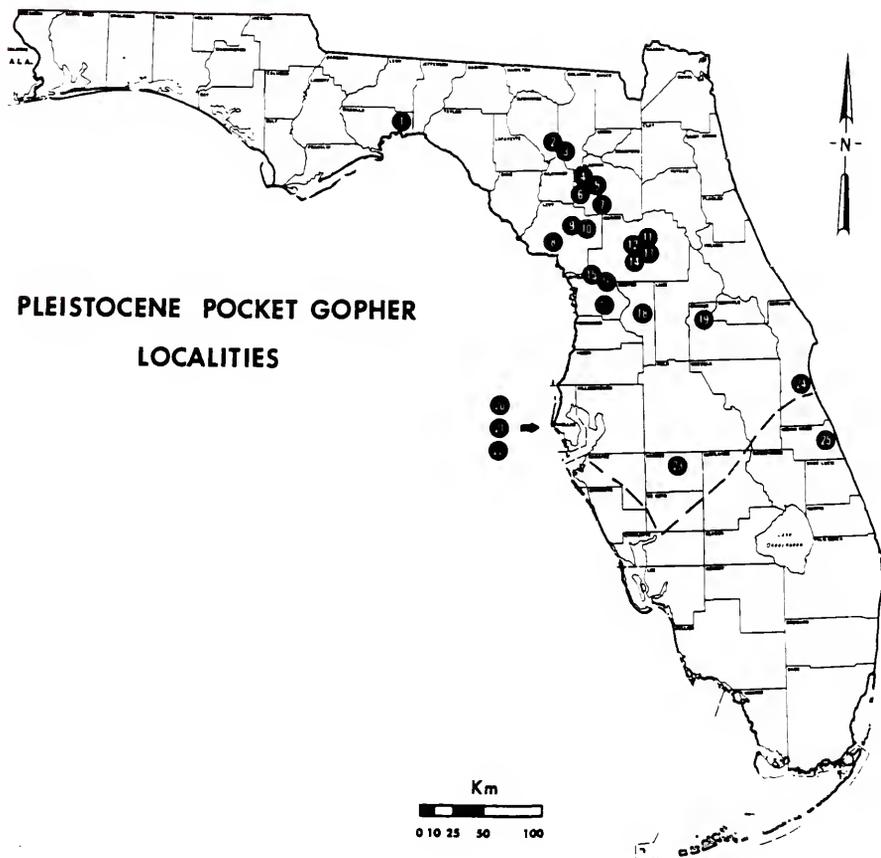


Table 1.--Florida fossil sites bearing pocket gopher material, listed in chronological sequence. N indicates number of dentaries included in analyses. Map number refers to site numbers in Fig. 2.

Site	Map Number	County	Mammal Age	Stage	N
Vero 3	25	Indian River	Recent	Holocene	1
St. Mark's River	1	Wakulla	Recent/ Rancholabrean	Holocene	0
Devil's Den	9	Levy	Rancholabrean	Holocene	4
Ichetucknee River	2	Columbia	Rancholabrean	Late Wisc.	17
Melbourne 2	24	Brevard	Rancholabrean	Late Wisc.	4
Orange Lakes Cave	11	Marion	Rancholabrean	Late Wisc.	0
Seminole Field	20	Pinellas	Rancholabrean	Late Wisc.	4
Vero 2	25	Indian River	Rancholabrean	Late Wisc.	1
Haile XIV	6	Alachua	Rancholabrean	Full Wisc.	3
Waccasassa River	8	Levy	Rancholabrean	Full Wisc.	3
Sabertooth Cave	17	Citrus	Rancholabrean	Wisc. or Sang. (uncertain)	0
Arredondo IA, IB, IIA	5	Alachua	Rancholabrean	Sangamonian	28
Haile VIIIA, XIB, XIIIA, XIIIB, XX	6	Alachua	Rancholabrean	Sangamonian	36
Kendrick IA	11	Marion	Rancholabrean	Sangamonian	4
Mefford Cave IA	12	Marion	Rancholabrean	Sangamonian	0
Reddick IA, IIC	13	Marion	Rancholabrean	Sangamonian	68
Rock Springs	19	Orange	Rancholabrean	Sangamonian	6
Williston IIIA, IIIB	10	Levy	Rancholabrean	Sangamonian	0
Withlacoochee River VIA	16	Citrus	Rancholabrean	Sangamonian	0

Table 1.--Continued.

Site	Map Number	County	Mammal Age	Stage	N
Santa Fe River IIA	3	Gilchrist	Rancholabrean	Late Illinoian	0
Eichelberger Cave	14	Marion	Rancholabrean	Uncertain	1
Maximo Moorings	21	Pinellas	Rancholabrean	Uncertain	3
Renegade Sink	4	Alachua	Rancholabrean	Uncertain	0
Riverview	23	Hardee	Rancholabrean	Uncertain	0
St. Petersburg	22	Pinellas	Rancholabrean	Uncertain	5
Wade's Cave	7	Alachua	Rancholabrean	Uncertain	1
Coleman IIA	18	Sumter	Late Irvingtonian	*	16
Haile XVI	6	Alachua	Mid-Irvingtonian	*	0
Inglis IA	15	Citrus	Early Irvingtonian	*	231

\*Unsafe to predict glacial/interglacial stage earlier than Rancholabrean due to numerous cycles during and before Illinoian (see Shackleton and Opdyke, 1973).

Prime pocket gopher habitat is the sandhill association of the co-dominants longleaf pine (Pinus palustris) and turkey oak (Quercus laevis), and a fire-perpetuated ground cover of grasses (especially wire grass, Aristida stricta), forbs, and sedges from which G. pinetis selects its diet. Terrain in the sandhill ecosystem is rolling and the sandy soils are well-drained. Xeric hammocks are dominated by live oaks (Quercus virginiana) and a variety of other hardwood species; soils are moister and contain more organic material than in sandhill or sand scrub situations.

Longleaf pine dominated one of the three types of pine flatwoods in Florida before intensive land clearing activities (for cultivation, timber, etc.) removed most virgin stands (Quarterman and Keever, 1962; Monk, 1968). Although some longleaf pine flatwoods still remain, the faster-growing slash pine (Pinus elliotii) preferred by commercial foresters has supplanted longleaf pine in most flatwoods. Flatwoods are topographically flat areas subjected to seasonal flooding. Soils are sandy and usually moist enough to exclude pocket gophers. The characteristic dense understory of palmetto (Serenoa repens), apparently not suitable for pocket gopher digging or feeding, further contributes to the undesirable nature of flatwoods for Geomys habitation. In at least two longleaf pine flatwoods situations I have either collected specimens (2.5 miles E Woodville, Leon Co.) or seen pocket gopher sign (Morningside Nature Center, Gainesville, Alachua Co.; see also Ross, 1976).

The sand scrub association is characterized by a very dense forest dominated by sand pine (Pinus clausa), palmetto (Sabal etonia), and an assemblage of scrubby oaks and other angiospermous shrubs and trees. Because ground cover provided by shrubs is so dense, forbs and grasses suitable for Geomys diet are not abundant. Hubbell and Goff (1939:133) remarked that the pocket gopher cannot be regarded as a "characteristic scrub-inhabitant." Generally, ground not covered by shrubs and trees is heavily exploited by mats of xerically-adapted fruticose lichens. Soils in the sand scrub ecosystem contain less organic material and are by far the driest of the four associations discussed here.

The role of fire in maintaining many ecosystems (e.g., sandhill, flatwoods, sand scrub) is well-documented (Monk, 1968:444-445; Veno, 1976:498). Man's activities over the past century in Florida have resulted in control of wildfire. As a result, the role of fire has been greatly diminished. Removal of fire allows fire-intolerant hardwoods to gain a foothold in ecosystems dominated by fire-tolerant species (e.g., many pines), thereby competitively excluding the pyroclimax communities requisite for Geomys pinetis habitation.

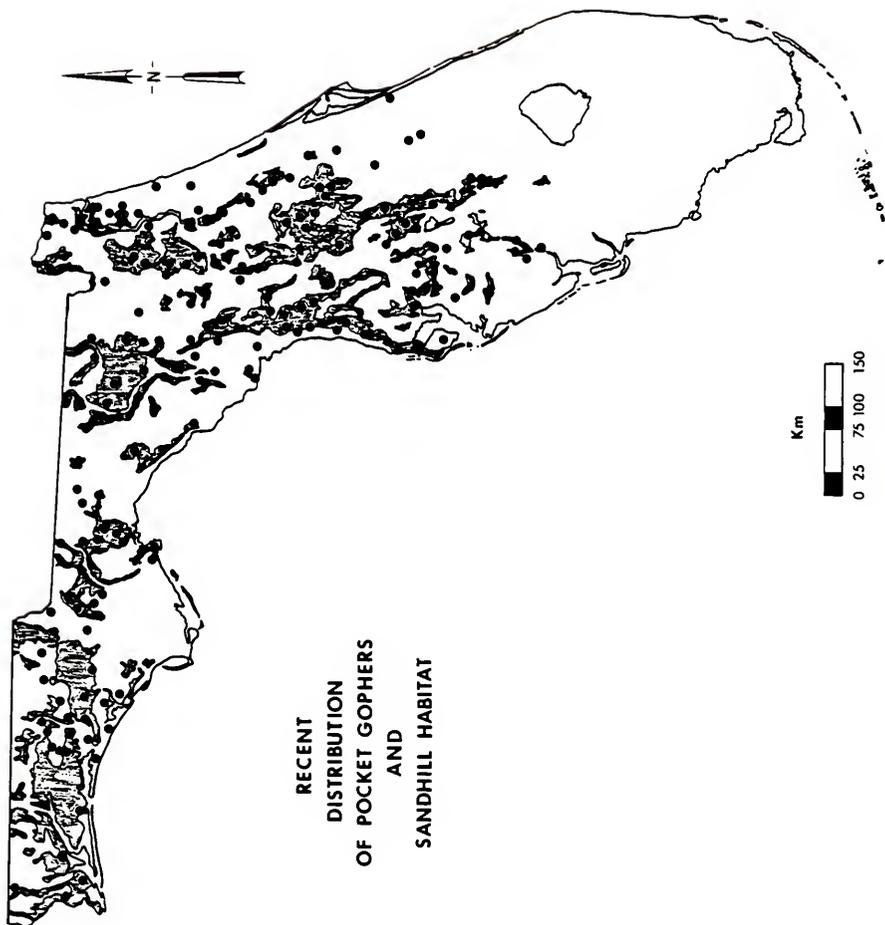
The pyroclimax community includes many herbaceous species comprising the diet of Geomys pinetis. Pocket gophers may be locally extirpated as a result of loss of these food sources. The general trend, then, is a reduction in the amount of land area suitable for habitation by pocket gophers. An example of such exclusion of Geomys due to removal of fire may be developed from field studies

in Levy Co., Florida. James N. Layne (pers. comm.) has collected field data on diversity and density changes in the mammalian fauna of sand ridges between Rosewood and Cedar Key (Levy Co.) from at least the early 1960's through his most recent visit to the area in 1979. His field notes for the years 1960-1963 indicate Geomys to be present in fairly continuous populations in the sand pine habitat of these relict dunes and along the roadside (Highway 24) between Rosewood and Cedar Key, a distance of about 11 km. Notes from 1965 to present either do not mention the presence of Geomys in the scrub areas or explicitly note their absence. My observations in Fall 1980 and Spring 1981 along this transect are that (1) the town of Rosewood, situated in an area of longleaf pine-turkey oak habitat, supports a thriving population of Geomys, but that (2) no Geomys now occur along Highway 24 from outside Rosewood to Cedar Key. I have not searched the ridge systems adjacent to the highway for Geomys activity; however, the visible scrub vegetation is so dense as to seem unfit for pocket gopher occupancy. Layne attributes the disappearance of Geomys from this habitat to the removal of fire from the ecosystem in the last two decades. Wildfires during the last two years might have opened this general area up to re-invasion by pocket gophers.

#### Habitat Mosaic

The distribution of the sandhill association, one of the four general habitats that Geomys pinetis occupies in Florida, is outlined in Fig. 3 (modified from Davis, 1980). Dots represent

Fig. 3.--Recent distribution of pocket gophers, Geomys pinetis, (dots) overlaid by the general distribution of sandhill habitat (shaded areas) in Florida.



localities (or clusters of localities) from which voucher specimens of pocket gophers are known. Over 125 of the more than 150 localities plotted coincide with or are at the edges of parcels of the sandhill association. Most of the remainder occur in xeric hammocks. Only a few records of pocket gophers are available for the sand scrub regions located sporadically on sand ridges along the Atlantic and Gulf coasts and in the interior of north-central peninsular Florida. The pine flatwoods ecosystem is the predominant habitat in the state (Monk, 1968:444). In most cases, parcels of the other three associations are bounded on all sides by pine flatwoods. Only a few pocket gopher specimens are known from the pine flatwoods of Florida.

Fig. 3 is a composite of the general distribution of sandhill habitat overlaid by specimen localities. The coincidence of a collecting site with a certain habitat need not always correctly indicate the actual microhabitat inhabited by pocket gophers. As an example, Ocala National Forest in eastern Marion Co. is depicted on this map (Fig. 3) as being characterized by single parcels of two distinct habitat types: sand scrub and sandhill. The misleading nature of this illustration is apparent to those who have visited Ocala National Forest. Sand scrub is the predominant association and is probably more extensive than depicted. The sandhill association is present also, but is not distributed quite as depicted; rather than comprising the entire northeastern section of the forest, longleaf pine-turkey oak stands (and some xeric

hammocks) occur as isolated parcels sprinkled through broad areas of sand scrub. Such parcels of sandhill habitats are referred to as "islands" in the local vernacular. It should be noted that the sites in which essentially all Geomys have been collected (or most sign has been observed) in Ocala National Forest coincide with such sandhill islands. Additionally, the range of G. p. goffi (a taxon no longer valid: Williams and Genoways, 1980) along the Pineda Ridge in the Melbourne-Eau Gallie area of eastern Brevard Co. is depicted on the Davis (1980) vegetation map as sand scrub surrounded by pine flatwoods. Personal visits to this area (October 1978) revealed the sandhill and xeric hammock associations to be present also.

From the preceding examples it is evident that microgeographic distribution of habitats in Florida is a mosaic. On a broader scale the statewide distributions of these habitats are also in a mosaic pattern (Fig. 3). Parcels of sandhill, xeric hammock, flatwoods, and sand scrub are all widely distributed throughout the state, but in a disjunct manner. Areas of a particular habitat are isolated from other areas of that same habitat by features that may form partial or complete barriers to dispersal of species that are adapted and restricted to the isolated habitat types. In the case of pocket gophers, these intervening barriers may take the form (1) of rivers or streams (Udvardy, 1969:14), or (2) of substrates unsuited to digging because of excessive moisture, hardness of soil, or shallowness or lack of soil, or (3) of communities lacking vegetation required in the diets of Geomys (Winchester and DeLotelle,

1978). In many species of plants and animals, and notably in other species of pocket gophers (Wright, 1943; Kennerly, 1954, 1963; Patton and Dingman, 1970; Patton et al., 1972; Honeycutt and Schmidly, 1979; Nevo, 1979), such isolation corresponds to patterns of geographic variation often to the point of defining subspecies or species. Hence, in Florida the opportunity for allopatric differentiation exists for pocket gophers in spite of what appears to be fairly uniform topography.

#### Habitats of Florida's Past: Palynological Evidence

A direct record of Pleistocene vegetation conditions in Florida is provided by pollen samples from lake sediments. These pollen records clearly indicate the waxing and waning of habitats more and less favorable to pocket gophers. Two of the most informative pollen cores have been taken from Lake Annie in south Florida and Sheeler Lake in north central Florida (Watts, 1980; Watts and Stuiver, 1980). Over the last 40,000 years dramatic changes have occurred in vegetation in the vicinities of these lakes. The general climatic trend indicated from Wisconsinan times into the Holocene is from colder, drier conditions to the warmer, moister situations of today; numerous minor excursions from this general trend are evident as well. For example, the following vegetation associations are recorded in sequence from the vicinity of Sheeler Lake:

- :
- :
- 24,000 - 18,500 B.P.    open pine forests with broadleaf trees and localized patches of prairie and sandhill herbs interspersed;
  - 18,500 - 16,600 B.P.    hiatus, probably due to lake's being empty during an extreme dry period;
  - 16,600 - 14,000 B.P.    dry oak-hickory with localized prairie;
  - 14,000 - 13,000 B.P.    mesic broadleaved trees;
  - 13,000 - 9,500 B.P.    oak and prairie plants;
  - 9,500 - 7,200 B.P.    pine forests mixed with oak plus swamp, cypress, and bayhead species.

The pollen profile from Lake Annie, extending from 44,000 B.P. to present, differs greatly from that of Sheeler Lake in many of the species and vegetation associations documented, but still demonstrates the general trend from cold, dry to warm, moist conditions. Such differences are easily reconciled when discrepancies existing in present-day floras are considered.

Two conclusions may be drawn from the palynological data. First, changes in rainfall and temperature regimes correspond to glacial phases, and hence to sealevel changes. In Florida, glacial periods tend to be cold and dry, whereas interglacials are warmer and moister; variations on this theme correspond to geographic location in the peninsula. Second, vegetation associations dominating localized areas are subject to swift, drastic change in response to climatic variation. For this reason, the suitability of local areas for habitation by various species (e.g., pocket gophers) has likewise fluctuated through time. Because of known habitat preferences of pocket gophers, it is conceivable that detailed chronological variation in the range of pocket gophers in Florida could be inferred if

pollen diagrams were available from throughout the state. Even with the present limited data, pollen cores support the general view that pocket gopher habitats were more extensive and surface water less extensive during glacial maxima, and that the reverse was true during interglacial stages (including the Recent).

Correspondence of Geomys Distribution with Geomorphology

The distribution of pocket gophers tends to follow certain physiographic features in various parts of the state. Two examples follow below. In the southwestern peninsula (Manatee, Sarasota, and DeSoto counties), the range boundary of G. pinetis corresponds closely with the edge of the DeSoto Plain (White, 1970: map 1-C and Fig. 43). Personal field trips to the area in May 1980 and March 1981 revealed such localities in south-central Manatee Co. (junction of Highways 64 and 675), southern DeSoto Co. (Fort Ogden), extreme western DeSoto Co. (sporadic occurrence of small colonies along Highway 72 and in adjacent fields and pastures within 5 km of the Sarasota Co. line; no vouchers known), and a suspected sight locality in NNE Sarasota Co. south of Verna. Proceeding south and west off the DeSoto Plain, the habitat changes from the sandhill association to lower, wetter pine flatwoods of the Gulf Coastal Lowlands from which no pocket gophers are known.

The pattern of occurrence of G. pinetis in Osceola Co. and eastern Polk Co. is another example of correlation of distribution with physiographic landforms. Most of Osceola Co. and extreme eastern Polk Co. consists of flat lands (the Osceola Plain)

supporting primarily pine flatwoods and wet prairies, but also cypress forests, swamp forests, and an occasional isolated sand scrub ridge (Davis, 1980; pers. obs.). Highway 441 tracks the more highly elevated portions of eastern Osceola Co. Geomys vouchers indicate their occurrence in Osceola Co. only at or near Kenansville, Nittaw, Illahaw, Mahaw, and St. Cloud, all in central or northern parts of the county. Within the last five years, James N. Layne (pers. comm.) says he has seen Geomys diggings in the vicinity of Yeehaw Junction in extreme southern Osceola Co. As determined from personal observations in March 1981, the habitat in the immediate vicinity of Yeehaw Junction, now developed into citrus groves, appears suitable for pocket gopher habitation although we saw none. This town is located in an area coinciding with a small parcel of sand scrub on the Davis vegetation map (1980). To my knowledge, no vouchers are available from Yeehaw Junction. The closest documented Geomys locality is about 20 km to the north in Kenansville.

The route from Yeehaw Junction westward into Lake Wales (Polk Co.) along Highway 60 traverses flat terrain and habitats excessively wet for Geomys until a point near Indian Lake Estates (Polk Co.) near the junction of Highways 60 and 630. Here, about 12 km west of the Osceola Co. line where the highway ascends the "Bombing Range Ridge" (White, 1970: map 1-C), we observed three or four lines of Geomys mounds along the roadside and in lawns for a 0.8 km stretch. The sandhill habitat of the ridge levelled and then dropped into pine flatwoods devoid of Geomys sign for about 13 km past which we ascended a second scarp, Lake Wales Ridge (White, 1970:

map 1-C) into Hesperides. These two ridges, at about 35 m elevation, represent the Wicomico shoreline (MacNeil, 1950: plate 19). Although no Geomys sign was noted for about an additional 11 km, the rolling sandhill habitat (mostly developed into citrus groves) appeared suitable. The Geomys activity closest to Hesperides was found 3 km east of Lake Wales. Upon entering the city of Lake Wales, situated in the Polk Upland (White, 1970: map 1-C), elevation increased to about 50 m. This elevation corresponds to the Okefenokee shoreline (MacNeil, 1950: plate 19).

#### Correspondence of Geomys Distribution with Soils

The general soils map of Florida (Fl. Agric. Exp. Sta., 1962) illustrates the distributions of approximately 37 soil associations in the state. These are classified into five major groups according to drainage characteristics. The only soil association not represented within the overall range of G. pinetis in Florida is rockland (type number 31), which is most common in the Everglades region. A general correspondence between Florida pocket gopher habitats and their component soils is evident by comparing distributions of soils with vegetation (Davis, 1980).

The most highly preferred habitat (sandhill) and xeric hammocks occur in the same well to moderately well drained soil types. The names of these associations and their identifying numbers from the 1962 soil map are (3) Lakeland-Eustis-Blanton, (3a) Lakeland-Eustis-Norfolk, (4) Jonesville-Chiefland-Hernando, (9) Hernando-Chiefland-Jonesville, (5) Arredondo-Gainesville-Fort Meade, (8) Hague- Zuber-

Fellowship, (12) Blanton-Klej, (12b) Kanapaha-Blanton, (17a) Rex-Blanton, (17b) Blanton-Bowie-Sequahanna, and (17c) Goldsboro-Lynchburg associations. Inland and coastal sand scrub ecosystems are found on two excessively drained soil associations: (1) St. Lucie-Lakewood-Pomello and (2) Palm Beach-Cocoa. Pine flatwoods occur in areas dominated by somewhat poorly drained soils: (13a) Leon-Plummer-Rutledge, (13b) Leon-Immokalee-Pomano, (13c) Leon-Pomello-Plummer, and (13d) Leon-Blanton-Plummer associations.

Pocket gophers apparently occur or have recently occurred (at various densities) in all of the above soil types in Florida. Variation between these soil types occurs in pH, organic content, moisture content, and size of component sand grains. However, all of these soils share a feature important in determining suitability for pocket gopher inhabitation: all are sandy and, therefore, are suitably friable for pocket gophers. Differences in abundance of pocket gophers in these soil associations appear not to be due to soil qualities per se, but to other parameters such as soil moisture and associated vegetation types.

#### Sealevel Changes

The primary mechanism governing the degree of isolation of populations of Geomys pinetis is tied to the role of the oceans as both source of glacial ice and as sink holding glacial melt waters. Sealevel changes during the Neogene period (Miocene through present) resulted from fluctuations in the extent of worldwide glaciation. The amount of emergent land characterizing Florida during the

Pleistocene varied with the magnitude of continental glaciers and the extent of their melting. During the high stands of earlier interglacials (i.e., those corresponding to the Coharie, Okefenokee, and Wicomico shorelines) seas covered most of the peninsula, leaving only an archipelago of islands to represent present-day peninsular Florida. Pocket gophers, if present on such islands at these times, were isolated from other such populations, and thereby were presented with opportunities to differentiate from each other. However, during ensuing glacials, sealevel fell well below the present level (by 100 m or more), thereby reconnecting islands with each other. With sea barriers so removed, habitats were once again in contact. Potentially, and quite probably, pocket gopher populations expanded and established a peninsula-wide interbreeding population. Such a population would likely have been phenotypically homogeneous. Thereby, any differentiation achieved during isolation (if it had not proceeded to the point of reproductive isolation) would likely be obliterated. The high sea stand during the middle of the Wisconsin glaciation (the Pamlico at 9 m) again formed a habitat mosaic probably inhabited by demes of pocket gophers. But divergence amongst these populations was likely swamped during range extension that accompanied the expansion of late Wisconsinan glaciers. At the height of the late Wisconsinan (about 19,000 B.P.), seas fell to about 90 to 130 m below present (Bloom et al., 1974; Harmon et al., 1978). Since then, the glaciers have been melting and the sea continuously rising towards its present level. Isolation of populations has increased with increasing sealevel.

Because Florida is characterized by low and gentle topographic relief, even minor sealevel changes have caused notable variation in the relative amounts of emergent land and water on the Florida Plateau (present-day Florida and surrounding continental shelf to a depth of about 100 m). Hence, many authors have investigated sealevel changes in Florida (e.g., Cooke, 1939, 1945; MacNeil, 1950; Alt and Brooks, 1965; Scholl and Stuiver, 1967; Healy, 1975). Evidence has been so variously interpreted by different authors, however, that little agreement exists on (1) the number of glacial-interglacial cycles whose effects are visible, (2) the correspondence of relict shoreline features (e.g., dune systems, scarps, marine terraces) at different statewide localities, or (3) even the ages of these shoreline features. Perhaps the sole point of agreement among these studies is that these shorelines "become progressively younger as they step down toward present sealevel" (Alt and Brooks, 1965:406). Healy (1975) offers a concise summary and comparison of findings of Florida shoreline investigations including a substantial list of pertinent references.

A traditional, composite interpretation drawn from various of these studies suggests that four glacial-interglacial cycles occurred during the Pleistocene. In order of occurrence, the four shoreline-terrace complexes (and approximate elevations above present sealevel) left at these interglacial maxima are (1) the Coharie (70 m) during the Aftonian interglacial, (2) the Okefenokee (50 m) during the Yarmouthian, (3) the Wicomico (35 m) during the Sangamonian, and (4) the Pamlico (9 m) during the mid-Wisconsinan. A fifth shoreline, the

Silver Bluff at 3 m, is regarded by some as a Recent (6,000-4,000 B.P.) high sea stand during a warmer climatic optimum (MacNeil, 1950:104). This interpretation of the Silver Bluff may be discounted on two counts. From south Florida data, Scholl and Stuiver (1967) showed that, at 4,400 B.P., sealevel was about 4 m below present and has been rising since then at varying rates. Furthermore, sealevel has been rising since the height of the late Wisconsinan Woodfordian glaciation between 22,000 B.P. and 12,500 B.P. (Watts, 1980). Additionally, numerous, more recent studies in the vicinities of New Guinea and the Caribbean Sea have shown that the last time sealevel exceeded its present height was about 125,000 B.P.; the estimates for this transgression range from 4 to 10 m (Broecker and Thurber, 1965; Osmond et al., 1965; Broecker et al., 1968; Mesolella et al., 1969; Cant, 1972; Bloom et al., 1974; Ku et al., 1974; Neumann and Moore, 1975; Chappell and Polach, 1976; Harmon et al., 1978; Marshall and Launay, 1978; and Bender et al., 1979). Of the shorelines visible in Florida, it is the Pamlico rather than the Silver Bluff which best corresponds with the 125,000 B.P. transgression. Therefore, a more reasonable explanation is that the Silver Bluff might represent a pause during recession of this particular 4-10 m high stand.

Other interpretations of the numbers and ages of these relict shoreline features have been proposed. Shackleton and Opdyke (1973) conclusively demonstrated (via oxygen isotope and paleomagnetic studies) the occurrence of approximately 22 cycles of sealevel change, rather than the traditional four, during the last 800,000

years of the Pleistocene. Many of these transgressions are not recorded as emergent shoreline features because many of these high stands were below present sealevel. All interglacial high stand terraces mapped and dated in New Guinea since the 125,000 B.P. 4 to 10 m sealevel were below present sealevel (Bloom et al., 1974; Chappell, 1974). The ages and approximate elevations with respect to present sealevel of these high sea stand terraces are: 30,000 B.P. (-50 m), 40,000 B.P. - 50,000 B.P. (-30 m), 60,000 B.P. (-20 m), 80,000 B.P. (-10 m), and 105,000 B.P. (-10 m). Bender et al. (1979) extended the record even further, documenting about 10 high stands between 140,000 B.P. and 640,000 B.P. These interglacial seas stood from near present sealevel to well below that of present. The general conclusion, then, is that seas have stood higher than present level only once in the last 700,000 years. It is very possible, then, that with regard to ages of these terraces Alt and Brooks (1965) were correct in assigning only the lowest terrace (Pamlico) to the Pleistocene. The designate Miocene and Pliocene ages for the Coharie, Okefenokee, and Wicomico shorelines.

From the preceding dates for high sea stands, it is evident that the amount of isolation now seen between populations of Florida Geomys pinetis is the greatest that has existed since the last time seas stood higher than present--about 125,000 B.P. when sealevel was about 4 to 10 m. The earlier Wisconsinan, from its beginning (at about 300,000 B.P.) to about 125,000 B.P., is characterized by about five more glacial-interglacial cycles, all having high stands near present sealevel. Following this 125,000 B.P. transgression,

which apparently corresponds to the Pamlico, seas fell to about -60 m at about 115,000 B.P. and then fluctuated through about five more cycles before attaining the current level. Estimates of the low sealevel stand at the maximum extent of the final glacial of the late Wisconsinan (at about 19,000 B.P.) range from around -90 m to -130 m (Blackwelder et al., 1979).

#### Analytical Approach

Both Recent and Pleistocene phases of this study are based on morphometric analyses of cranial, mandibular, and/or dental characters. The initial analyses in each phase were directed towards evaluating non-geographic sources of variation (e.g., sex, age, and individual variation). This step identified subsets of characters for which variation between samples exceeded that within samples. Next, samples were defined such that subsequent analyses would examine geographic variation with regard to features thought to comprise zoogeographic barriers. Both univariate (analyses of variance, Duncan's multiple range tests) and multivariate (clustering, principal components, canonical variates, multivariate analyses of variance) techniques were employed for study of geographic and chronological variation. Patterns of variation elicited are then discussed in terms of habitat preferences, geomorphology, and the effects of sealevel changes on pocket gopher distribution over the last 1.8 million years.

The primary hypotheses examined in this study concern the interaction of sealevel changes, existing dispersal barriers, and

the degree of isolation of pocket gopher populations in determining the patterns of morphological variation among these populations. The hypotheses tested and research directions pursued include the following:

- (1) It is hypothesized that the pattern of geographic variation in Recent Florida Geomys pinetis corresponds to the magnitude and geographic occurrence of dispersal barriers with rivers defining interbreeding populations. Multivariate analyses of variance testing inter-area and inter-region variation in morphological features address this hypothesis.
- (2) It is assumed that during the low sealevels of glacial intervals distribution of pocket gophers in the Florida peninsula was relatively widespread due to abundant and widespread suitable habitats. Such broad distribution enhanced gene flow, and populations became genetically more homogeneous. Genotypic constitution is assumed to be reflected by morphological characters. It is hypothesized, then, that morphometric differences between glacial stage samples (e.g., Wisconsinan) from distant peninsular localities are not significant.
- (3) Conversely, the high sea stands of interglacial intervals (e.g., Holocene or Sangamonian) restricted peninsular populations into isolated refugia. Reduced gene flow presented the opportunity for genetic divergence, which may be reflected in morphological traits. Therefore, it is hypothesized that interglacial stage samples from distant peninsular localities are significantly different morphometrically.

(4) Variation in each of 10 dentary characters represented in pocket gopher material spanning the last nearly two million years was examined for the purpose of describing morphological changes characterizing phylogeny of Florida geomyines.

## MATERIALS AND METHODS: CRANIAL MORPHOMETRICS

Conventional skin and skull preparations of 1,123 specimens of southeastern pocket gophers from Florida were examined (listed in Appendix B). Thirty-three of these specimens were collected from critical areas during the course of the study. Measuring of characters was restricted to the adult sample of 854 individuals. Although juveniles were not measured, their collecting localities were used to document the distribution of pocket gophers in Florida.

### Ageing

Mature adults were divided into two age groups on the basis of a suite of osteological features developed from the efforts of other investigators examining other geomyids: Dunnigan (1967), Thaeler (1968b), Hoffmeister (1969), Williams and Genoways (1977), and Honeycutt and Schmidly (1979). Younger adults (age class 1) and old adults (class 2) were distinguished according to (1) the degree of fusion of the basisphenoid and basioccipital bones, (2) the development of the temporal ridges, and (3) the degree of porosity in the maxillary process of the zygoma and the palatine. In younger adults, the basisphenoid-basioccipital suture is closed with no interlying gap, but yet not obliterated by accumulated bony material as in old adults. The temporal ridges in old adults (especially males) are highly rugose and usually contact each other to form a single 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 pronunciation increases with age. In both sexes, bone porosity in the palatine and maxilla decreases with age.

Age, determined as described above, and sex were noted for each specimen. When sex was not indicated or the assigned sex was doubtful, cranial morphology was used to designate the sex (see Merriam, 1895:20-21); however, specimens for which sex designation via cranial morphology remained ambiguous were deleted from consideration.

#### Measurements

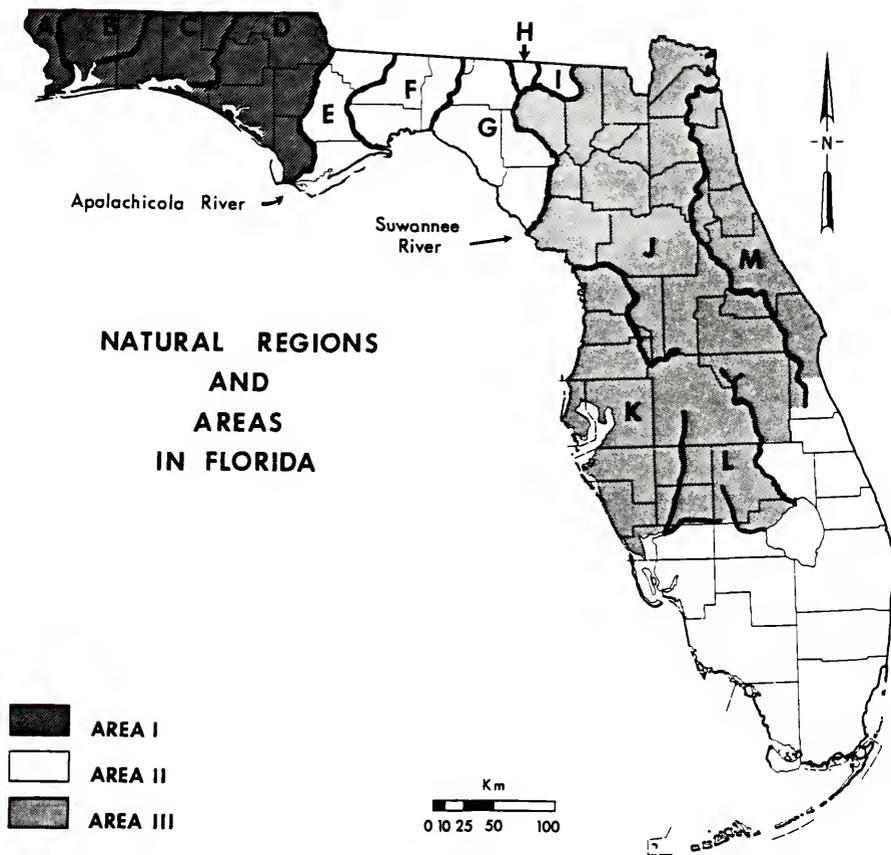
Descriptions and abbreviations of the 20 cranial features measured to 0.1 mm with Helios dial calipers for the 854 adults examined are as follows: greatest length of skull (GLS), from exoccipital to anterior surface of incisors; greatest zygomatic width (ZYGO); width across mastoid processes (WMAST); 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 or 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); and width of lower incisor (WLINC). These abbreviations are used in the remainder of this paper. Illustrations of Geomys pinetis crania may be found in Pembleton and Williams (1978), Hall (1981), and under the names Geomys tuza and G. mobilensis in Merriam (1895; plate 7).

#### Natural Region and Area Definitions

Geographic variation was examined using a scheme of combining specimens from adjacent localities into larger, more zoogeographically meaningful samples. The state was divided into "natural regions" delimited by physiographic features (e.g., rivers) suspected to define a number of discrete non-interbreeding populations that might be morphometrically distinguishable (Fig. 4). Evidence of the effectiveness of rivers in limiting ranges and dispersal of pocket gophers is readily available. Lowery (1974:47) noted that G. bursarius does not range east of a series of Louisiana rivers, including the Mississippi, Atchafalaya, Ouachita, and Little rivers. Similarly, G. pinetis occurs in a region bounded to the northeast by the Savannah River and to the west by the Mobile and Tombigbee rivers (Lowery, 1974:207). The natural region scheme used here differs slightly, but importantly, from that used by others studying

Fig. 4.--Areas and component natural regions of Florida (A-M) divided by rivers (heavy black lines). The unshaded portion of the southern peninsula lies outside the current range of Geomys pinetis.



this problem. Williams and Genoways (1980) grouped adjacent samples with the primary purpose of enhancing sample size. In at least one instance, such grouping included in one sample specimens from opposite sides of the Suwannee River--a feature determined in this study to be an important zoogeographic barrier for Geomys pinetis.

The regions in the Florida panhandle and in the far northern peninsula (regions A through I) are discretely defined by rivers on two or three sides, and most are bounded by the coastline of the Gulf of Mexico to the south; each of these regions opens northward into the state of Alabama or Georgia (Fig. 4). Region A is comprised of the westernmost county in Florida, Escambia Co.; the Perdido River forms the stateline boundary with Alabama, and the Escambia River separates regions A and B. The northern portions of Santa Rosa Co. and Okaloosa Co. comprise region B which is delimited from region C by the Yellow River. Region C includes parts of four counties: Santa Rosa, Okaloosa, Walton, and Holmes. Region D, between Choctawhatchee and Apalachicola Rivers, is composed of portions of Walton Co. and Holmes Co. plus five other entire counties. Region E is situated between the Apalachicola and Ocklockonee Rivers. The Aucilla River separates regions F and G; region G includes extreme northeastern Jefferson Co. and all of four other counties. The eastern border of region G is jointly comprised of the Suwannee River from the Gulf of Mexico to its confluence with the Withlacoochee River which separates Madison Co. (region G) and Hamilton Co. (region H). Hamilton Co. is divided between two regions, with regions H and

I consisting entirely of the western and eastern portions of this county, respectively. The Alapaha River segregates regions H and I. The continuation of the Suwannee River forms the southern and eastern edges of region I.

Region J in the north-central peninsula is bounded by the Suwannee River and the Gulf Coast to the west, by the St. Johns River and Atlantic Ocean to the east, and the St. Marys River and Okefenokee Swamp region to the north. The Withlacoochee River forms part of the southern boundary of region J. Farther to the south in the central highlands of Lake, Orange, Osceola, and Polk Counties, region J merges with regions K and L. Region K extends from Citrus Co. bounded by the Withlacoochee River southward to include Sarasota Co. and western parts of Charlotte, DeSoto, and Hardee Counties. The boundary between regions K and L in DeSoto Co. and Hardee Co. is the Peace River. The southern extent of region L is denoted by Prairie Creek. The southernmost reaches of region J (Osceola Co.) are isolated from region L by the Kissimmee River. Region M is well-defined by the St. Johns River, the Atlantic coastline, and marshy habitat unsuitable to pocket gophers to the south in Brevard Co. The names of counties comprising each natural region (as well as those from which Geomys pinetis is known) may be obtained from the list of Specimens Examined (Appendix B).

Polk Co. in the central peninsula is potentially split between three natural regions (J, K, and L). No Polk Co. localities were included with region J to the north and northeast because of their isolation from region J (Lake Co. and Osceola Co.) by (1) the Green

Swamp in northern Polk Co. and southern Lake Co., and by (2) Snell and Lake Marion creeks, Dead River and other creeks, swamps and areas impassable to pocket gophers in northeastern Polk Co. Because no good physiographic feature was found to partition central from southern Polk Co., and thereby to allow assignment of localities to either region K or L, all Polk Co. localities were arbitrarily assigned to region K. Specimens that might be argued as equally likely to belong to region L are from the Frost-proof and Lake Wales vicinities. This difficulty of discretely defining regions K and L (and even J) suggests that study of zoogeographic relationships of Florida Geomys pinetis might be better accomplished at a grosser level.

Therefore, each region is considered to belong to one of three multi-region "areas." All regions west of the Apalachicola River (regions A, B, C, and D) comprise area I. Those between the Apalachicola and Suwannee Rivers (regions E, F, G, H, and I) fall into area II, whereas the four peninsular regions (J, K, L, and M) constitute area III. These area designations emanated from results of initial exploratory analyses (e.g., clustering and principal components analyses); hence, assignment of regions to areas was not an arbitrary, a priori exercise.

#### Analyses Conducted

Variation observed in a sample from a particular locality may result from differences between individuals of different sex or age. Before undertaking an analysis of inter-population variation,

intra-population variation was examined in the pocket gophers from Gainesville (Alachua Co.), the largest available local sample (n = 209). Several univariate statistics were computed for each character for each of the four sex/age combinations using the MEANS and TTEST procedures of the Statistical Analysis System (SAS, Helwig and Council, 1979).

In studies of geographic variation, trends between samples are usually evaluated for each character examined. Clinal variation among samples may correspond to a variety of environmental parameters (e.g., temperature, precipitation, elevation, habitats, etc.), especially if the samples are taken from a large geographic area. In the present study of Geomys pinetis in Florida, clinal variation was examined in 16 cranial characters separately for each of the four sex/age categories. Maximally non-significant subsets of regional samples were determined using the Duncan's multiple range test option of PROC GLM of SAS.

Multivariate statistical techniques are of great value in systematic studies because, unlike the univariate approach of examining one character at a time, they permit simultaneous evaluation of large numbers of characters, perhaps reflecting the way that nature interacts simultaneously with an organism's entire phenotype. Two general categories of multivariate analyses were conducted. Clustering and the associated principal components analyses explore phenetic relationships between samples. Multivariate analyses of variance and the associated canonical variates analyses are included in a category of techniques that test the significance of differences between samples.

The first series of clustering and principal components analyses (PCA) assessed the similarities among the 13 regional populations (separately for each sex/age category; see section on non-geographic variation below). In accordance with conventional morphometrics methodology (e.g., Baumgardner and Schmidly, 1981), input data used were the mean values for each of the 16 characters for each regional sample. Regions represented by only one specimen were omitted from clustering and PCA on the assumption that individual specimens might not accurately characterize the population. 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). Phenograms and principal components projections overlaid by computer-generated minimum spanning trees illustrate clustering and PCA results.

A problem inherent with this approach to cluster analyses is that mean values provide no measure of the variation within a sample. Use of individual specimens, therefore, is preferable. A cluster analysis using standardized values for measure values for each of the 187 age 1 male specimens as input was conducted to check the feasibility of a "single specimen" approach over the "mean value" approach. The inter-specimen relationships resulting from this experimental run did not follow any comprehensible geographic pattern. The probable causes for this patternless arrangement are that (1) the amount of ontogenetic size variation occurring within this age class is greater than the variation that may be attributed to geography, and (2) overall variation throughout Florida is slight. Hence, the "mean value" method is used throughout the study.

Several series of multivariate analyses of variance (MANOVA) were conducted for each sex/age category to test the null hypotheses of no significant differences (1) between all regional samples, (2) between regional samples within their respective areas, and (3) between area samples. MANOVA's, using character measurements for individual specimens as input data, were computed by PROC GLM of SAS. The test statistics generated were the Hotelling-Lawley and Pillai's traces, Wilks' lambda, and Roy's maximum root criterion.

Canonical variates analyses (CVA) provide a means of pictorially representing relationships between samples by two-dimensional plotting of specimens along pairs of canonical axes. For clarity, only the points representing centroid means (bounded by  $\pm 1$  standard deviation bars) are plotted, rather than plots of individual specimens. The score of each specimen on each axis is the sum of all measured characters multiplied by their respective coefficients which indicate their contribution to the variation reflected in a particular axis. The relative importance of a character to a particular variate may be determined by a procedure modified slightly from that outlined in Baumgardner and Schmidly (1981:13). For a given vector, the mean value of each character is multiplied by the absolute value of its corresponding loading (i.e., coefficient, eigenvalue); the products so obtained are then summed. The proportionate influence of a character, then, is the product of its mean and the absolute value of its coefficient divided by the sum of all such character-coefficient products.

## Multivariate Statistics Rationale

Correct interpretation of the results of multivariate statistical methods requires a general acquaintance with the techniques. Presented in the following section is a general discussion of the purpose, operation, and applications of the techniques used in this study.

### Cluster Analyses

Clustering is a classificatory procedure in which entities (operational taxonomic units or OTU's) are placed in a hierarchical arrangement in multidimensional space on the basis of phenetic similarities of the entities. The degree of similarity between each pair of OTU's is expressed by a coefficient (of either similarity or of dissimilarity). For example, the method used in this study (Ward's method) employs a squared Euclidean distance coefficient that varies such that an indistinguishable sample pair has a coefficient value of 0.0; this value increases with increasing dissimilarity of OTU's. Relationships may be depicted in two-dimensional phenograms.

### Principal Components Analyses

Ordination procedures (such as principal components analyses, PCA) may also be applied in an effort to express the relationships between entities in fewer dimensions than originally measured. In ordination (as in clustering procedures) data are made dimensionless via standardization to zero mean and unit standard deviation. Thereby, new axes are formed with the new origin (centroid) being a point corresponding to the mean value for each point;

each entity now possesses new coordinates defined in terms of standard deviation units.

Multidimensional rotation of axes follows such that perpendicular distances of the entities from the first new axis (first principal component, first eigenvector, or first latent root) are minimized. Such a rotation serves to maximize the spread of entities along the length of this axis. So situated, this first principal component (PC) accounts for the maximum amount of total variance that can be explained by a single axis through a particular n-dimensional cloud of observations. Additional axes, also passing through the centroid, are positioned at right angles to the first, with each successively generated axis accounting for less variance (eigenvalues) than the preceding one.

It should be noted that none of the new axes directly reflects the measured attributes, but instead each vector represents a different linear combination to which each measured character contributes. The relative contribution of each character to any particular vector is indicated by the respective character loadings. The actual percent contribution of a character to a particular component equals the square of the corresponding character loading (Neff and Marcus, 1980:54-55). The magnitudes of these loadings, which may range from -1 to +1, indicate the relative importance of the original variables in the newly derived component. The position of any entity along any vector is a linear combination of the products of measured attributes and their corresponding character loading coefficients.

The prime objective underlying principal components analyses is to reduce the number of dimensions (original attributes) from many to a few that are easily visualized but still preserve the inter-entity relationships described by the original data set. Conventionally, spatial relationships between entities are depicted in bivariate plots having two of the first three principal components as axes. Proximity of entities on these plots generally reflects their similarities. Using principal components I, II, and III as axes, three-dimensional plots may be constructed, especially when two dimensions do not adequately segregate entities. However, as Clifford and Stephenson state (1975:186), "addition of further dimensions in this fashion runs counter to the entire objective of ordination."

As a further aid to visualizing relationships between entities plotted in principal components projections, minimum spanning trees can be overlaid. By this method, pairs of points are joined by a set of lines such that no closed loops occur (Calinski and Harabasz, 1970, unpublished manuscript cited in Wishart, 1975:123). The result is that all  $n$  entities are connected by  $n-1$  lines (edges) of minimal total length. The comparative value of this method is evident where samples widely separated in multi-dimensional space may lie close together in two-dimensional principal components plots (Clifford and Stephenson, 1975:123-124).

### Multivariate Analyses of Variance

Multivariate analysis of variance (MANOVA) is a procedure that tests for differences between three or more samples on the basis of simultaneous consideration of many characters (i.e., dependent variables). Unlike clustering and principal component methods, MANOVA groups observations into samples on an a priori basis. MANOVA operates by determining for each individual specimen a single value that is a simple linear combination of the products of actual character measurements and corresponding character loadings. The set of loadings so obtained allows maximal discrimination of the a priori designated samples (Harris, 1975:101).

MANOVA examines the null hypothesis that all samples have the same joint mean or centroid. Rejection of the null hypothesis indicates that some statistically significant differences exist in the joint means of the populations sampled. It is not the intent of MANOVA to identify which samples differ significantly from which other samples nor to indicate the number of significantly different subsets of samples present in the analysis. Several different test criteria are available for establishing the significance of differences observed between samples. The MANOVA subroutine of PROC GLM of SAS computes and presents the test statistics and associated  $F$ , degrees of freedom (d.f.), and probability values for three such criteria (Hotelling-Lawley trace, Pillai's trace, and Wilks' criterion) plus the  $F$ -value and associated degrees of freedom for Roy's maximum root criterion.

Some controversy exists over which is (are) the best test(s) to use (Neff and Marcus, 1980:153-154). Wilk's lambda, which is a function of the product of the eigenvalues, requires large samples for correct probability levels (i.e., is an asymptotic test). The Hotelling-Lawley and Pillai's criteria are sums of eigenvalues (i.e., traces) of the matrices resulting from different manipulations of the effect and error matrices (Helwig and Council, 1979:249, 262). Harris (1975:109-110) argues strongly and convincingly of the merits of greatest characteristic root criteria over Wilks' lambda; because Roy's maximum root criterion is an exact test (unlike the preceding three), smaller samples suffice for correct probability levels. Although the SAS MANOVA output does not present probability values for greatest characteristic roots, the latter is indicated to be statistically significant if the null hypothesis of centroid equality is rejected by the other criteria mentioned above (Neff and Marcus, 1980:154).

#### Canonical Variates Analyses

Canonical variates analysis (CVA) is an extension of the MANOVA technique discussed above. Placement of individuals into samples is performed a priori as in MANOVA. CVA maximizes differences between these samples on the basis of measured attributes and determines a single score for each specimen. As for PCA and MANOVA, such a score is the summation of the products of character measurements and appropriate weighting coefficients. Because these coefficients are chosen such that within-sample variances are minimized while between-sample variances are maximized, the series

of canonical axes projected through the multidimensional scatter of points, in contrast to PCA, are usually not positioned at right angles to each other (Clifford and Stephenson, 1975:183; Blackith and Reyment, 1971:49). Each of the canonical vectors describes different portions of the between-sample variance, and because characters generally contribute differently to the various vectors, a unique set of character loading coefficients accompanies each variate.

## MATERIALS AND METHODS: DENTARY MORPHOMETRICS

The fossil material examined in this study was restricted to cranial specimens, although some post-cranial material is available from several sites. Dentaries were the only type of cranial material present in relatively large numbers from most sites; hence, features of only the dentaries and of the mandibular teeth were measured.

### Measurements

Using both a 10X Gaertner measuring microscope (to 0.01 mm) and Helios dial calipers (to 0.1 mm), 25 features were measured wherever possible for each of the 526 fossil dentaries and for a Recent reference sample of 50 males and 50 females from Gainesville, Alachua Co., Florida. The following characters are measured features of the dentary: (1) The dorsoventral distance from the level of the lingual edge of the alveolar toothrow to the mental foramen (MFDV); (2) the dorsoventral distance from the level of the lingual edge of the alveolar toothrow to the ventralmost point of the masseteric ridge (MRDV); (3) anteroposterior distance from mental foramen to dorsoventral plane through the anterior edge of p4 alveolus (MFAP); (4) anteroposterior distance from masseteric ridge to dorsoventral plane through anterior edge of p4 alveolus (MRAP); (5) diastema, the alveolar distance from p4 to incisor (DIAST); (6) mediolateral width of the dentary at highest point of

masseteric ridge (WDENT); (7) height of the condyle from level of lingual edge of alveolar toothrow (HTCOND); (8) anteroposterior distance from posterior of m2 to posterior edge of angle (M2ANG); (9-10) alveolar distances between p4 and m2 (P4M2) and p4 and m3 (P4M3); (11-13) length (LRMF), width (WRFM), and depth (DRMF) of retromolar (= basitemporal) fossa; (14) distance from m2 alveolus to deepest point of retromolar fossa (M2RMF); (15) distance from m2 posterior alveolus to dental (= mandibular) foramen (DFOR). The remaining 10 characters pertain to individual teeth: (16) width of lower incisor (WLINC); (17-20) lengths and widths of m1 (LM1, WM1), and m2 (LM2, WM2); (21) length of p4 (LP4); (22) length of anterior loph of p4 (LANTP4); (23-24) widths of anterior (WANTP4) and posterior (WPOSTP4) lophs of p4; and (25) width of p4 isthmus (WISTHP4).

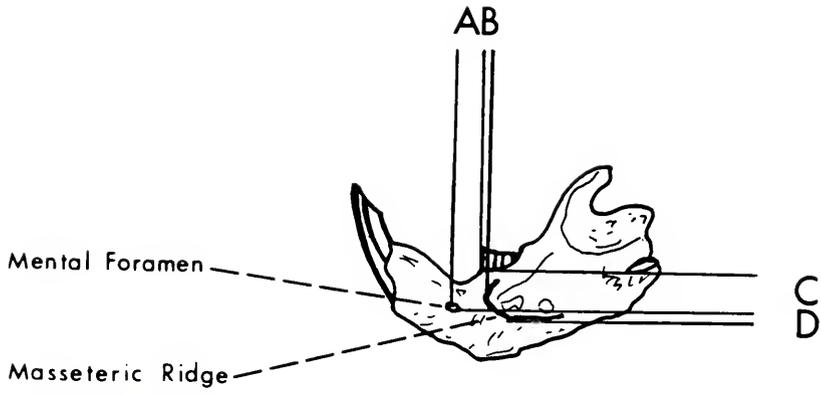
From the above measurements, values for four other characters were computed: (1) distance from the mental foramen to the incisor (MFINC = DIAST - MFAP); (2) relative dorsoventral positions of mental foramen and masseteric ridge (MFMRDV = MFDV - MRDV); (3) distance between the mental foramen and the anteriormost point of the masseteric ridge (MFMR = MFAP + MRAP); and (4) length of posterior loph of p4 (LPOSTP4 = LP4 - LANTP4). Lateral and medial views of a Geomys dentary with endpoints of various of the measured characters are illustrated in Fig. 5.

#### Materials Examined

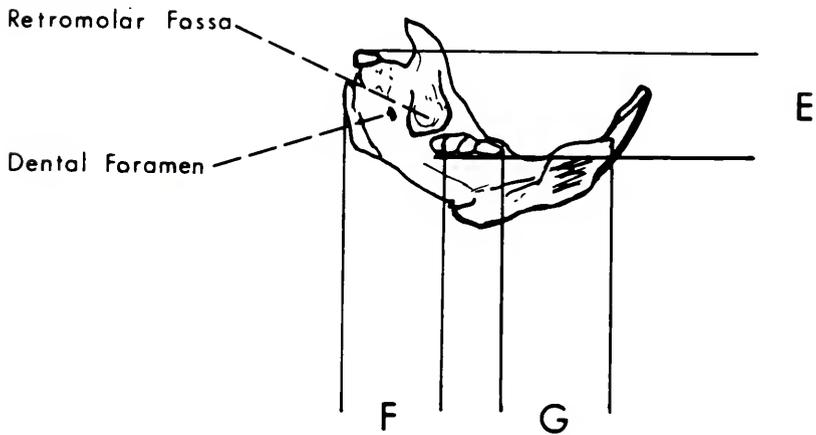
Table 1 lists 27 Florida sites and their component deposits that have yielded fossil pocket gopher material; the number of

Fig. 5.--Drawings of lateral and medial views of Geomys mandible indicating several anatomical features and endpoints of seven measurements: (A) MFAP, (B) MRAP, (C) MFDV, (D) MRDV, (E) HTPCOND, (F) M2ANG, and (G) DIAST. Names and descriptions of these measurements may be found in text. After Akersten (1973).

## LATERAL



## MEDIAL



dentaries is indicated for each site. With the exception of two mandibles from Melbourne borrowed from the United States National Museum, all fossil material is housed in the Vertebrate Paleontology Collection of the Florida State Museum, University of Florida (UF); Appendix C lists fossil geomyid material examined in this study. No dentaries were measured from Sabertooth Cave as none are included in the UF collection, although such material exists elsewhere (e.g., 4 lower jaws, 2 partial skulls at the American Museum of Natural History; listed in Simpson, 1928:2). Dentaries from four other deposits (Orange Lakes Cave, Haile XIV and XVI, and Williston III B) were not included in this study because the vertebrates in these faunas are presently being studied by Mike Frazier (Mississippi Museum of Natural Sciences) and by Robert A. Martin (Farleigh Dickinson College). Assignment of samples to land mammal ages and to glacial/interglacial stages was based on consultation of a number of references (Auffenburg, 1957, 1958, 1963; Martin, 1969; Webb, 1974; Gillette, 1976; Kurten and Anderson, 1980) and through re-examination of associated materials and discussions with Dr. S. David Webb. Specimens comprising the Recent reference sample are housed in the Recent Mammal Collection, Florida State Museum.

#### Procedural Rationale and Analyses Conducted

##### Non-Geographic Variation

In studies of geographic variation for any taxon, it is desirable to determine what proportion of the variation between and within samples is due to factors other than geographic occurrence. These factors may include sex, age, individual variation,

and experimental error. Once identified, the effects of these factors should be eliminated (as in the craniometric segment of this study).

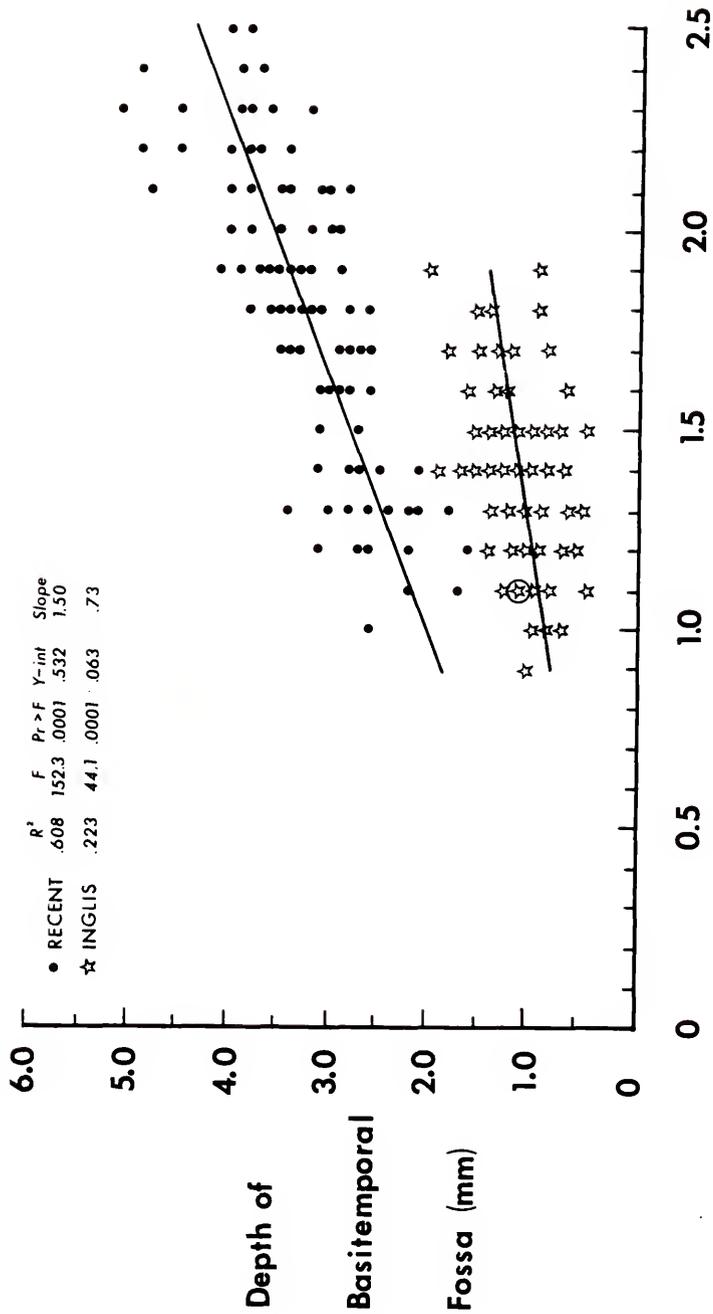
Ideally, the same procedure would be followed in analyses of geographic and chronological variation in the fossil pocket gopher material from Florida. Unfortunately, the nature of this (as with most) fossil material disallows certain analytical procedures. In rare instances where a relatively intact cranium may be found, knowledge of sexual dimorphism in living geomyids permits an inference of the sex of a fossil specimen; however, the sex of a fossil pocket gopher specimen can never be known with certainty. Even in living forms, the only mandibular characters useful in distinguishing sexes are related to size; no qualitative features are apparent. The value of relative size or dimensions is limited because of the great overlap in males and females. Pocket gopher crania and mandibles generally increase in size (in most characters) with increasing ontogenetic age, with old males being larger than old females. Only in the zone of non-overlap at the upper end of the size range of males can the sex be inferred with greater than 50% confidence.

Because of the marked ontogenetic variation, comparisons between samples should involve subsamples not only of the same sex, but also of the same age. Although actual age of fossil specimens can never be determined, width of the lower incisor (WLINC) can provide a reasonable index of age. However, it is not known whether the ontogenetic rate of increase of WLINC is the same for

both sexes; to my knowledge, this information is not available for any living geomyid species. Furthermore, the constancy of these rates over the phylogenetic history of geomyids in Florida is unknown. Nevertheless, width of the lower incisor (WLINC) was used as an index of specimen size. Although such a relationship has not been empirically demonstrated for any geomyids, it is apparent from observation of an ontogenetic series of Recent Geomys pinetis. Fig. 6 illustrates ontogenetic variation in Geomys pinetis of one of the characters (DRMF, depth of retromolar fossa) examined in this study relative to WLINC. Incisor width is known to be strongly correlated with ontogenetic age in other rodents (e.g., in Marmota monax, Ruckel and Scanlon, 1978), so that incisor width increases with increasing age of the individual.

One means of dealing with ontogenetic variation is to subdivide samples by increments (0.1 mm) of WLINC and then to restrict all statistical comparisons to subsamples of like WLINC. There is a major problem with this approach. Subdivision of fossil samples (already of limited size) reduces statistical power and confidence. It may also reduce the number of comparisons that can be made, particularly if not all WLINC categories are present in local fauna samples. These difficulties may be overcome by combined pairs of subsamples of consecutive WLINC values. For this approach to be valid, however, the ascending (or descending) arrangement of character means (for all characters) must correspond to a consecutive arrangement of subsamples according to 0.1 mm increments (or decrements) of WLINC. Because such a correspondence between means

Fig. 6.--Relationship between depth of retromolar fossa and width of lower incisor (an indicator of ontogenetic age) for the early Irvingtonian Inglis IA sample (stars) and for the Recent reference sample from Gainesville, Alachua County (dots). Circled star represents only overlap of Recent and fossil data sets.



and WLINC's was seen for most characters in only a general way, combination of adjacent WLINC subsamples was deemed undesirable.

An alternative (and preferable) means of accounting for age variation without subdividing samples by incisor width is via analyses of covariance. In such analyses, the total variation in the dependent variable (i.e., the various measured dentary features) is partitioned among three sources: (1) the independent treatment variable of major interest (i.e., locality, glacial/interglacial stage, mammal age, or other means of identifying samples), (2) the covariate (i.e., WLINC which is a measure of ontogenetic age), and (3) an error term. The importance of the variation from each of these sources is examined via F-tests. If the covariate is found to significantly influence overall variability, then comparisons of individual samples are conducted via t-tests for differences in corresponding adjusted means. Steel and Torrie (1960:315-316) outlined formulae and procedures for adjustment of treatment means.

In an effort to understand variability in fossil pocket gophers due to sex and age, non-geographic variation was examined in a Recent reference sample of Geomys pinetis from Gainesville, Alachua Co., Florida. The sample included 50 males and 50 females selected from over 200 available specimens such that all widths of incisor represented in the Florida State Museum mammal collection were included. All characters measured and computed for the Pleistocene material were similarly measured in this Recent reference sample. The occurrence of significant sexual variation was

examined, separately for each of 28 dental and osteological characters, in the Recent sample using a series of t-tests (PROC TTEST of SAS). WLINC, the 29th character, was used to group specimens; comparisons were made only between subsamples of males and females of like WLINC. Coefficients of variation were computed for each of these 29 characters by sex for each WLINC in the Recent reference sample. Evaluation of individual character variation was restricted to the largest male (WLINC = 2.2 mm; n = 7) and female (WLINC = 1.9 mm; n = 9) subsamples. Variation due to ontogenetic age (as indicated by WLINC) was examined within each sex using Duncan's multiple range tests (PROC GLM of SAS). The purpose of these analyses of non-geographic variation was to indicate which characters should be retained for subsequent analyses.

#### Geographic and Chronological Variation

Analyses of covariance, using width of lower incisor as the covariate to indicate ontogenetic age, provided adjusted character means for each sample and for the represented glacial/interglacial stages. Multivariate analyses examining chronological and geographic variation utilized these adjusted values as input. Relationships between samples were first explored via clustering (Ward's method) and principal components analyses using the CLUSTAN computing package (Wishart, 1975). Univariate and multivariate analyses of variance (SAS) were then used to test the significance of (1) overall variation among samples, (2) chronological variation between samples from geographically proximal areas, and (3) geographic variation between samples of similar geological age.

The significance of variation between samples can be assessed using several multivariate test statistics (e.g., Hotelling-Lawley and Pillai's traces, Wilks' criterion, and Roy's maximum root criterion). Calculation of these statistics requires that the error sum of squares matrix be inverted. Such matrices can be inverted only if the number of observations or samples included exceeds the sum of the number of variables examined and the number of groups recognized. Matrices which for this reason cannot be inverted are referred to as "singular." In several of the comparisons made in this study, matrix singularity has precluded calculations of multivariate test statistics. For those cases, statistical testing consists of univariate analyses of variance and Duncan's multiple range tests. Background information developing the rationale for use of various multivariate statistical procedures is presented in an earlier section of this dissertation.

## RESULTS: CRANIAL MORPHOMETRICS

### Non-Geographic Variation

Coefficient of variation values (CV) were used to assess within-sample variation in the 20 cranial characters. Because of extremely large CV values (Table 2), four characters (TEMP, AWINT, PWINT, LINT) were omitted from further analyses.

Variation due to sex and age was evaluated using t-tests; t-values and associated probability levels are presented in Table 3. For age class 1, males were larger than females in all of the remaining 16 cranial characters; LWNAS was the only feature for which the sexes were not different ( $P > 0.05$ ). For the older adults (age class 2), females were slightly, but not significantly, larger than males in GWNAS. The sexes were similar in size for IOC, LWNAS, and PMEXT. Males were significantly larger than females in the remaining measurements (Table 3).

Male Geomys pinetis of both age categories were similar in size in four characters: IOC, LWNAS, GWNAS, and PMEXT. Old adult males were significantly larger than younger adult males in all other features examined (Table 3). For females, mean values for IOC in both age groups were equal. In the remaining characters, older adult females were larger than younger adults; 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

Table 2.--Univariate statistics for 20 cranial characters for Gainesville, Alachua Co., Florida, of Recent *Geomys pinetis* for each sex/age combination. 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.

Character	Male (N=87)		Female (N=122)	
	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 (ZYG0)	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

Table 2.--Continued.

Character	Male (N=87)		Female (N=122)	
	Age 1 (N=53)	Age 2 (N=34)	Age 1 (N=84)	Age 2 (N=38)
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

Table 2.--Continued.

Character	Male (N=87)		Female (N=122)	
	Age 1 (N=53)	Age 2 (N=34)	Age 1 (N=84)	Age 2 (N=38)
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 (LDDIAST)	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

Table 3.--Student's  $t$ -values and associated probability levels for sex variation (within each age class) and for age variation (within each sex) in 16 cranial characters for Recent Geomys pinetis. Computed from the Gainesville, Alachua Co., Florida, sample (N = 209). Character abbreviations are defined in text.

Character	Sex Variation				Age Variation			
	Age Class 1		Age Class 2		Males		Females	
	$t$	$P > t$	$t$	$P > t$	$t$	$P > t$	$t$	$P > t$
GLS	12.486	0.0001	11.465	0.0001	5.835	0.0001	3.574	0.0008
ZYGO	11.878	0.0001	11.431	0.0001	6.939	0.0001	5.766	0.0001
WMAST	4.325	0.0001	6.610	0.0001	3.299	0.0014	4.609	0.0001
DCRAN	9.522	0.0001	6.862	0.0001	3.084	0.0028	3.673	0.0001
DROST	9.188	0.0001	6.512	0.0001	3.310	0.0014	4.143	0.0001
WROST	9.526	0.0001	8.157	0.0001	4.357	0.0001	4.704	0.0001
IOC	2.233	0.0272	0.591	0.5564	0.645	0.5215	0.280	0.7793
LMNAS	1.555	0.1221	0.091	0.9272	0.055	0.9557	0.687	0.4959
GWNAS	2.897	0.0033	0.278	0.7820	0.473	0.6368	1.192	0.2400
PMEXT	3.013	0.0031	0.516	0.6073	0.709	0.4802	1.398	0.1646

Table 3.--Continued.

Character	Sex Variation				Age Variation			
	Age Class 1		Age Class 2		Males		Females	
	$\bar{x}$	$P > \bar{x}$	$\bar{x}$	$P > \bar{x}$	$\bar{x}$	$P > \bar{x}$	$\bar{x}$	$P > \bar{x}$
LUDIAST	13.121	0.0001	11.475	0.0001	6.226	0.0001	5.544	0.0001
LMXTR	4.339	0.0001	3.947	0.0002	3.096	0.0027	3.087	0.0026
WUINC	4.976	0.0001	6.038	0.0001	3.184	0.0020	2.880	0.0047
LLDIAST	8.461	0.0001	8.160	0.0001	4.286	0.0001	5.221	0.0001
LMNDTR	5.051	0.0001	5.616	0.0001	4.550	0.0001	3.284	0.0013
WLINC	6.306	0.0001	6.248	0.0001	3.322	0.0013	3.092	0.0032

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.

### Geographic Variation

#### Univariate Clinal Variation

Geographic variation between samples was examined to assess the importance of rivers comprising region boundaries, particularly the Apalachicola and Suwannee Rivers. For a character to warrant further examination, significant differences between regional samples for that character were required; otherwise, the character was disregarded. Trends in characters with mean regional values falling into two or more significant subsets were studied on the basis of regional "area" membership (i.e., areas I, II, or III; refer to cluster section). In a descending sequence of regional means (Table 4), regional samples from the same area (i.e., geographically contiguous) would be expected to be adjacent to each other and to be separate from samples comprising other areas. Subsets for which included regions represented all three areas or non-adjacent areas (I and III) were considered to indicate no trend. Furthermore, maximally non-significant subsets whose memberships corresponded to regional composition of areas such that any subset contains regions from only one area, were judged to support the contention that the Apalachicola and Suwannee Rivers have served as barriers to pocket gopher dispersal.

Table 4.--Clinal variation in Recent *Geomys pinetis* from Florida in 16 cranial characters. Letters, representing means of samples from designated natural regions, are arranged left to right in order of decreasing mean value. Samples belonging to the same maximally significant subsets occur on the same horizontal line. Condensed from Appendix A.

Characters	Males, Age 1	Males, Age 2	Females, Age 1	Females, Age 2
GLS	DJLMKCGAI KCGAIFE	LBCJFHMDGE	LMJCBKAFGDHE	GCMDFJALEB
ZYGO	MAJLKCDG AJLKCDGFIE	DBLKFCJMGE	MKGJALBFC GJALBFCDEH	GCKFMDLJAEB
WMAST	LKJMGACFDIE	LKBFJCG BFJCGMED	GKMJLFBHC BHCDAE	GFKJMCDALEB
DGRAN	JMLKFGIDECA	FKMGLJBE KMGJLJBE GLJBECD	M KJLGFH LGFHC GFHCDEAB	MFK FKJCGAEDL JCGAEDLB
DROST	J MDKLGAI LGAICEF	JKLBEMFCD LBEMFCDG	AHJMBCKGLDFE	JBGCMCKADFEL
WROST	JMAC MACKDLIG ACKDLIGFE	MBKJCFDE BKJCFDEL ELG	MJCKGLFB CKGLFBDHAE	MDFCJKELBGA
IOC	ACDIMGJKL IMGJKLFE	CBDMF BDMFJGLKE	ACDHBMJL HBMJLKEGF	ACBMDGE BNDGKFKJL

Table 4.--Continued.

Character	Males, Age 1	Males, Age 2	Females, Age 1	Females, Age 2
LMNAS	AJKIGMCFLDE	EKJMCFLGDB	EHCABJKMGFLD	BAKJMGCELDF
CWNAS	AGJKCED GJKCEDMIF CEDMIFL	CEK EKJDMFBLG	AHCBCDKJGFML	BCAGJDKELMF
PMEXT	IFMDLJECAG	GLBFE LBFEJMKDC	HGFMBKDJLCAE	FEGDM EGDMKLJACB
LUDIAST	DJMLCKA JMLCKAG LCKAGFIE	CBLD BLDKFJMG	CMABKLDJCGFHE	GDCJAFKMLEB
LMXTR	AJMLKGDG IJMLKGDGCFE	LKMFIJIBECG	LMJFAKDB MJFAKDBCHGE	MEJLF EJLFBGGDA
WUINC	MJLKDCG LKDCGFAEI	DMKEJFLCB KEJFLCBG	KJMLB LBCFGAH BCFGAHE	MK KJFGDGLEAB
LLDIAS	DCJL CJLMKAGFIE	CBDLF BDLFJKGME	DML MLJOCKFABHE	GDCA CAJMKFLEB
LMNDR	IILMAJKDGCFE	MLKFJBCEDG	ALMGJKBCDFHE	MEAD EADKJCLFGB
WLINC	LMJKDCIFG DCIGFAE	MKLEJDBGFC	LKMJAB ABCFGEDH	MKL KLJFDGGA LJFDGGAFF

Appendix A consists of four tables (one for each sex/age category) enumerating the results of univariate statistical analyses of 16 cranial characters on a regional basis. Included for each regional sample are sample size, mean, standard deviation, extreme values, and coefficient of variation. Samples for any particular character are sequenced in order of decreasing mean values. The information contained in Appendix A has been reduced to a single table showing regional sample sequencing and significant subset membership for each character, separately for each sex/age category (Table 4). The ensuing results emanate from consideration of this table.

Males, age class 1. Only five characters failed to show significant variation between regional samples: WMAST, DCRAN, LWNAS, PMEXT, and LMNDTR. Two significantly different subsets of regional samples describe variation in seven additional characters. In six of those (GLS, ZYGO, IOC, LMXTR, WUINC, WLINC), the larger subset contains regional samples from all three areas; the larger subset of LLDIAST embraces samples from only areas I and II. The smaller subsets of IOC and WLINC are comprised of regions of areas II and III and areas I and II, respectively; regions from all areas compose the smaller subset of the remaining five two-subset characters.

DROST, WROST, GWNAS, and LUDIAST are characters with three significantly different sample subsets. Samples from all three areas fall into the intermediate and smaller subsets of all four characters, as well as into the larger subset of GWNAS. The larger subset of WROST and of LUDIAST embodies samples from areas

I and III; region J (area III) alone comprises the larger subset for DROST.

Only three of these 16 characters appear to be of value in evaluating clinal trends for age class 1 males. The pattern of IOC variation suggests the importance of the Apalachicola River as a discontinuity between area I and areas II and III. Here regions A, C, and D (area I) are adjacent to each other and have means of greatest value whereas the rest of the sequence is an irregular assortment of samples from areas II and III. In an opposite direction, but in a similar manner, WLINC and WUINC regional means vary such that regions J, K, L, and M have the four greatest mean values and the balance of the sequence includes mixed area I and II samples. The pattern of variation exhibited by WLINC and WUINC points to the possible influence of the Suwannee River in dissecting the range of Geomys pinetis in Florida. It should be noted, however, that regional sample alignments in IOC, WUINC, and WLINC correspond only to sequences of means, not to breaks between maximally significant subsets.

Males, age class 2. GLS, ZYGO, LWNAS, LMXTR, LMNDTR, and WLINC showed no significant geographic variation in old adult males. Two significantly different subsets of regional mean values were discerned in each of eight additional characters: WMAST, DROST, IOC, GWNAS, PMEXT, LUDIAST, WUINC, and LLDIAST. Regional composition of the smaller subsets of all eight characters and of the larger subsets of all characters except LUDIAST is such that all three areas are represented in each. Only areas I and III are

present in the larger subset of LUDIAST. Only DCRAN and WROST are characterized by three subsets. All three subsets of DCRAN and the two larger subsets of WROST include samples representing all three areas; regions of areas II and III comprise the smallest subset of WROST.

Unlike the other three sex/age categories, none of the character sample sequences for age 2 males are ordered with the means of the four peninsular regions being consecutive and of greatest value. Samples of two characters, IOC and LLDIAS, are arranged with area I regional samples (B, C, and D) having the three largest means in the sequences; an irregular ordering of area II and III regions completes these sequences. However, significant subset breaks for IOC and LLDIAS do not coincide with area membership of regions.

Females, age class 1. No significant differences were seen between samples of young adult females in seven characters: GLS, DROST, LWNAS, GWNAS, LUDIAS, and LMNDTR. Seven characters were represented by samples falling into two significant subsets, thereby indicating no geographic trend. For five of these (ZYGO, WMAST, WROST, IOC, LMXTR), both the large and small subsets contained regional samples representing all three areas. No geographic trend was evident in the other two-subset characters. The larger subset in both LLDIAS and WLINC included samples from areas I and III; the smaller subset of WLINC included samples from areas I and II whereas areas I, II, and III were represented in the smaller subset of LLDIAS. Three significant regional subsets describe variation

in WUINC; the intermediate subset contains regions from all three areas, whereas areas I and III and areas I and II are represented in the largest and smallest subsets, respectively.

Variation in DCRAN is described by four significant subsets (Table 4) with a general trend of increasing size from area I to II to III. That the mean cranial depth of the region M sample is greatest and that M alone comprises this subset may suggest a significant role of the St. Johns River in isolating populations east of this river from other Florida populations. This same effect is shown by variation in ZYGO and WROST where samples with the largest mean character values represent populations located east of the St. Johns River. Large character means for region M may be a part of a more general pattern for which samples from all four peninsular regions tend to have greater character means than those from areas I and II. DCRAN, WUINC, and WLINC are characters for which peninsular samples J, K, L, and M comprise the four largest mean values in the sample sequence.

Females, age class 2. Significant variation was lacking in the following eight cranial features in old adult females: GLS, ZYGO, WMAST, DROST, WROST, LWNAS, GWNAS, and LUDIAST. Samples of six additional characters grouped into two significantly different subsets; the smaller subset for all six contained samples from all three areas. IOC, PMEXT, and LMNDTR are characters in which all three areas are represented in the larger subset as well. Samples from areas I and II occur in the larger subset of LLDIAST, whereas the larger subset of LMXTR and WUINC include regional samples from areas II and II and area III, respectively.

Characters with samples falling into three significant subsets are DCRAN and WLINC. The intermediate and smaller subsets for both characters include regions from all three areas. Areas II and III are represented in the largest subset of DCRAN, as is area III for WLINC.

Region M has the greatest mean value for five characters exhibiting significant differences: DCRAN, LMXTR, WUINC, LMNDTR, and WLINC. WLINC is the only character for which the four peninsular regions are the samples with the four largest means. The arrangement of WLINC samples could support the importance of the Suwannee River as a dispersal barrier, yet area III regions occur in all three subsets, and therefore are not significantly different from certain regions of other areas. The remainder of the WLINC sequence comprises a seemingly random jumbling of area I and II regions.

Summary of univariate clinal variation. The preceding univariate examination of characters on a regional and area basis failed to demonstrate any convincing overall clinal trends that (1) occur in all four sex/age categories or (2) consistently include a particular subset of characters. The variation in nine characters, however, hints at the possible importance of three rivers in partitioning Florida pocket gopher populations.

In at least one character in each sex/age category, region M possesses the greatest mean value. However, only for DCRAN (females, age 1) is this value for M significantly different from all other regions. Sequencing of means with the value for M being greatest

suggests that populations east of the St. Johns River in peninsular Florida may be isolated from other Florida populations. Characters for which the four greatest mean values include peninsular regions J, K, L, and M indicate that peninsular forms may be separated from panhandle Geomys by the Suwannee River. No characters showed this pattern in age 2 males, although this trend is evident in as many as three characters (DCRAN, WUINC, WLINC) in the other sex/age groups. These area III region means were not significantly different from means of regions of areas I and/or II in any of these comparisons.

In only three of the possible 64 cases (from 16 characters for each of the four sex/age classes) do all regional samples from area I group together at the end of a character sequence. In the LLDIAST and IOC sequences for old adult males, area I regions have the three greatest sample means. The area I regions represented in the young adult male analysis also are the samples with the three greatest means. Such contiguous alignment of area I regions (concomitant with patternless mixing of the area II and III samples) tends to emphasize the role of the Apalachicola River in separating western panhandle Geomys from those in the remainder of Florida. Again, however, breaks between significant subsets do not correspond with area membership of regional samples.

#### Cluster Analyses

In this study it was expected that phenetic similarities between samples of like sex and age would provide insight into the degree of past or present gene flow between populations in adjacent

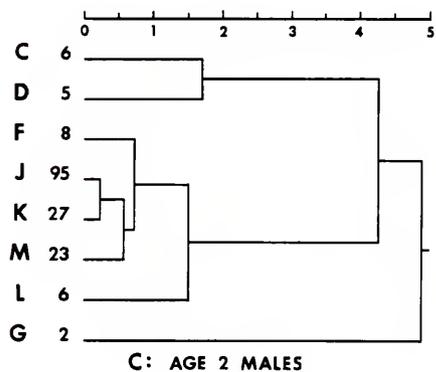
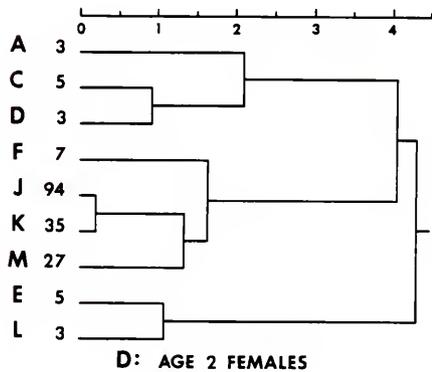
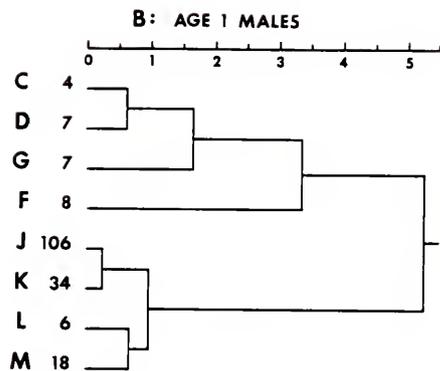
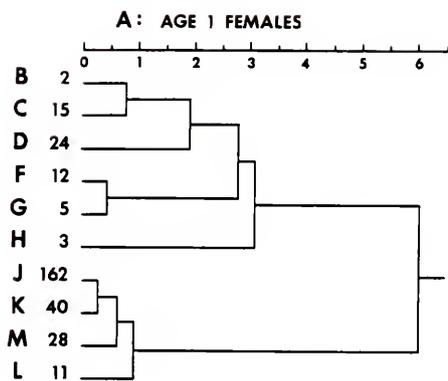
regions. The manner of cluster formation in the following analyses addresses the relative importance of the various rivers (inter-region boundaries) in inhibiting pocket gopher dispersal.

Males, age class 1. The dendrogram depicting similarities between samples of males of age class 1 bears a strong resemblance to the arrangement above. The four peninsular regions cluster tightly with each other, yet distantly from all area I and II regions (Fig. 7B). 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 each more closely connected to area I samples than to area III samples.

Males, age class 2. Fig. 7C presents the phenetic relationships of samples of old adult males. The clarity of separation of samples with respect to the Suwannee and Apalachicola Rivers seen previously is not as evident in this comparison due to the positioning of the area II regions F and G. G bears little resemblance to any regions, whereas F is included with area III. Still, the two regions from area I (C and D) form a distinct cluster emphasizing the importance of the Apalachicola River as a barrier. Additionally, three of the four peninsular regions comprise another group; the fourth peninsular region (L) occurs in the same major cluster as regions J, K, and M.

Females, age class 1. In the dendrogram generated for females of age class 1, two primary clusters are evident (Fig. 7A). One of these clusters contains all four peninsular regions (regions J, K, L, and M) that collectively are designated area III. The remaining

Fig. 7.--Results of cluster analyses of the four sex/age categories of Recent Geomys pinetis in Florida. Dendrograms computed from distance matrices using Ward's method. Letters indicate natural regions; associated numbers represent sample sizes.



regions, all occurring 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). Area II includes those regions situated between the Suwannee and Apalachicola rivers. Of the three area II regions included in this analysis, two (F and G) are closely united in one cluster. Region H, however, is closely joined to neither the area I or II clusters, although its affinity is clearly with the samples west of the Suwannee River.

Females, age class 2. The age class 2 females dendrogram (Fig. 7D) most closely resembles that for old age males. Region A, C, and D, the only area I samples included in this analysis, 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 very different from all other regions.

In each of the four analyses, all of the included area I regions were consistently and exclusively grouped together. In two of the four dendrograms (Figs. 7A and 7B) the four peninsular regions formed exclusive, highly similar clusters, while in Figs. 7C and 7D 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 indicate 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.

### Principal Components Analyses

Males, age class 1. PC I and PC II for age 1 males account for 72.39% of the observed variance; PC III represents an additional 15.24%. Character loadings for PC I are positive for all 16 characters except PMEXT (Table 5), suggesting that differentiation between samples along this component reflects general cranial size. The highest coefficient for PC I is 0.340 for length of maxillary toothrow. Positive correlations for PC II are with various dental characters (maxillary and mandibular toothrows, lower incisor width), certain rostral features (least width of nasals, extension of pre-maxilla past nasals), cranial breadth and depth, and others. Least and greatest widths of the nasals were most important characters for PC III; various other positively correlated characters reflect rostral and posterior cranial dimensions.

Table 6 enumerates coordinates of regional samples along the first three PC's for each of the four sex/age analyses. Computer-generated minimum spanning trees superimposed on these PC plots connect the most closely related regional samples and indicate relationships that might not be evident otherwise; Table 7 presents minimum spanning tree edge lengths. For age class 1 males, inter-sample relationships are similar in plots of PC I vs. PC II and PC I vs. PC III, which explain 72.39% and 64.14% of the variance, respectively (Fig. 8). The peninsular regions (J, K, L, and M of area III) comprise a single cluster of close-lying points in Fig. 8A and a more scattered group in Fig. 8B. Samples from regions C and D (area I) are more or less closely associated in Figs. 8A and

Table 5.--Results of principal components analyses of relationships between natural region samples of Recent *Geomys pinetis* from Florida. Character loadings along, and proportion of variance accounted for by, the first three vectors are presented separately for each sex/age category.

Character	MALES					
	Age 1			Age 2		
	I	II	III	I	II	III
GLS	0.310	-0.164	-0.200	0.330	0.073	-0.314
ZYGO	0.323	0.006	-0.069	0.207	-0.224	0.010
WMST	0.211	0.267	0.146	0.191	0.282	-0.384
DCRAN	0.151	0.433	0.051	0.023	0.392	-0.067
DROST	0.321	-0.035	0.154	0.401	0.053	0.018
WROST	0.314	-0.075	0.103	0.301	-0.119	0.313
IOC	0.094	-0.448	-0.107	0.014	-0.396	0.032
LWNAS	0.173	0.225	0.441	0.200	0.231	-0.092
GWNAS	0.046	-0.227	0.554	0.226	-0.275	-0.027
PMEXT	-0.058	0.198	-0.479	-0.337	0.211	-0.181
LUDIAST	0.256	-0.314	-0.184	0.190	-0.268	-0.412
LMXTR	0.340	0.113	0.101	0.338	0.158	-0.027
WUINC	0.336	-0.035	-0.113	0.233	-0.108	0.489
LIDIAST	0.119	-0.426	-0.185	0.091	-0.332	-0.371
LMNDTR	0.326	0.070	-0.146	0.341	0.195	0.017
WLINC	0.267	0.257	-0.205	0.160	0.329	0.246
Total Variance	48.90%	23.49%	15.24%	37.01%	31.75%	14.70%

Table 5.--Continued.

Character	FEMALES								
	Age 1			Age 2					
	I	II	III	I	II	III	I	II	III
GLS	0.324	-0.139	0.136	0.358	0.174	-0.143			
ZYGO	0.301	0.216	0.144	0.324	0.046	-0.175			
WMAST	0.238	0.400	-0.013	0.361	-0.058	-0.006			
DCRAN	0.223	0.274	-0.096	0.371	-0.139	0.083			
DROST	0.005	0.279	0.416	0.292	0.202	0.238			
WROST	0.308	0.064	0.236	0.314	-0.035	-0.253			
IOC	-0.129	-0.398	0.322	0.006	0.325	0.261			
LMNAS	-0.210	0.187	0.449	-0.027	0.095	0.588			
GNAS	-0.289	-0.002	0.367	0.008	0.428	0.175			
PMEXT	-0.134	0.435	-0.179	0.004	-0.278	-0.344			
LUDIAST	0.194	-0.237	0.392	0.200	0.384	-0.203			
LMXTR	0.285	-0.134	-0.153	0.077	-0.400	0.172			
WLINC	0.240	0.123	0.193	0.377	-0.130	0.165			
LLDIAST	0.186	-0.368	-0.145	0.082	0.382	-0.256			
LMNDTR	0.344	-0.101	-0.035	0.204	-0.123	0.286			
WLINC	0.335	0.016	0.121	0.281	-0.204	0.112			
Total Variance	46.12%	19.95%	16.21%	35.99%	27.68%	16.30%			

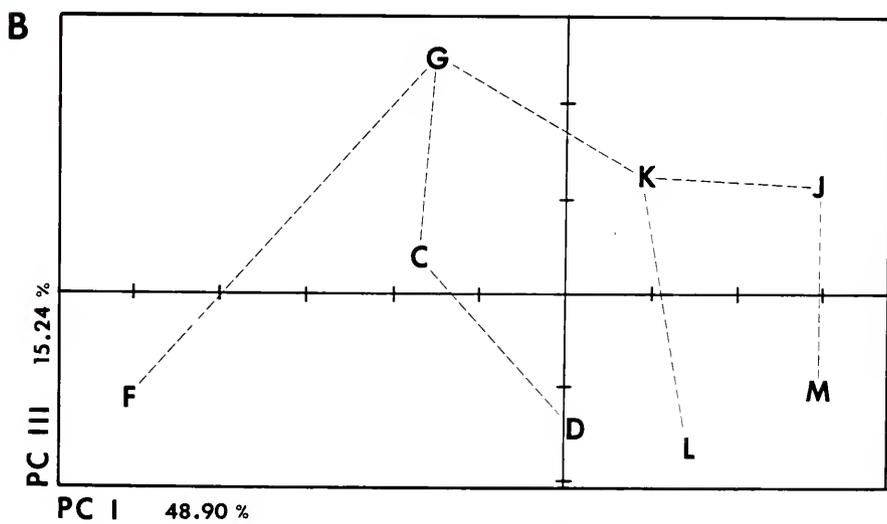
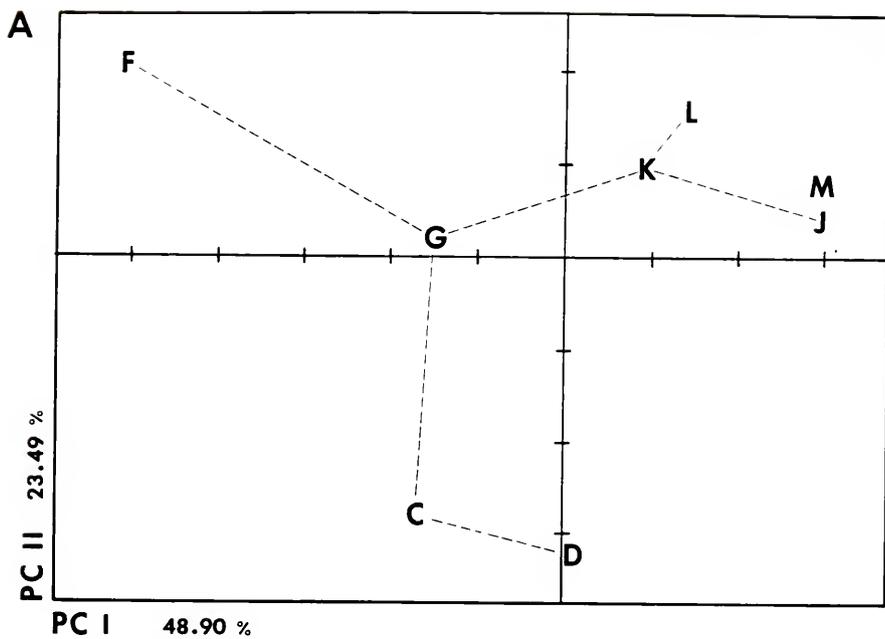
Table 6.--Results of principal components analyses of relationships between natural region samples of Recent *Geomys pinetis* from Florida: coordinates of natural region samples for principal components I, II, and III used for plotting principal components projections.

Natural Region	Males, Age 1			Males, Age 2		
	I	II	III	I	II	III
	Natural Region			Natural Region		
C	-1.7706	-2.7702	0.3852	0.579	-3.4756	-1.966
D	0.1153	-3.1906	-1.4680	-0.545	-3.7047	1.410
F	-5.2469	2.0812	-1.1311	0.150	0.5974	-0.234
G	-1.5628	0.1984	2.5530	-5.694	1.3669	-0.256
J	3.0567	0.4080	1.1596	0.895	0.9227	0.746
K	0.9001	0.9517	1.2722	2.052	1.5689	0.113
L	1.4626	1.5635	-1.6799	1.426	1.8653	-2.131
M	3.0461	0.7579	-1.0910	1.137	0.8592	2.318
Females, Age 1						
B	-1.427	-0.2540	1.6968	-2.465	2.484	2.067
C	-1.0550	-2.1025	2.5721	1.502	3.021	-0.214
D	-1.8236	-3.4822	-1.8039	0.112	2.457	-2.606
F	-0.6622	0.7364	-2.3282	-3.497	-1.735	0.117
G	-0.2778	1.9618	-1.2220	1.228	-1.984	-2.304
H	-5.4775	1.8312	0.2293	0.917	0.008	1.142
J	1.7776	0.2593	1.0601	1.489	-0.557	0.716
K	1.8078	1.4155	0.5704	-2.839	-1.814	-0.464
L	3.2253	-1.2393	-1.3431	3.556	-1.881	1.547
M	3.6291	0.8738	0.5692			
Females, Age 2						

Table 7.--Results of principal components analyses between natural region samples of Recent *Geomys pinetis* from Florida: minimum spanning tree parameters including edge lengths.

Males, Age 1			Males, Age 2		
Edge No.	Vertices	Edge Length	Edge No.	Vertices	Edge Length
1	C to G	1.139	1	C to F	1.659
2	D to C	0.820	2	D to C	1.718
3	F to G	2.131	3	F to J	0.500
4	G to K	0.765	4	G to F	2.397
5	J to M	0.690	5	J to M	0.349
6	K to J	0.456	6	K to J	0.229
7	L to K	0.848	7	L to F	0.837
Females, Age 1			Females, Age 2		
1	B to J	0.981	1	A to J	1.559
2	C to B	0.923	2	C to J	0.930
3	D to F	1.560	3	D to C	0.965
4	F to G	0.586	4	E to L	1.118
5	G to K	1.095	5	F to K	0.968
6	H to B	2.063	6	J to K	0.252
7	J to M	0.522	7	K to M	0.966
8	K to J	0.441	8	L to J	1.651
9	L to J	0.751			

Fig. 8.--Relationships between regional samples of age 1 male Geomys pinetis as shown on plots of principal components I vs. II and I vs. III. Percent variance contained within each component indicated along axes. Most similar samples connected by a minimum spanning tree (dashed lines).



AGE 1 MALES

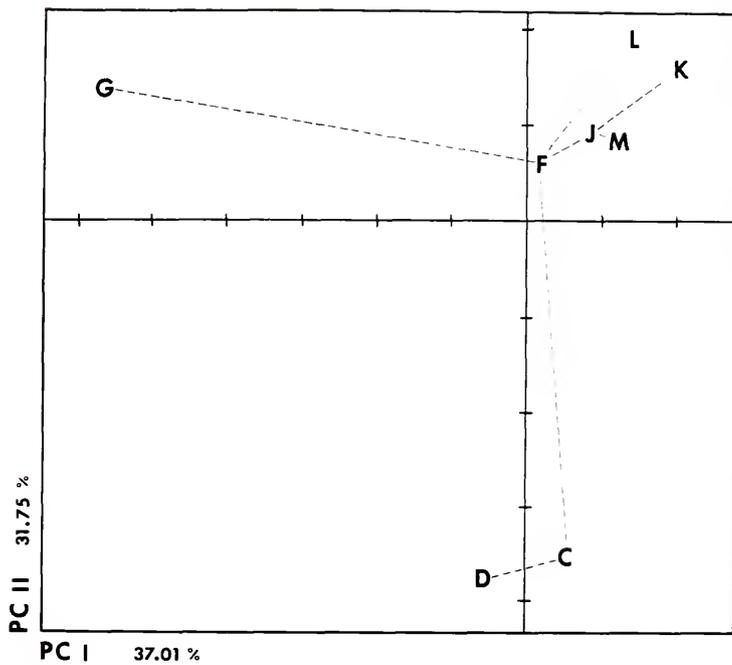
8B, respectively. Region F, a distant outlier in both plots, is most similar to region G, the only other area II sample in this analysis.

Males, age class 2. Over 83% of the total variance is explained by the first three PC's (Table 5). The pattern of character loadings for PC I here is very similar to that for PC I in the younger males; the only negatively correlated character is PMEXT. The greatest coefficients in PC I for old adult males are for rostral depth, length of mandibular and maxillary toothrows, and skull length. The loadings for PC II in both old and younger adult males are similar; the primary differences are sign reversals for skull length, zygomatic breadth, and rostral depth. Width of the upper incisor was the greatest contributing factor to PC III; other important characters were width of the lower incisor and rostral width.

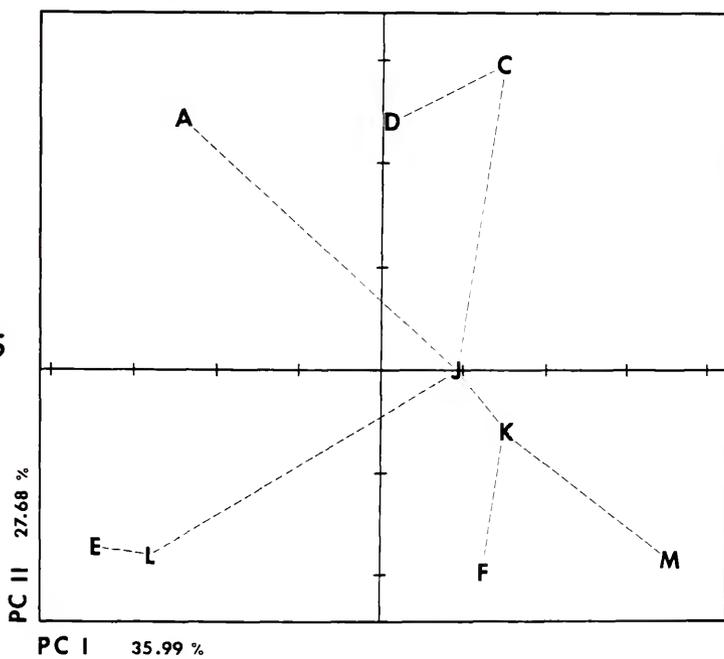
The plot of PC I vs. PC II depicts a central core of samples from which two arms radiate (Fig. 9A). One arm is composed of regions C and D, the only area I samples represented in this analysis. Region G, also distant from the major cluster, is most similar to region F, the only other area II sample in the analysis. The five regions comprising the central cluster are divisible into two groups. Region L (area III) lies separate from the other peninsular samples (J, K, and M of area III) that are most similar to region F. This plot explains 68.76% of the variance in the data set.

Fig. 9.--Relationships between regional samples of age 2 male (A) and age 2 female (B) Geomys pinetis as shown on plots of principal components I vs. II. Percent variance contained within each component indicated along axes. Most similar samples connected by a minimum spanning tree (dashed lines).

A

AGE 2  
MALES

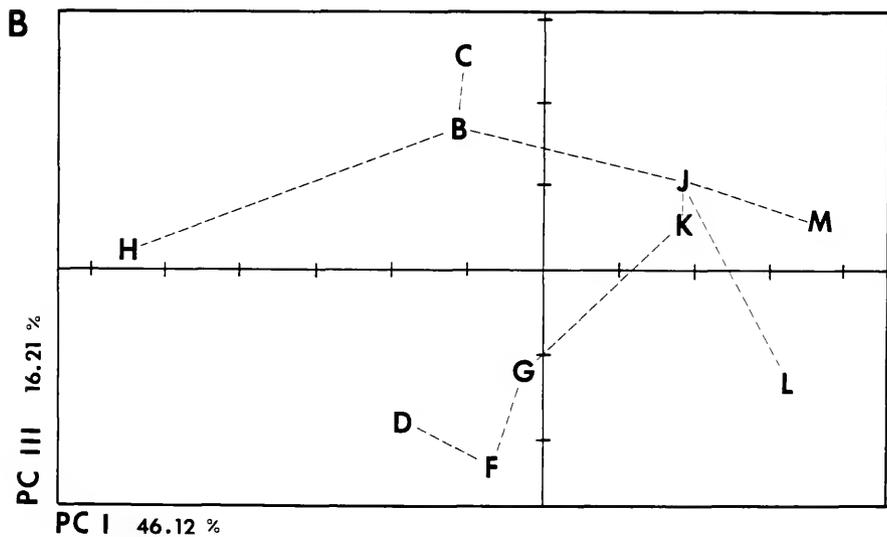
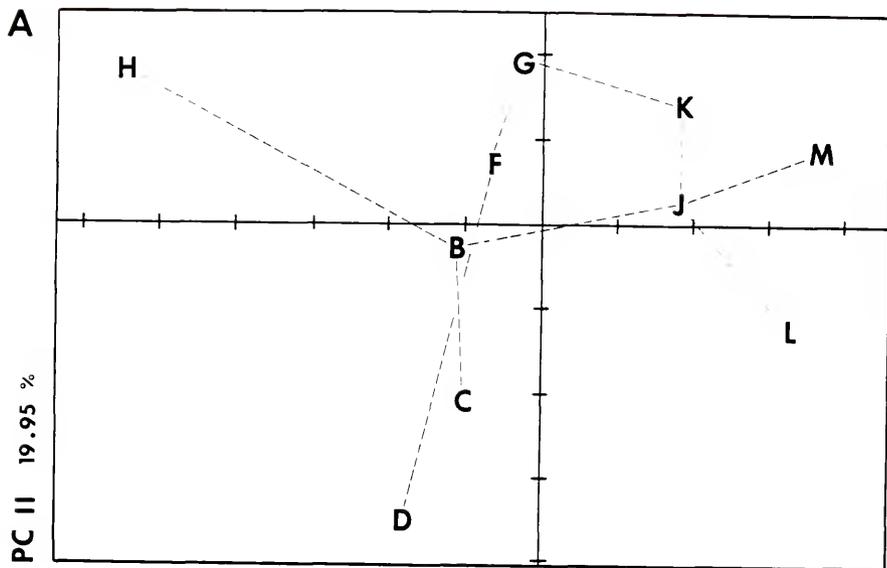
B

AGE 2  
FEMALES

Females, age class 1. The first PC's account for 82.28% of the variation between the younger adult female samples. While PC I reflects a general size component, the character loading pattern is slightly different from those of the other three sex/age categories. Negative loadings were produced for characters evaluating shape and positioning of the nasals and adjacent maxilla and for width of the interorbital constriction (Table 5). Factors contributing most importantly to PC II include PMEXT, mastoid width, cranial and rostral depths, and zygomatic width. Variation explained by PC III results primarily from a suite of characters assessing various rostral features: least and greatest nasal widths, depth and width of rostrum, length of upper diastema, and width of interorbital constriction.

Plots of PC I vs. PC II (Fig. 10A) and PC I vs. PC III (Fig. 10B) illustrate 66.07% and 62.33% of the total data set variance, respectively. Relationships between regional samples, obscured in two-dimensional plottings, are clarified through examination of edges connecting various vertices (regional samples). Area III regions J, K, L, and M comprise relatively discrete clusters in both illustrations. Through region K, this cluster is connected to two area II regions (G and F) and thence to area I region D. Regions B and C, the other area I samples, comprise a cluster most similar to the peninsular regions (via region J). As plotted in two dimensions (especially in Fig. 10A), region D falls close to its area I neighbors, but the minimum spanning tree shows region F to be its most similar sample; region D and regions B and C are

Fig. 10.--Relationships between regional samples of age 1 female Geomys pinetis as shown on plots of principal components I vs. II and I vs. III. Percent variance contained within each component indicated along axes. Most similar samples connected by a minimum spanning tree (dashed lines).



**AGE 1 FEMALES**

phenetically linked only in a very roundabout manner. Region H (area II), linked with, but still distant from region B, is positioned far from other area II regions.

Females, age class 2. Principal components I, II, and III account for almost 80% of the variance among old adult female samples. The PC I character loading pattern seen in both male analyses is similar to that for this analysis; all characters (except least width of nasals) are positively correlated (Table 5). The highest loadings are generally for characters assessing gross cranial dimensions. PC II emphasized features in the rostral region (e.g., greatest nasal width, length of upper diastema, width of interorbital constriction, rostral depth) as well as length of the lower diastema. Least width of nasals is the most strongly correlated character in PC III; a variety of dental features have positive correlations as do certain rostral characters.

Four sample groups are evident in the plot of PC I vs. PC II (Fig. 9B). Region A, which comprises one of these groups, is circuitously connected to the other included area I regions (C and D) by way of region J. Three of the four area III regions (J, K, and M) form a cluster with area II region F. The fourth group includes two regions (E and L) from different areas.

#### Multivariate Analyses of Variance: Variation Between Regions

The occurrence of statistically significant morphological differences between samples characterizing different natural regions is demonstrated for each sex/age category by each of the test criteria computed (Table 8). For all test statistics, the probability

Table 8.--Results of multivariate analyses of variance for differences between regional samples of Recent Geomys pinetis from Florida. Included are parameters 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.

Parameter	MALES		FEMALES	
	Age 1	Age 2	Age 1	Age 2
Hotelling-Lawley				
Trace	1.7571	2.3766	1.8625	1.9108
<u>F</u>	1.74	2.36	2.86	1.78
<u>d.f.</u>	160,1582	144,1289	176,2972	160,1492
Prob > <u>F</u>	0.0001	0.0001	0.0001	0.0001
Pillai's				
Trace	1.3032	1.5997	1.2528	1.2951
<u>F</u>	1.58	2.07	2.27	1.49
<u>d.f.</u>	160,1690	144,1377	176,3102	160,1600
Prob > <u>F</u>	0.0001	0.0001	0.0001	0.0002
Wilk's				
Criterion	0.2224	0.1456	0.2230	0.2130
<u>F</u>	1.67	2.23	2.54	1.62
<u>d.f.</u>	160,1385	144,1161	176,2504	160,1308
Prob > <u>F</u>	0.0001	0.0001	0.0001	0.0001
Roy's Maximum				
Root Criterion	0.5326	0.7899	0.9610	0.9553
<u>F</u>	9.32	14.04	25.07	15.86
<u>d.f.</u>	10,175	9,160	11,287	10,166

of exceeding  $F$  was less than or equal to 0.0001, except for age 2 females for which the probability of being greater than  $F$  for Pillai's trace was 0.0002.

Males, age class 1. For age 1 males, 10 canonical variates were required to describe the total variation observed. The first three variates represent 30.31%, 25.87%, and 19.94% of the variation, respectively, for a total of 76.12%; the remaining vectors each entail less than 8% of the total variation (Table 9). GLS (18.14%) and LMXTR (16.23%) contributed most to separation of regional samples along variate I (Table 9). The only other characters on variate I with more than 8% influence were IOC and DROST. Over 70% of the dispersion along variate II resulted from five characters: WMAST, LUDIAST, IOC, LMXTR, and DCRAN. For variate III GLS, WMAST, and LMNDTR were most important in discriminating between samples. Sample sizes of the regions included in this analysis are: A (1), C (4), D (7), E (1), F (8), G (4), I (1), J (104), K (34), L (6), and M (17).

Plots of regional sample centroids and corresponding  $\pm 1$  standard deviation bars on canonical variate axes I vs. II and I vs. III (Figs. 11A, 11B) both show two sample clusters where regions C and D (area I) form one group and regions from areas II and III collectively form the other. Regions represented only by single specimens were plotted but are not considered in presentation of results. In the plot of variate I vs. II, regions C and D broadly overlap each other but do not overlap other samples. In both plots, the area II samples (F and G), intermediate between

Table 9.--Results of multivariate analyses of variance for differences between regional samples of Recent *Geomys pinetis* from Florida. Presented for each of the first three canonical variates are coefficients and relative importance (%) for each character, characteristic root, and percentage of variance explained by that variate. Mean values for each character, used for determining character contributions, also included. Presented separately for each sex/age category.

Character	MALES, AGE I						Mean Value
	Variate I		Variate II		Variate III		
	Coefficient	Impt.	Coefficient	Impt.	Coefficient	Impt.	
GLS	-0.02272033	18.14	0.00038122	0.36	-0.03019676	21.31	48.80
ZYGO	0.01046501	4.98	0.00283676	1.59	0.02174222	9.15	29.11
WMAST	0.00676266	2.83	-0.04262071	20.95	0.05170566	19.14	25.59
DCRAN	0.02304297	5.57	-0.04365982	12.39	-0.02318831	4.95	14.77
DROST	0.07308372	8.58	0.01851625	2.55	0.00458802	0.48	7.18
WROST	0.03581378	6.12	-0.01886213	3.78	-0.02410258	3.64	10.44
IOC	-0.07668162	8.78	0.09550897	12.84	-0.02064286	2.09	7.00
LWNAS	0.13570593	5.02	-0.01908797	0.83	0.02827389	0.92	2.26
GWNAS	-0.09260121	4.29	0.07963780	4.33	0.10823243	4.43	2.83
PNEXT	0.01154787	0.60	-0.02884202	1.77	-0.00918219	0.42	3.19
LUDIAST	0.0174813	5.30	0.04193981	15.22	-0.01676455	4.58	18.89
LMXTR	0.10001469	16.23	0.06550090	12.48	0.00677946	0.97	9.92
WUINC	-0.07887571	2.97	0.01405377	0.62	0.07075305	2.35	2.30
LLDIAST	-0.03682026	6.97	0.01200783	2.67	0.04086779	6.84	11.57
LMNDTR	0.00021931	0.03	0.01062776	1.79	-0.10866924	13.77	8.76
WLINC	0.10352338	3.61	-0.14281484	5.84	-0.16064475	4.95	2.13
Char. Root	0.53259619		0.45460447		0.35032937		
Percent Var.	30.31%		25.87%		19.94%		

Table 9.--Continued.

Character	MALES, AGE 2						Mean Value	
	Variate I		Variate II		Variate III			
	Coefficient	Impt.	Coefficient	Impt.	Coefficient	Impt.		
GLS	0.01164875	10.93	-0.01479442	15.66	-0.01906701	14.03	52.37	
ZYGO	0.00676555	3.86	-0.01098622	7.06	-0.02104854	9.59	31.82	
WMAST	0.00984052	4.82	-0.01683534	9.29	0.04354723	17.04	27.32	
DCRAN	0.03102579	8.53	0.02702325	8.38	-0.03958665	8.70	15.34	
DROST	0.06860734	9.53	0.06433559	10.08	0.05702151	6.33	7.75	
WROST	-0.00921983	1.84	0.11147863	25.07	0.01568712	2.50	11.13	
IOC	-0.07913358	10.02	0.01907071	2.72	-0.04172463	4.23	7.07	
LWNAS	0.12380144	5.08	-0.02178115	1.01	0.06999349	2.30	2.29	
GWNAS	-0.11034262	5.75	0.00874061	0.51	0.02502227	1.04	2.91	
PMEXT	0.02180010	1.34	-0.03954178	2.73	-0.03044278	1.49	3.42	
LUDIAST	-0.02552244	9.68	0.00099349	0.43	0.05649467	17.13	21.17	
LMXTR	0.08628282	15.94	-0.00663780	1.38	-0.02966021	4.38	10.31	
WUINC	-0.07806884	3.47	0.11494937	5.76	-0.16129885	5.73	2.48	
LLDIAST	-0.02845070	6.71	-0.02658795	7.08	-0.00954535	1.80	13.17	
LMNDR	-0.01501705	2.47	0.01387987	2.57	-0.02147977	2.82	9.17	
WLINC	-0.00139783	0.06	0.00570213	0.26	-0.01866270	0.61	2.27	
Char. Root	0.78988564		0.61063397		0.41935603			
Percent Var.	33.24%		25.69%		17.65%			
			FEMALES, AGE 1					
GLS	0.00239812	2.32	-0.00127091	1.13	0.00334873	4.61	44.42	
ZYGO	-0.01736084	9.90	0.03232438	17.00	-0.02914341	23.70	26.22	
WMAST	-0.01829405	9.39	0.02104371	9.96	-0.00222413	1.63	23.60	
DCRAN	-0.04498402	13.68	-0.03220417	9.03	0.00376727	1.63	13.98	
DROST	-0.00005176	0.01	0.03303296	4.31	0.13005581	26.22	6.50	
WROST	-0.04206971	8.71	-0.02164677	4.13	-0.00407245	1.20	9.52	

Table 9.--Continued.

Character	Variate I		Variate II		Variate III		Mean Value	
	Coefficient	Impt.	Coefficient	Impt.	Coefficient	Impt.		
IOC	0.10770888	16.11	-0.07751280	10.70	0.03289603	7.02	6.88	
LWNAS	-0.09892787	4.71	-0.03848285	1.69	0.04707166	3.20	2.19	
GWNAS	0.13864969	8.11	0.12902276	6.96	0.00443824	0.37	2.69	
PMEXT	0.00413934	0.26	0.01997360	1.18	-0.01084627	0.99	2.94	
LUDIAST	0.03140192	11.18	-0.00686873	2.26	0.00278566	1.41	16.38	
LMXTR	0.00496126	1.03	-0.01489342	2.85	0.01652893	4.89	9.54	
WUINC	-0.11757222	5.39	0.05248305	2.22	0.14901301	9.75	2.11	
LLDIAST	0.01809930	4.00	-0.03828359	7.81	-0.00370488	1.17	10.17	
LMNDTR	0.01740158	3.18	-0.07285161	12.29	-0.04574528	11.93	8.41	
WLINC	-0.04752419	2.02	-0.16572994	6.48	0.00469604	0.28	1.95	
Char. Root	0.96099782		0.30843790		0.19115308			
Percent Var.	51.60%		16.56%		10.26%			
			FEMALES, AGE 2					
GLS	-0.01100215	7.67	0.02044381	14.84	-0.00528879	4.89	46.16	
ZYGO	-0.00938978	3.93	-0.00783232	3.41	-0.02876500	15.95	27.69	
WMAST	-0.00331505	1.23	-0.05135854	19.86	-0.03411076	16.80	24.60	
DCRAN	-0.04287031	9.30	-0.02480698	5.60	-0.00625402	1.80	14.36	
DROST	0.07605704	7.79	-0.08360011	8.91	0.04494477	6.10	6.78	
WROST	-0.05019784	7.56	0.00257255	0.40	-0.01527144	3.05	9.97	
IOC	0.01222809	1.28	0.12766931	13.89	-0.00335912	0.47	6.92	
LWNAS	-0.17934610	6.10	0.00968901	0.34	0.02681282	1.21	2.25	
GWNAS	0.20474127	8.54	-0.03048026	1.32	0.00087156	0.05	2.76	
PMEXT	-0.03302843	1.55	0.00737721	0.36	-0.01683960	1.05	3.11	
LUDIAST	0.03962621	10.44	0.00220292	0.60	0.00051996	0.18	17.44	
LMXTR	0.05406227	8.00	-0.04749644	7.32	0.15533631	30.48	9.80	

Table 9.--Continued.

Character	Variate I		Variate II		Variate III		Mean Value
	Coefficient	Impt.	Coefficient	Impt.	Coefficient	Impt.	
WUINC	-0.21493768	7.14	0.02647459	0.92	-0.10253499	4.52	2.20
LLDIAS	0.02579059	4.25	0.04794667	8.22	0.01650671	3.60	10.90
LMNDR	-0.09550855	12.60	0.09153379	12.56	0.03265986	5.71	8.73
WLINC	-0.08553844	2.61	-0.04547204	1.44	0.10312421	4.17	2.02
Char. Root	0.95527005		0.32225726		0.19835477		
Percent Var.	49.99%		16.86%		10.38%		

Fig. 11.--Canonical variates projections showing relationships between regional samples (without regard to area membership) for age 1 and age 2 male Geomys pinetis. Bars indicate one standard deviation to either side of sample means (indicated by position of letters). Character loading coefficients and percentage variance attributed to each vector listed in Table 9. Sample sizes indicated in text.



those of area I and area III regions, broadly overlap various of the area III regions. A slight overlap between areas I (region C) and II (region F) is apparent in the plot of variates I vs. II. No pattern was evident in the plot of variates II vs. III; samples were intermingled in one general cluster (not illustrated).

Males, age class 2. Nine variates describe the variation between regional samples of age 2 males (Table 9). 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. LMXTR, GLS, IOC, LUDIAST, and DROST, the five most influential variables for variate I, individually explained greater than 9% (and collectively the majority) of the observed variability (Table 9). Three-quarters of the dispersion along variate II was attributable to five characters: WROST, GLS, DROST, WMAST, and DCRAN. Along variate III, five characters (LUDIAST, WMAST, GLS, ZYGO, DCRAN) accounted for over 56% of the variation. Regions and respective sample sizes for this analysis are: B (1), C (6), D (5), E (1), F (8), G(2), J (95), K (26), L (6), and M (24).

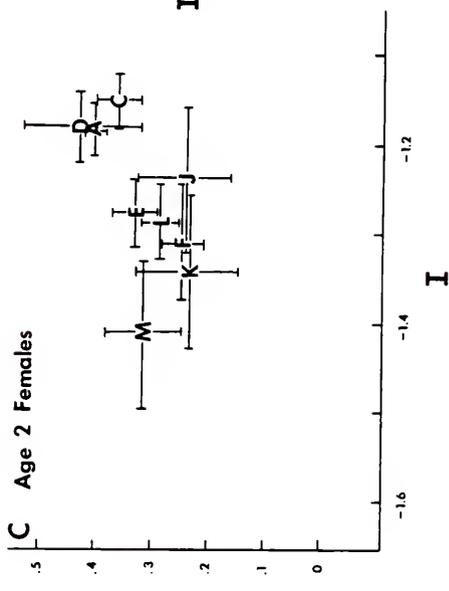
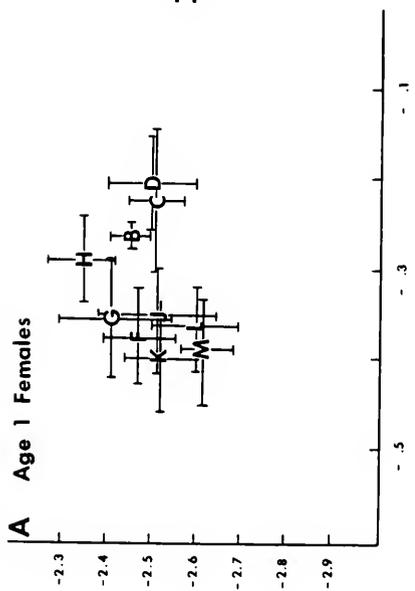
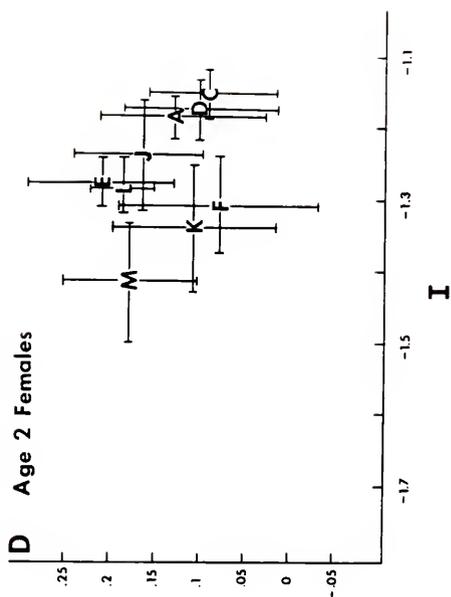
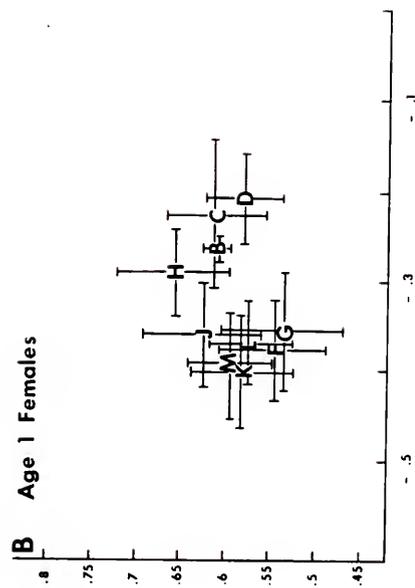
Two distinct sample clusters are evident in plots of regional sample centroids for both variate I vs. II and I vs. III (Figs. 11C, 11D). Samples C and D (area I) overlap variously in these plots, but are widely separated from the cluster comprised of area II and III samples. Overlap of the confidence bars of regions F (area II) with those of regions J, K, L, and M (area III) is extensive in both plots. Sample G is positioned quite closely to centroids of

other area II and III samples in Fig. 11D (plot of variates I and III) and somewhat less closely with the same in the plot of variates I and II (Fig. 11C); still, in the latter graph, G is much nearer area II and III centroids than area I centroids. As for age 1 males, plotting regional centroids on vectors II and III revealed no pattern; all samples are mixed and are extensively overlain (not illustrated).

Females, age class 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 total variation, respectively (Table 9). 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 (Table 9). 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. Regional sample sizes for this analysis are: 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).

Generally similar relationships between regional samples are shown in both plots of canonical variates I vs. II and I vs. III (Figs. 12A, 12B). Area I samples B, C, and D group together closely and are situated distinctly separately from samples of areas II and III. In Fig. 12A (plot of variates I vs. II) their  $\pm 1$  standard

Fig. 12.--Canonical variates projections showing relationships between regional samples (without regard to area membership) for age 1 and age 2 female Geomys pinetis. Bars indicate one standard deviation to either side of sample means (indicated by position of letters). Character loading coefficients and percentage variance attributed to each vector listed in Table 9. Sample sizes indicated in text.



III

III

II

II

I

I

deviation bars contact, but do not overlap those of samples of areas II or III. In Fig. 12B (plot of variates I vs. III), confidence bars of B and C moderately overlap those of H and J. Although samples from all area II and III regions broadly overlap in both plots, the different relative positions of the centroids in the two plots suggest varying degrees of distinctness of areas II and III. Centroids of F, G, and H are interspersed among J, K, L, and M in the plot of vectors I and III. Although still overlapping, when plotted on axes representing variates I and II, however, area II region centroids (F, G, and H) lie adjacent to one another; similarly, area III regions J, K, L, and M form a different adjacent subgroup. Despite the variable interpretation of relationships between areas II and III, both plots clearly depict area I as distinct from the cluster including samples of areas II and III. The plot of regional centroids on variates II vs. III imparts no further information regarding inter-group relationships (not illustrated).

Females, age class 2. Variability among regional samples of age 2 females is contained within 10 characteristic roots. Variates I, II, and III entail 49.99%, 16.86%, and 10.38% of the variation individually and 77.23% collectively (Table 9). Less than 8% of the variation is explained by each of the remaining vectors. The equitability of explained variability among characters for variate I is greater than for any of the other variates for this and other sex/age categories. LMNDTR, at 12.6% influence, was the most important character, whereas the least influential attribute was

WMAST (1.23%). For variate I, less than 49% of the variability resulted from the top five characters (Table 9). The five most important characters along variate II were WMAST, GLS, IOC, LMNDTR, and DROST; all except DROST each contributed greater than 12%. Three characters (LMXTR, WMAST, and ZYGO) on variate III explain 61% of the observed dispersion; the remaining 13 characters each contribute 6% or less influence. Regions (and their sample sizes) represented in this analysis are: A (3), B (1), C (5), D (3), E (5), F (7), G (1), J (93), K (34), L (5), and M (27).

Scatter plots of regional centroids on variates I vs. II (Fig. 12C), I vs. III (Fig. 12D), and II vs. III (not depicted) all show regions A, C, and D to comprise an overlapping cluster separated, to various degrees, from samples representing areas II and III. No overlap between regions A, C, and D and areas II and III occurs in the plot along vectors I and II; some overlap does occur in the other two plots. Component samples of the area II-III cluster are positioned sporadically such that no sub-clusters corresponding to area II regions or area III regions can be envisaged. A point of interest in plots of vectors I vs. II and I vs. III is that sample M is situated as an outlier, whereas it is more centrally located in vector II vs. III space. Such positioning might correspond to the effects of the St. Johns River in isolating region M from the rest of Florida.

Multivariate Analyses of Variance: Variation within Areas

This series of MANOVA's examined variation between natural regions separately for each area, with the objective of determining if within-area variation was greater than between-area variation. Test statistics and associated probability levels assessing the significance of between-region differences are presented in Table 10.

Because of the requirements of matrix algebra, the number of characters included in this series of MANOVA's was reduced from 16 to eight. Calculations of test statistics entail inversion of the error sums of squares--cross-products matrix. Matrix inversion for MANOVA (and all other discriminant analysis procedures) is possible only when the sample size is greater than the number of variables examined plus the number of groups recognized (Neff and Marcus, 1980:150). The smallest sample in this series of analyses was 11 (for age 2 males from area II); hence, only eight characters could be used. Characters were deleted on the basis of coefficient of variation (CV) values computed for age 1 males from the Gainesville (Alachua Co.) sample (Table 2). The eight characters deleted all had CV's of 7% or greater; CV's for the remaining eight characters were less than 7%.

No significant differences were found among regions in area I for any of the sex/age categories. In area II, only for age 2 females were differences between component regions significant ( $\underline{P} = 0.0448$  or less). Variation between regions of area III, however, was significant in three of the four sex/age comparisons

Table 10.---Results of multivariate analyses of variance for differences between regional samples (separately for each area) of Recent *Geomys pinetis* from Florida. Included are parameters 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.

Parameter	Males, Age 1			Males, Age 2		
	Area I	Area II	Area III	Area I	Area II	Area III
	12	14	160	12	11	149
N	10.0459	4.6344	0.2215	6.4289	94.4119	0.5884
Hotelling-Lawley Trace	0.63	0.32	1.36	0.40	0.00	3.35
F	16,2	24,5	24,443	16,2	16,0	24,410
d.f.	0.7660	0.9734	0.1188	0.8855	1.0000	0.0001
Prob > F	1.4605	1.5368	0.1994	1.0361	1.8772	0.4609
Pillai's Trace	1.02	0.66	1.34	0.40	3.82	3.18
F	16,6	24,15	24,453	16,6	16,4	24,420
d.f.	0.5327	0.8264	0.1293	0.9314	0.1018	0.0001
Prob > F	0.0448	0.0828	0.8106	0.1144	0.0013	0.5954
Wilks' Criterion	0.93	0.53	1.35	0.49	3.38	3.27
F	16,4	24,9	24,432	16,4	16,2	24,400
d.f.	0.5981	0.8982	0.1239	0.8636	0.2523	0.0001
Prob > F	8.7575	2.8896	0.1449	6.2172	86.4341	0.3808
Roy's Maximum Root Criterion	39.41	9.63	7.54	27.98	345.74	18.41
F	2,9	3,10	3,156	2,9	2,8	3,145
d.f.						

Table 10.--Continued.

Parameter	Females, Age 1			Females, Age 2		
	Area I	Area II	Area III	Area I	Area II	Area III
N	42	21	240	12	13	152
Hotelling-Lawley Trace	1.0466	2.2859	0.3130	34.6448	49.8059	0.4306
F	1.29	0.83	2.97	0.00	6.23	2.51
d.f.	24,89	24,26	24,683	24,-1	16,4	24,419
Prob > F	0.1924	0.6801	0.0001	1.000	0.0448	0.0001
Pillai's Trace	0.7580	1.1654	0.2794	2.2789	1.7410	0.3562
F	1.39	0.95	2.97	1.19	3.36	2.41
d.f.	24,99	24,36	24,693	24,9	16,8	24,429
Prob > F	0.1296	0.5411	0.0001	0.4154	0.0437	0.0003
Wilks' Criterion	0.4124	0.2032	0.7442	0.0034	0.0050	0.6766
F	1.35	0.90	2.97	0.89	4.93	2.46
d.f.	24,90	24,29	24,664	24,3	16,6	24,409
Prob > F	0.1584	0.5970	0.0001	0.6394	0.0291	0.0002
Roy's Maximum Root Criterion	0.4835	1.1858	0.1582	30.0656	46.6040	0.2836
F	6.12	6.72	12.45	80.18	233.02	13.99
d.f.	3,38	3,17	3,236	3,8	2,10	3,148

( $P = 0.0003$  or less); age 1 males showed no significant variation by region ( $P > 0.11$ ). The apparent trend is that within each of the two panhandle areas, pocket gopher populations are generally homogeneous, whereas peninsular populations are more variable.

Significant variability among regions J, K, L, and M suggested that area III might consist of subunits by a barrier more effective in restricting pocket gopher movements than the rivers delimiting regions within the two panhandle areas.

The St. Johns River is the logical choice for such a barrier in the peninsula. Using the full 16 character data set, a series of four MANOVA's, one for each sex/age category, was conducted to test for significant variability between the area III regions west of the St. Johns River (regions J, K, and L). Despite deletion of region M specimens from these analyses, significant variation was found between samples from regions J, K, and L. For age 1 males,  $F$ -probabilities of the Hotelling-Lawley and Pillai's traces and Wilks' criterion were all less than 0.07. These values for the other three sex/age comparisons were more highly significant at probabilities of 0.0187 or less. Hence, variability between the four peninsular regions cannot be entirely attributed to the isolating effects of the St. Johns River. This problem is treated further under geographic variation in the fossil section of this dissertation (page 143).

Multivariate Analyses of Variance: Variation between Areas

The null hypothesis of no differences between joint means of samples representing the three areas of Florida was rejected for all sex/age categories on the basis of the test criteria listed in Table 11. Probabilities associated with Wilks' lambda and Pillai's trace for age 2 females are 0.0002 for both statistics, and 0.0001 for the Hotelling-Lawley trace. The probability of exceeding  $F$  is 0.0001 for these three test statistics for age 1 females and males of ages 1 and 2. Hence, Geomys pinetis from the three areas of Florida differ significantly in cranial dimensions.

Males, age class 1. Canonical variates I (65.67%) and II (34.33%) explain all observed variation between samples of young adult males from the three areas. In order of decreasing influence, the five most important characters along variate I are GLS, IOC, DCRAN, DROST, and LMXTR (Table 12). Along variate II, LUDIAST, GLS, WMAST, LMXTR, and DCRAN are the five most influential characters. The plot of area centroids with  $\pm 1$  standard deviation bars on axes representing variates I and II reveals overlap of areas 2 and 3 with area 1 isolated to the left in the graph (Fig. 13A). Sample sizes for the three areas are: 1 ( $n = 12$ ), 2 ( $n = 14$ ), and 3 ( $n = 161$ ).

Males, age class 2. All variation between samples due to area occurs along only two vectors: variate I, 78.65% and variate II, 21.35%. DCRAN, LMXTR, LUDIAST, DROST, and LLDIAST are the five most important characters on variate I (Table 12). The five top

Table 11.--Results of multivariate analyses of variance for differences between area samples (samples from all regions in an area combined) of Recent Geomys pinetis from Florida. Included are parameters for three tests for significant differences between samples plus Roy's test for significance of the first canonical variate. Presented separately for each sex/age category.

Parameter	MALES		FEMALES	
	Age 1	Age 2	Age 1	Age 2
Hotelling-Lawley				
Trace	0.7324	0.9282	0.9651	0.4744
$\underline{F}$	3.82	4.38	8.54	2.34
$\underline{d.f.}$	32,334	32,302	32,566	32,316
Prob > $\underline{F}$	0.0001	0.0001	0.0001	0.0001
Pillai's Trace	0.5257	0.5874	0.5808	0.3676
$\underline{F}$	3.77	3.98	7.29	2.25
$\underline{d.f.}$	32,338	32,306	32,570	32,320
Prob > $\underline{F}$	0.0001	0.0001	0.0001	0.0002
Wilks' Criterion	0.5396	0.4824	0.4786	0.6597
$\underline{F}$	3.79	4.18	7.91	2.30
$\underline{d.f.}$	32,336	32,304	32,568	32,318
Prob > $\underline{F}$	0.0001	0.0001	0.0001	0.0002
Roy's Maximum Root				
Criterion	0.4810	0.7300	0.8123	0.3590
$\underline{F}$	44.01	60.95	121.43	31.24
$\underline{d.f.}$	2,183	2,167	2,299	2,174

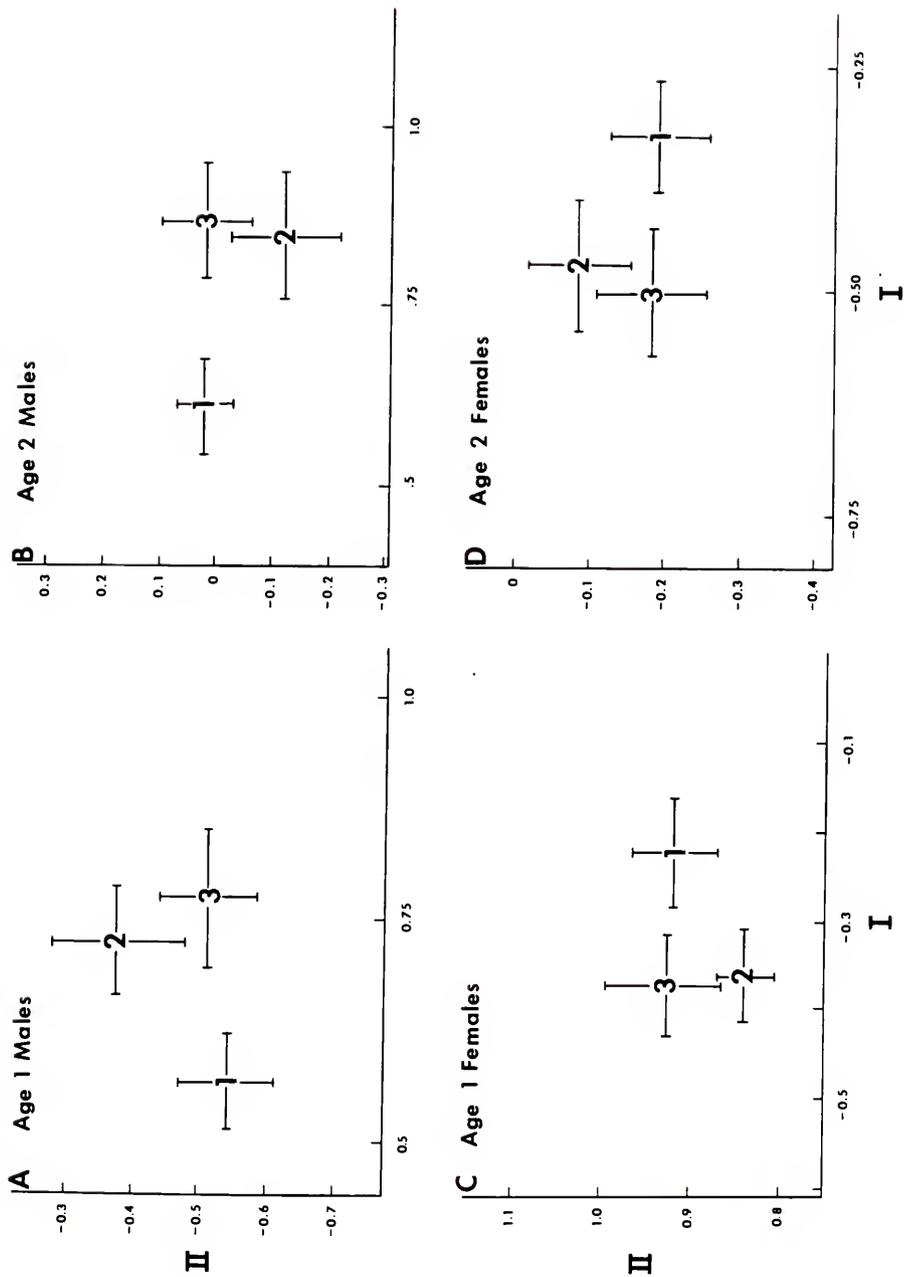
Table 12.--Results of multivariate analyses of variance for differences between area samples (all regions within an area combined) of Recent *Geomys pinetis* from Florida. Presented for the first two canonical variates are coefficient and relative importance (%) for each character, characteristic root, and percentage of variance explained by that variate. Mean values for each character, used for determining character contributions, also included. Presented separately for each sex/age category.

MALES, AGE 1					
Character	Variate I		Variate II		Mean Value
	Coefficient	Impt.	Coefficient	Impt.	
GLS	-0.02035315	16.38	0.01736425	16.55	48.80
ZYGO	0.00485932	2.33	0.00152245	0.87	29.11
WMAST	0.01769486	7.47	0.02768689	13.83	25.59
DCRAN	0.04328179	10.54	0.03231818	9.32	14.77
DROST	0.07288084	8.63	-0.01755453	2.46	7.18
WROST	0.03947840	6.80	0.00556880	1.14	10.44
IOC	-0.11649224	13.45	-0.03264868	4.46	7.00
LWNAS	0.12306629	4.59	-0.04816182	2.13	2.26
GWNAS	-0.11242114	5.48	-0.00809001	0.45	2.83
PMEXT	0.01640158	0.86	0.02670759	1.66	3.19
LUDIAST	0.00403681	1.26	-0.06935367	25.58	18.89
LMXTR	0.05120614	8.38	-0.05242569	10.16	9.92
WUINC	-0.02814396	1.07	-0.09243295	4.15	2.30
LLDIAST	-0.03975033	7.59	0.00171413	0.39	11.57
LMNDTR	-0.00013087	0.02	-0.03253304	5.56	8.76
WLINC	0.15309988	5.38	0.03122799	1.30	2.13
Char. Root	0.48096533		0.25142908		
Percent Var.	65.67%		34.33%		
MALES, AGE 2					
GLS	0.00642467	6.54	0.00381982	3.49	52.37
ZYGO	-0.00932896	5.77	-0.00964372	5.36	31.82
WMAST	0.00928280	4.93	-0.00586303	2.80	27.32
DCRAN	0.04684268	13.97	-0.07431390	19.90	15.34
DROST	0.06260377	9.43	0.10625848	14.38	7.75
WROST	0.01490007	3.22	0.05518988	10.72	11.13
IOC	-0.06381418	8.77	-0.04024141	4.97	7.07
LWNAS	0.12383819	5.51	-0.06443571	2.58	2.29
GWNAS	-0.10867448	6.15	0.06551319	3.33	2.91
PMEXT	0.01435574	0.95	-0.03769491	2.25	3.42
LUDIAST	-0.02346001	9.65	0.02777831	10.27	21.17
LMXTR	0.06829617	13.69	0.02590462	4.66	10.31
WUINC	-0.03212596	1.55	-0.06111956	2.65	2.48
LLDIAST	-0.03435415	8.79	-0.03524451	8.10	13.17
LMNDTR	-0.00480746	0.86	-0.00833520	1.33	9.17

Table 12.--Continued.

Character	MALES, AGE 2				Mean Value
	Variate I		Variate II		
	Coefficient	Impt.	Coefficient	Impt.	
WLINC	-0.00485380	0.21	0.08111931	3.21	2.27
Char. Root	0.72999376		0.19820663		
Percent Var.	78.65%		21.35%		
	FEMALES, AGE 1				
GLS	-0.00026180	0.28	-0.00024965	0.31	44.42
ZYGO	-0.01471255	9.18	-0.03063213	22.46	26.22
WMAST	-0.01756291	9.86	-0.01314848	8.68	23.60
DCRAN	-0.04331557	14.40	0.00562067	2.20	13.98
DROST	-0.03249426	5.03	0.00799135	1.45	6.50
WROST	0.00007744	0.02	0.00306624	0.82	9.52
IOC	0.10122700	16.57	0.08425900	16.21	6.88
LWNAS	-0.09333027	4.86	0.03514125	2.15	2.19
GWNAS	0.11173756	7.15	-0.04528405	3.41	2.69
PMEXT	0.00182208	0.13	-0.02798623	2.30	2.94
LUDIAST	0.03257563	12.70	0.01645129	7.53	16.38
LMXTR	-0.00441557	1.00	0.00797306	2.13	9.54
WUINC	-0.14550762	7.30	0.11460219	6.76	2.11
LLDIAST	0.01456875	3.53	0.01328716	3.78	10.17
LMNDTR	0.02878491	5.76	0.03217179	7.56	8.41
WLINC	-0.04811040	2.23	0.22486098	12.26	1.95
Char. Root	0.81226092		0.15285860		
Percent Var.	84.16%		15.84%		
	FEMALES, AGE 2				
GLS	0.00866174	7.81	0.01752482	18.37	46.16
ZYGO	0.00190131	1.03	0.00235829	1.48	27.69
WMAST	-0.03416289	16.42	0.02528124	14.13	24.60
DCRAN	-0.03633483	10.19	-0.01575347	5.14	14.36
DROST	-0.01191007	1.58	-0.04549913	7.01	6.78
WROST	-0.01493034	2.91	0.01276239	2.89	9.97
IOC	0.11684137	15.80	-0.02198053	3.45	6.92
LWNAS	-0.12093167	5.32	-0.10361581	5.30	2.25
GWNAS	0.11334008	6.11	-0.01374788	0.86	2.76
PMEXT	-0.00743451	0.45	0.07791855	5.50	3.11
LUDIAST	0.02187136	7.45	-0.02903383	11.50	17.44
LMXTR	-0.06035079	11.56	0.00539845	1.20	9.80
WUINC	-0.02993972	1.29	0.08798155	4.40	2.20
LLDIAST	0.02312861	4.93	-0.00428928	1.06	10.90
LMNDTR	0.01207239	2.06	-0.02108932	4.18	8.73
WLINC	-0.12935620	5.11	-0.29473315	13.52	2.02
Char. Root	0.35903104		0.11534455		
Percent Var.	75.68%		24.32%		

Fig. 13.--Canonical variates projections showing relationships between areas (without regard to region membership) for all four sex/age classes of *Geomys pinetis*. Bars indicate one standard deviation to either side of sample means (indicated by position of letters). Character loading coefficients and percentage variance attributed to each vector listed in Table 12. Sample sizes indicated in text.



characters accounting for the majority of the variability along variate II are DCRAN, LMXTR, LUDIAST, DROST, and LLDIAS. Overlap of area 2 and 3 samples on the plot of canonical variate I vs. II is more extensive than for age 1 males (Fig. 13B). The area 1 sample is distinct from areas 2 and 3. The number of specimens representing these areas are: 1 (n = 12), 2 (n = 11), and 3 (n = 151).

Females, age class 1. All of the observed variation in cranial morphometrics of young adult females representing the three areas of Florida is accounted for in canonical variates I (84.16%) and II (15.84%). IOC, DCRAN, LUDIAST, WMAST, and ZYGO contribute most importantly to the spread of area samples along variate I (Table 12), whereas the five variables most influential for variate II are ZYGO, IOC, WLINC, WMAST, and LMNDTR. On the plot of specimen scores on axes representing canonical variates I and II, the area 1 sample stands separately from other area samples which overlap each other slightly (Fig. 13C). Area sample sizes are: 1 (n = 41), 2 (n = 21), and 3 (n = 240).

Females, age class 2. As for the other three sex/age categories, canonical axes I (75.68%) and II (24.32%) account for all differences between samples due to areas represented by the samples. The five most important characters explaining dispersion on variate I are WMAST, IOC, LMXTR, DCRAN, and GLS (Table 12). Over half of the variation along variate II is due to the five most influential features: GLS, WMAST, WLINC, LUDIAST, and DROST. The canonical variate plot for age 2 females depicts the same inter-area relationships as

shown for the other sex/age analyses (Fig. 13D). Areas 2 and 3 broadly overlap each other, and area 1 is located separately from areas 2 and 3. The numbers of specimens representing the three areas are: 1 (n = 12), 2 (n = 13), and 3 (n = 157).

#### Summary of Results

The following section briefly highlights the results of the preceding studies of craniometric variation in Recent Geomys pinetis in Florida.

(1) Non-geographic variation due to sex and ontogenetic age is significant in nearly all characters examined. Therefore, four sex/age categories were recognized, and all subsequent analyses of geographic variation involved comparisons of samples of like sex and age.

(2) Univariate examination of characters on a regional and area basis failed to demonstrate any overall clinal geographic trends. Variation in nine characters, however, variously hints at the possible importance of three rivers (Alalachicola, Suwannee, St. Johns) in partitioning populations of Florida pocket gophers.

(3) Multivariate analyses (clustering and PCA) exploring the phenetic relationships within the four data sets determined that geographically proximal samples are more similar than were distant samples. Relatively large and small gaps between regional samples correspond to the relative effectiveness of the Apalachicola and Suwannee Rivers, respectively, in inhibiting dispersal of pocket gophers.

(4) Series of multivariate analyses of variance tested the significance of differences between samples comparing (a) inter-region, (b) intra-area, and (c) inter-area relationships. The findings follow: (a) Significant differences exist in all four tests (one for each sex/age category) simultaneously comparing centroid means of the 13 regional samples. Hence, pocket gopher populations are not morphometrically similar throughout the peninsula. (b) Three series of analyses (one for each area) tested variation among regions comprising their respective areas. Each test series included four tests--one for each sex/age category. No intra-area differences were found for any sex/age groups in area I. For area II, significant differences were found only for age 2 females. Variation in the peninsula (area III) is significant for three of four sex/age classes. (c) In assessing inter-area variation, component samples of each area were pooled without regard to regional affiliation. Significant differences exist in all four tests (one for each sex/age category) simultaneously comparing centroid means of the three area samples.

## RESULTS: DENTARY MORPHOMETRICS

### Non-Geographic Variation

#### Sex Variation

Because of great ontogenetic variation in Geomys pinetis, analysis of sex variation necessarily overlaps that of age variation. Width of incisor measurements in the Recent female sample ranged from 1.0 mm to 2.1 mm, whereas the observed range for males was 1.1 mm to 2.5 mm. Presumably, even smaller incisor widths occur in both sexes in juvenile and fetal pocket gophers that are not represented in the UF collections. Of most interest is the upper end of the range, which is comprised only of males. In my examination of hundreds of Recent specimens, I have found such large incisor widths to occur only in old adult males. Hence, within the WLINC range of 2.2 mm to 2.5 mm, the represented sex is almost certainly male. For samples containing widths of incisor less than or equal to 2.1 mm, however, both sexes are probably present. It is for such mixed samples that sex variation must be considered when examining geographic and chronological variation. A crucial assumption here is that this distribution of sexes by WLINC is representative of that for all populations in peninsular Florida throughout the Pleistocene. As size ranges may have evolved with time and under different environmental conditions, this assumption may not be valid in every case.

Overall, 16 different characters showed significant ( $P < 0.05$ ) sexual dimorphism. But for any particular WLINC, only eight or fewer characters differed significantly. Table 13 indicates sexually variable characters for six WLINC comparisons. For three other WLINC (i.e., 1.4 mm, 1.6 mm, and 1.8 mm), no characters showed significant sexual variation. Samples of remaining WLINC's were comprised of only one sex, and therefore could not be tested.

#### Individual Variation

Coefficients of variation (CV) were computed for every character by sex for each WLINC to assess variability within samples. Evaluation of individual character variation was restricted to the largest male and female subsamples. Six characters had CV values greater than 15% for the largest male subsample (WLINC = 2.2 mm,  $n = 7$ ): MRAP, MFAP, M2RMF, MRDV, MFMRDV, and MFMR. For the largest female subsample (WLINC = 1.9 mm,  $n = 9$ ), CV values exceeded 15% in five characters: MFAP, MRAP, MFMRDV, MFMR, and WISTH. Table 14 lists CV values for each character for those two subsamples. Similar trends in character variability were seen for the subsamples corresponding to other widths of incisor.

It should be noted here that all except one (WISTH) of these seven highly variable characters are measurements of distances whose endpoints cannot be neatly or precisely defined. For example, the greatest depth of the retromolar fossa, which is an endpoint of M2RMF, may occur at one point, but more often extends over a broader expanse. In most specimens the anteriormost point of the masseteric ridge is ill-defined. Orientation of the specimen for

Table 13.--Sexual variation in dentary characters from Recent reference sample (Gainesville, Alachua Co., Florida) for various subsamples designated by width of lower incisors. Asterisk indicates significant sexual variation ( $P < 0.05$ ) for a character in a particular subsample.

Character	Width of Lower Incisor (mm)					
	1.2	1.3	1.7	1.9	2.0	2.1
MFDV	-	-	-	-	-	*
DIAST	-	-	-	-	-	*
M2ANG	-	-	-	*	-	-
P4M2	*	-	-	-	-	-
P4M3	-	-	-	*	-	-
MFAP	-	-	-	-	*	*
WIDENT	-	-	-	*	-	*
HTCOND	*	-	-	-	-	-
MRDV	-	*	-	-	-	*
LM1	-	-	*	-	-	-
LM2	-	-	*	-	-	-
MFINC	-	-	-	-	-	*
MFMR	-	-	-	*	-	*
Sample Size						
Male	2	4	3	2	5	4
Female	3	4	7	9	5	4
Total	5	8	10	11	10	8

Table 14.--Coefficient of variation values (in %) for the 28 character data set for the largest male (WLINC = 2.2 mm) and female (WLINC = 1.9 mm) subsamples of the Gainesville, Alachua Co., Florida, Recent reference sample.

Character	Male (N = 7)	Female (N = 9)
MFDV	13.95	10.27
MRDV	17.58	12.15
MFAP	24.55	34.51
MRAP	67.56	39.32
DIAST	6.82	4.43
WDENT	5.74	3.64
HTCOND	11.53	6.35
M2ANG	5.86	3.02
P4M2	3.11	5.46
P4M3	3.01	3.84
LRMF	10.35	4.40
WRMF	15.45	10.51
DRMF	12.52	10.41
M2RMF	18.77	14.48
DFOR	8.74	10.74
LM1	7.17	7.39
WM1	3.77	7.62
LM2	4.49	8.73
WM2	3.28	7.85
LP4	4.26	5.31
LANTP4	4.29	6.56
WANTP4	3.79	7.79
LPOSTP4	4.62	6.81
WPOSTP4	3.34	5.75
WISTHP4	14.39	16.46
MFINC	6.01	6.76
MFMRDV	114.88	114.07
MFMR	25.20	16.74

measurements of the masseteric ridge and/or of the mental foramen is difficult. The mental foramen is variable in its position, and to further complicate matters, it occurs occasionally as two adjacent foramina. Russell (1968:527) noted that the position of the mental foramen varies both "with individuals and according to species." The relative positioning of the masseteric ridge and mental foramen has been regarded as an important character in understanding geomyid phylogeny; the difficulty of quantifying this relationship suggests that its value may be only qualitative.

Therefore, the decision was made to delete from further consideration the following 17 characters showing significant sexual and/or excessive individual variation: MFDV, MRAP, DIAST, M2ANG, P4M2, P4M3, MFAP, WDENT, HTCOND, M2RMF, MRDV, LM1, LM2, WISTHP4, MFINC, MFMRDV, and MFMR. The remaining 11 features (LRMF, WRMF, DRMF, LANTP4, DFOR, LP4, WANTP4, LPOSTP4, WPOSTP4, WM1, and WM2) show no significant sexual variation for any WLINC examined and have CV values less than or equal to 15%. In eight of these 11 characters, the CV was less than 8%. This set of 11 characters was used in subsequent analyses of geographic and chronological variation in Recent and Pleistocene pocket gophers from Florida.

Although 11 characters are deemed suitable for analyses of geographic and chronological variation, it should be noted that not every comparison includes all 11 characters. Multivariate analyses require that all characters be represented for each included observation; otherwise the character(s) for which any observation lacks data is (are) deleted from the entire analysis. In each of the

following comparisons, as many as possible of the 11 characters were included.

#### Age Variation

A series of analyses (F-tests, Duncan's multiple range tests), in which sexes were combined, addressed age variation in the remaining 11 characters. The hypothesis of equal means for all WLINC subsamples was rejected (F-tests, P < 0.0001) for each character. Duncan's multiple range tests defined significantly different subsets from the 16 levels of WLINC for each character. The number of subsets ranged from four (LRMF) to eight (WM1).

A series of analyses of covariance (using PROC GLM of SAS) for each of the 10 dentary characters examined the null hypotheses of (1) no significant covariation with WLINC, and (2) no significant differences among the 18 samples. For every character, both hypotheses were rejected (P ≤ 0.0001). The results indicate the important role of ontogenetic age in within-sample variation and the existence of significant differences among samples. Subsequent analyses addressed the latter source of variation, and examined the relative contributions of geographic and chronological variation to differences among samples.

#### Overall Relationships between Samples

This section investigates the phenetic relationships between 18 Pleistocene Florida Geomys samples and tests the significance of the observed differences. In subsequent sections, the effects of geographic occurrences and chronological ages will be examined separately as sources of morphological variation (not separated here).

Comparison of samples without regard to chronology. The first of two series of multivariate analyses was used to determine relationships between the 18 fossil samples without regard to their relative ages or geographic occurrence. (Although pocket gopher material is known from at least 37 deposits, only 18 of these samples include measureable Geomys dentaries.) The input data consisted of a series of adjusted means (obtained through analyses of covariance with WLINC as the covariate) for each measured character for each sample (Table 15). Because of missing values for three characters in several samples, only seven characters (WRMF, DRMF, LANTP4, LP4, WANTP4, WPOSTP4, and WML) were included in these analyses. The first analysis produced a dendrogram with five clusters; membership in these clusters showed no correspondence to geographic or chronological occurrence. Suspecting small size of a number of samples as the cause of incoherence of the dendrogram, samples with five or fewer specimens (Table 1) were deleted and the data reanalyzed.

The resulting dendrogram (Fig. 14A) consists of two major clusters. One cluster included the Inglis and Coleman samples (of early and late Irvingtonian age, respectively). Two subgroups comprise the other major cluster; one includes the three Sangamonian sites (Arredondo, several Haile sites, and Reddick), and the other the Wisconsinan Ichetucknee River material and the Recent reference sample.

In the corresponding principal components analysis, the same relationship is apparent (Fig. 14B). Vectors I (56.62% of the total

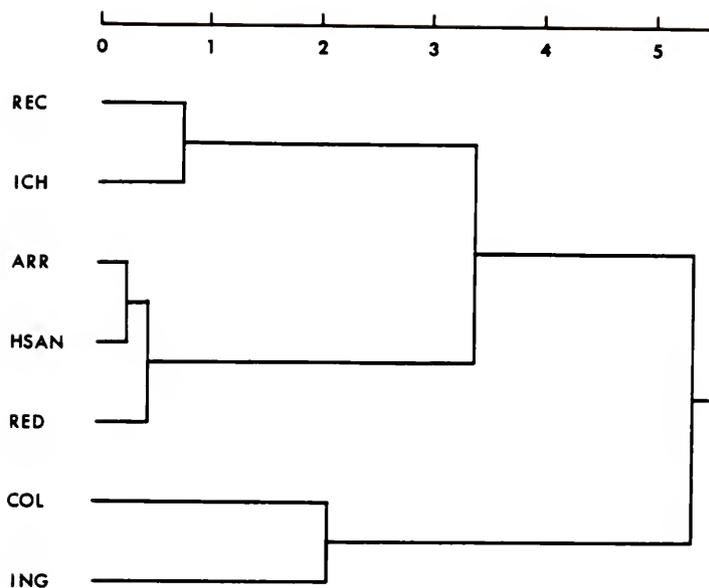
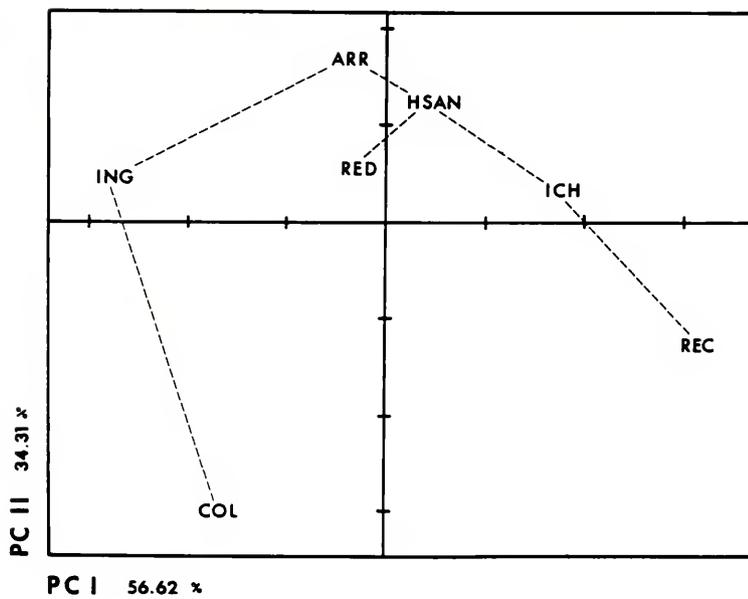
Table 15.--Adjusted means and associated standard errors (positioned below means) and sample size (N) for 10 dentary characters for each of 18 samples. These adjusted means (obtained via covariance analyses) comprise input data for various subsequent multivariate analyses. Measurements in millimeters.

Locality	N	LRMF	WRMF	DRMF	LANTP4	DFOR	LP4	WANTP4	WPOSTP4	WMI	WM2
Recent	100	4.83 0.05	2.55 0.03	3.14 0.04	1.62 0.02	5.93 0.05	2.74 0.02	1.81 0.01	2.35 0.02	2.46 0.02	2.42 0.02
Vero 3	1	4.76	1.91	1.65	1.41	5.74	2.59	1.63	2.28	2.16	2.20
Devil's Den	4	4.95 0.32	2.10 0.14	2.74 0.20	1.44 0.16	4.77 0.38	2.55 0.23	1.61 0.12	2.20 0.15	2.58 0.18	- -
St. Petersburg	5	- -	2.31 0.29	1.66 0.39	1.78 0.07	- -	2.98 0.11	1.87 0.06	2.30 0.07	2.42 0.10	2.41 0.16
Maximo Moorings	3	- -	2.13 0.29	1.32 0.39	1.85 0.16	- -	3.44 0.23	2.09 0.12	2.90 0.15	3.11 0.18	- -
Vero 2	3	- -	1.91 0.17	1.46 0.28	1.18 0.16	- -	2.37 0.23	1.50 0.12	2.20 0.15	2.05 0.18	- -
Seminole Field	4	- -	2.18 0.21	2.07 0.28	1.63 0.08	- -	2.89 0.12	2.03 0.07	2.29 0.09	2.35 0.13	2.38 0.16
Melbourne	4	5.19 0.27	2.12 0.17	1.87 0.20	1.63 0.08	5.65 0.32	2.90 0.12	1.84 0.06	2.24 0.08	2.42 0.09	2.30 0.09
Ichetucknee River	17	5.13 0.26	2.46 0.09	2.35 0.12	1.65 0.07	5.34 0.31	2.89 0.10	1.79 0.06	2.30 0.07	2.35 0.10	2.28 0.09

Table 15.--Continued.

Locality	N	LRMF	WRMF	DRMF	LANTP4	DFOR	LP4	WANTP4	WPOSTP4	WM1	WM2
Waccasassa River	3	-	1.70	2.11	1.38	-	2.51	1.56	1.77	2.31	2.27
		-	0.17	0.23	0.10	-	0.14	0.09	0.11	0.13	0.16
Haile XIV	3	4.74	2.17	1.75	1.68	6.00	2.89	1.64	2.17	2.31	2.29
		0.45	0.16	0.28	0.09	0.53	0.13	0.07	0.09	0.10	0.09
Wade's Cave	1	3.82	1.63	1.91	1.54	-	1.67	1.52	1.95	2.30	2.24
Reddick	68	4.51	1.92	2.03	1.64	5.25	2.84	1.73	2.20	2.33	2.30
		0.15	0.05	0.07	0.04	0.23	0.05	0.03	0.03	0.04	0.05
Kendrick	4	3.82	1.93	1.93	1.69	4.61	2.92	1.90	2.31	2.43	2.45
		0.32	0.14	0.20	0.11	0.54	0.16	0.09	0.11	0.12	0.11
Haile (Sangamonian)	36	4.60	2.12	1.80	1.65	5.43	2.92	1.81	2.22	2.36	2.26
		0.11	0.06	0.08	0.03	0.17	0.05	0.03	0.03	0.04	0.04
Arredondo	28	3.97	2.09	1.35	1.68	-	2.93	1.76	2.23	2.27	2.22
		0.26	0.09	0.15	0.05	-	0.07	0.04	0.04	0.06	0.07
Coleman	16	4.17	2.17	1.98	1.49	5.12	2.61	1.54	2.17	2.19	2.11
		0.17	0.09	0.12	0.09	0.24	0.13	0.07	0.09	0.09	0.09
Inglis IA	231	3.65	2.01	1.45	1.66	4.58	2.85	1.52	2.09	2.12	2.08
		0.06	0.03	0.04	0.02	0.08	0.04	0.02	0.02	0.03	0.04

Fig. 14.--Results of cluster (A) and principal components (B) analyses depicting relationships between samples represented by six or more specimens. Scale for dendrogram is a distance measure computed using Ward's method. Distance between tickmarks on axes in B is one unit; dashed line connecting samples is a minimum spanning tree. Sample abbreviations: REC, Recent reference; ICH, Ichetucknee River; ARR, Arredondo; HSAN, Sangamonian Haile sites; RED, Reddick; COL, Coleman; ING, Inglis IA.

**A****B**

variance) and II (34.31%) together reflect 90.93% of the total variation. Character coefficients (Table 16) indicate that all characters contributed positively to the first vector, and hence, this may be viewed as a "size component" (Bryant and Turner, 1979: 764). The three most important characters in PC II are LANTP4, WANTP4, and LP4.

#### Chronological Comparisons of Samples

The objective of the second series of clustering and principal components analyses was to display the relationships of material representing six different blocks of Pleistocene time: Recent, Holocene, Wisconsinan, Sangamonian, late Irvingtonian, and early Irvingtonian. Input data for each stage consisted of an adjusted mean for various of nine measured characters. Adjusted means were obtained from covariance analyses (using WLINC as the covariate) wherein all specimens from all sites falling within each particular stage were considered as units (Table 17).

Clustering of these data yielded two major clusters each with three members. The two oldest samples (early and late Irvingtonian) curiously grouped with the much younger Holocene material, whereas the two most similar samples (Sangamonian and Recent reference) clustered with the Wisconsinan samples. The only seemingly discordant sample is the Holocene, represented by just five specimens from two sites. On the suspicion that this small sample might not accurately represent the Holocene, this sample was deleted and the analysis conducted again with five samples. Except for the absence of the Holocene, this second dendrogram (Fig. 15A) closely resembles

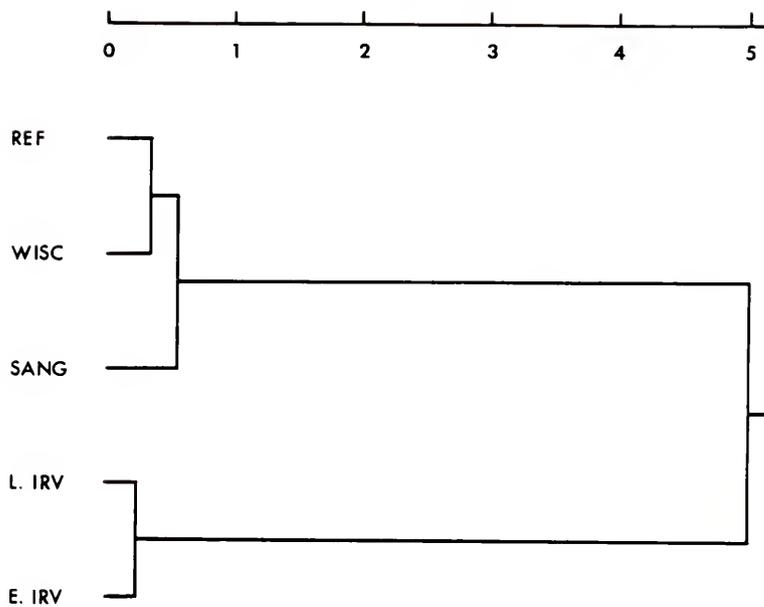
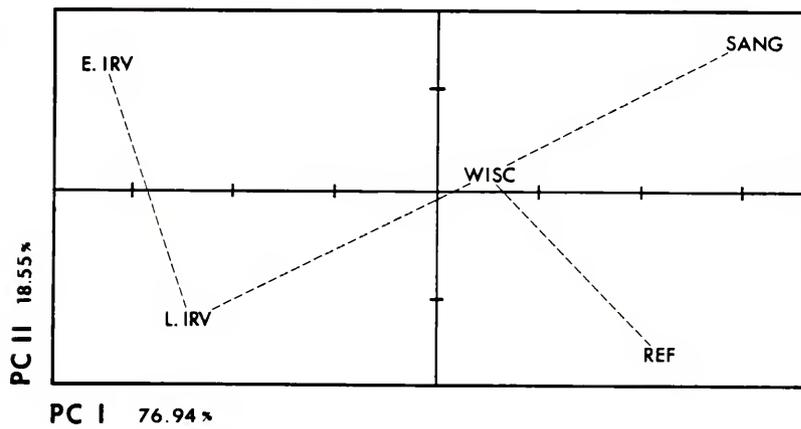
Table 16.--Results of principal components analyses of relationships between samples and between various Pleistocene stages for Florida Geomys pinetis dentaries. Included are character coefficients for components I and II, percentage of variance explained in these components, and factor scores for each sample or stage on these axes.

Character	Coefficient		Sample or Stage	Factor Score	
	PC I	PC II		PC I	PC II
Between Samples					
WRMF	0.404	-0.228	Inglis	-2.800	0.441
DRMF	0.411	-0.314	Coleman	-1.680	-2.883
LANTP4	0.092	0.599	Arredondo	-0.400	1.623
LP4	0.047	0.634	Haile (Sang.)	0.402	1.185
WANTP4	0.429	0.288	Reddick	-0.354	0.532
WPOSTP4	0.493	-0.033	Ichetucknee	1.711	0.316
WM1	0.479	0.060	Recent reference	3.121	-1.215
Percent of Variance	56.62%	34.31%			
Between Stages					
LRMF	0.309	-0.139	Recent	2.199	-1.555
WRMF	0.328	-0.271	Wisconsinan	0.490	0.160
DRMF	0.280	-0.411	Sangamonian	3.014	1.422
LANTP4	0.213	0.568	Late		
DFOR	0.349	-0.179	Irvingtonian	-2.431	-1.228
LP4	0.206	0.602	Early		
WANTP4	0.352	0.139	Irvingtonian	-3.271	1.202
WPOSTP4	0.355	-0.023			
WM1	0.360	0.017			
WM2	0.359	0.048			
Percent of Variance	76.94%	18.55%			

Table 17.--Adjusted means and associated standard errors (positioned below means) for 10 dentary characters for each of six Pleistocene stages. Number of specimens and sites comprising samples indicated. These adjusted means (obtained via covariance analyses) comprise input data for various subsequent multivariate analyses. Measurements in millimeters.

Stage	Number of Sites	Number of Specimens	LRMF	WRMF	DRMF	LANTP4	DFOR	LP4	WANTP4	WPOSTP4	WMI	WM2
Recent	1	100	4.82	2.55	3.13	1.62	5.92	2.74	1.81	2.35	2.46	2.42
Holocene	2	5	4.83 0.28	2.08 0.13	2.50 0.18	1.43 0.12	5.04 0.32	2.57 0.17	1.61 0.10	2.24 0.12	2.37 0.13	2.20 0.15
Wisconsinan	8	42	5.02 0.19	2.23 0.06	2.00 0.09	1.63 0.04	5.49 0.22	2.88 0.05	1.79 0.03	2.25 0.04	2.38 0.05	2.30 0.05
Sangamonian	4	135	4.75 0.08	2.43 0.04	2.33 0.05	1.79 0.02	5.83 0.16	3.12 0.04	1.94 0.02	2.41 0.02	2.53 0.03	2.49 0.03
Late Irvingtonian	1	16	4.13	2.18	1.96	1.49	5.08	2.62	1.53	2.17	2.19	2.11
Early Irvingtonian	1	231	3.70	1.99	1.48	1.66	4.63	2.84	1.53	2.09	2.13	2.09

Fig. 15.--Results of cluster (A) and principal components (B) analyses depicting relationships between samples representing five segments of Pleistocene-Recent time. Abbreviations: E. IRV, early Irvingtonian; L. IRV, late Irvingtonian, SANG, Sangamonian; WISC, Wisconsinan; REF, Recent. Other pertinent explanations as for Fig. 14.

**A****B**

the first. Again, the Wisconsinan and Recent reference samples join the Sangamonian samples to form one of two major clusters. The two most similar samples, the early and late Irvingtonian material, form the other cluster.

Over 95% of all intersample variation is explained by principal components I (76.94%) and II (18.55%). That all 10 characters have positive coefficients for vector I (Table 16) suggests that the samples differ primarily in size. The strongest contributors to vector II are LP4 and LANTP4. Plotting the samples on vectors I and II shows relationships to be similar to those in the dendrogram (Fig. 15B).

A multivariate analysis of variance was conducted to determine if the observed differences among samples representing these six stratigraphic ages were significant. Input data (shown in Table 15) were the adjusted character means for each of the 18 samples. The null hypothesis of no overall effect due to chronological age was accepted ( $P \geq 0.3632$ ) on the basis of three test statistics (e.g., Hotelling-Lawley trace,  $F = 0.51$ ; Pillai's trace,  $F = 1.13$ ; Wilks' criterion,  $F = 0.94$ ).

Further multivariate analyses of variance involved pairwise comparisons of the various geochronological ages. This approach was expected to show significant differences, even though the previous more generalized comparison did not. The former analyses were affected by the gradual nature of evolutionary trends of geomyids (especially over the relatively short span of time covered here) and by the relatively continuous chronological coverage

offered by the Florida material. To enhance significance testing, chronological gaps between samples were created by deleting samples of intermediate age. Of particular interest are (1) tests for differences between the youngest and oldest available material from Florida (e.g., post-Wisconsinan vs. Irvingtonian), and (2) tests between samples of adjacent stages (e.g., Recent vs. Wisconsinan, Wisconsinan vs. Sangamonian, Sangamonian vs. Irvingtonian).

Irvingtonian vs. post-Wisconsinan. One series of analyses of variance tested for differences between post-Wisconsinan (Recent reference, Devil's Den, and Vero 3) and Irvingtonian (Inglis and Coleman) samples using nine characters (LRMF, WRMF, DRMF, LANTP4, DFOR, LP4, WANTP4, WPOSTP4, and WML). Only for LRMF were differences significant ( $\underline{P} = 0.0201$ ,  $\underline{F} = 20.55$ , d.f. = 1). The mean values and 95% confidence limits for the Irvingtonian and post-Wisconsinan samples are 3.91 mm (3.40 - 4.42 mm) and 4.85 mm (4.43 - 5.26 mm), respectively. Singularity of the error matrix precluded calculation of multivariate test statistics.

For a second series of ANOVA's, the Devil's Den (n = 4) and Vero 3 (n = 1) samples were deleted due to small sample size. In this comparison of Irvingtonian (Inglis and Coleman) and post-Wisconsinan (Recent reference) sites, WANTP4 was the only significantly variable character ( $\underline{P} = 0.0393$ ,  $\underline{F} = 251.33$ , d.f. = 1). Means and 95% confidence limits were 1.53 mm (1.40 - 1.66 mm) and 1.81 mm (1.63 - 1.99 mm) for the Irvingtonian and Recent stages, respectively. No multivariate tests could be made because of singularity of the error matrix.

These results suggest that only two (LRMF, WANTP4) of the nine features tested here have changed significantly over the 1.8 million years from which geomyines are known in Florida. The following series of narrower comparisons were designed to determine the interval(s) of Pleistocene during which these changes occurred.

Irvingtonian vs. Sangamonian. Samples representing the Irvingtonian sites in this comparison are Inglis and Coleman; whereas Arredondo, various Haile samples, Kendrick, and Reddick represent the Sangamonian interglacial. Of the eight characters tested (LRMF, WRMF, DRMF, LANTP4, LP4, WANTP4, WPOSTP4, and WML), three were significantly different: WANTP4 ( $\underline{P} = 0.0086$ ,  $\underline{F} = 23.14$  d.f. = 1), WPOSTP4 ( $\underline{P} = 0.0657$ ,  $\underline{F} = 6.33$ , d.f. = 1), and WML ( $\underline{P} = 0.0239$ ,  $\underline{F} = 12.57$ , d.f. = 1). For the Irvingtonian samples, character means and 95% confidence intervals are: WANTP4 (1.53 mm, 1.40 - 1.66 mm), WPOSTP4 (2.13 mm, 2.03 - 2.23 mm), and WML (2.16 mm, 2.03 - 2.28 mm). Corresponding values for the Sangamonian samples are WANTP4 (1.80 mm, 1.40 - 1.66 mm), WPOSTP4 (2.24 mm, 2.17 - 2.31 mm), and WML (2.35 mm, 2.26 - 2.43 mm). Duncan's multiple range tests demonstrated significant differences (at  $\underline{P} \leq 0.05$ ) only for WANTP4 and WML. No multivariate test statistics could be calculated for this comparison.

Sangamonian vs. Wisconsinan. Two series of analyses of variance examined differences in character means representing Sangamonian sites and Wisconsinan sites. The former were the same as those used in the previous test; the Wisconsinan samples were Haile XIV, Ichetucknee River, Melbourne, Seminole Field, Vero 2 and Waccasassa

River. DFOR was omitted from both test series because values for this measurement were not available for all samples. In the first series, none of seven characters (WRMF, DRMF, LANTP4, LP4, WANTP4, WPOSTP4, and WM1) evaluated showed significant differences at  $\underline{P} \leq 0.05$ . Three multivariate tests statistics (Hotelling-Lawley and Pillai's traces and Wilks' criterion:  $\underline{F} = 1.03$ , d.f. = 7,3,  $\underline{P} = 0.5760$ ) indicated no overall differences between Sangamonian and Wisconsinan samples.

The second test series included these same seven characters plus LRMF. Significant differences were found for LRMF ( $\underline{P} = 0.0278$ ,  $\underline{F} = 9.42$ , d.f. = 1) and WRMF ( $\underline{P} = 0.0819$ ,  $\underline{F} = 4.72$ , d.f. = 1). For the Sangamonian sample, LRMF and WRMF means and 95% confidence limits are 4.23 mm (3.79 - 4.66 mm) and 2.02 mm (1.83 - 2.2 mm), respectively. These statistics for LRMF and DRMF for the Wisconsinan sample are 5.01 mm (4.51 - 5.51 mm) and 2.25 mm (2.03 - 2.46 mm), respectively. Matrix singularity disallowed calculation of multivariate test statistics.

Wisconsinan vs. post-Wisconsinan. The sites included in these two series of analyses of variance are the six Wisconsinan localities listed above and three post-Wisconsinan sites (Recent reference, Devil's Den, and Vero 3). Seven characters (WRMF, DRMF, LANTP4, LP4, WANTP4, WPOSTP4, and WM1) were examined in the first analyses; none were significantly different at  $\underline{P} \leq 0.05$ . The null hypothesis of no difference between samples from these glacial and post-Wisconsinan (= early interglacial) stages was accepted; three test statistics produced  $\underline{F}$  values of 50.50 (d.f. = 7,1) with  $\underline{P} = 0.1097$ .

The second series of ANOVA's included all of the above characters plus LRMF. Because values for LRMF are missing from the Seminole Field, Waccasassa River, and Vero 2 sites, these samples were deleted from analyses of all characters. LP4 was the only character showing significant differences ( $\underline{P} = 0.0100$ ,  $\underline{F} = 21.19$ , d.f. = 1). The means and confidence intervals for LP4 for the Wisconsinan and post-Wisconsinan samples, respectively, are 2.89 mm (2.78 - 3.01 mm) and 2.63 mm (2.51 - 2.74 mm). Multivariate test statistics were not computed for this comparison.

Summary. Six of the nine dentary characters varied significantly over various spans of the Pleistocene and Recent. In the tests comparing the endpoints of the entire period (Irvingtonian vs. post-Wisconsinan), length of the retromolar fossa (LRMF) and width of the anterior loph of p4 (WANTP4) were significantly different. Further analyses shows that the significant shift in LRMF occurred during the Sangamonian-Wisconsinan interval. Significant change in WANTP4 occurred during the Irvingtonian to Sangamonian interval. The other four of these six characters showed significant variation in various intervals: Wm1 and WPOSTP4, (Irvingtonian to Sangamonian), WRMF (Sangamonian to Wisconsinan), and LP4 (Wisconsinan to post-Wisconsinan).

For those comparisons where multivariate test statistics could be computed, observed differences between samples were not significant. Differences in many of these characters, although not statistically significant, may indeed still be evolutionarily important. Chronological trends in these features and their adaptive significance are treated in a separate section.

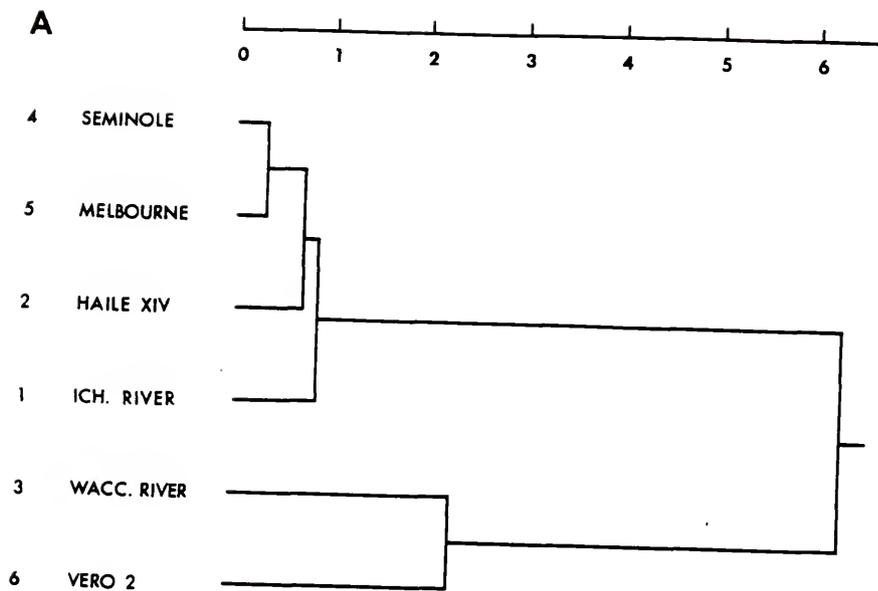
## Geographic Variation

### Wisconsinan Glacial

Of the six intervals of Pleistocene to Recent time represented in the Florida material, only the Wisconsinan includes enough samples to permit testing of geographic variation within a single time interval. The six Wisconsinan samples may be classified into three groups: the central peninsular (Haile XIV, Ichetucknee River, Waccasassa River), the east coastal (Melbourne, Vero 2), and the west coastal (Seminole Field) populations (Fig. 16). During the Wisconsinan glacial, sealevels were lower and soils were drier than at present. Present-day barriers (e.g., St. Johns River and various unsuitable lowland habitats) presumably did not at that time isolate the populations represented by these six samples. If such barriers did not function during glacial periods, then gene flow would have been enhanced and distant populations would be morphologically similar. It may be hypothesized, then, that if Wisconsinan populations from the above sites were not isolated, then morphometric differences among these samples will not be significant.

Comparisons of similarly located samples representing interglacial periods when gene flow was interrupted should result in rejection of the same hypothesis. Such interglacial comparisons cannot be made for fossil pocket gopher samples in Florida due to lack of material from peripheral locations. This dearth of material is, of course, the result of inundation of low-elevation peripheral regions of the state during interglacials. However, if one accepts

Fig. 16.--Geographic variation amongst Wisconsinan samples from central peninsula, east coast, and west coast. A: Dendrogram showing relationships between six sites; numbers to left of site names identify their locations on map (B). Dashed line in B approximates sealevel (about 100 m below present sealevel) at height of Wisconsinan glaciation.



the present-day Geomys pinetis samples as an example of early interglacial conditions, they can provide a standard of comparison against which to examine the effects of interrupted gene flow.

Multivariate analyses of variance were applied to geographic variation within the Wisconsinan glacial and Recent (= early interglacial) cases. Input data consisted of the adjusted means of seven dentary characters (WRMF, DRMF, LANTP4, LP4, WANTP4, WPOSTP4, and WM1) for each of the six Wisconsinan sites. For the Recent, input data consisted of 16 cranial characters for individual specimens from (1) central peninsular Gainesville, Alachua Co., (2) east coastal Brevard Co. (including specimens formerly recognized as G. p. goffi from Melbourne and Eau Gallie), and (3) west coastal Pinellas Co. Separate MANOVA's were computed for each of the four sex/age classes. Sample sizes for fossil and Recent sites are indicated in Tables 15 and 18, respectively.

Variation between Wisconsinan glacial samples. Cluster analysis of the six Wisconsinan samples demonstrated that similarity among the samples does not correspond to geographic location. Two major clusters comprise the dendrogram (Fig. 16). One contains only a central peninsular site (Waccasassa River) and an east coastal site (Vero 2). The other four samples fall into the second major cluster. The two most similar samples are Melbourne (an east coastal site) and Seminole Field (the only west coastal site). The Haile XIV and Ichetucknee River sites, both from the central peninsula, are also members of this cluster. In short, no geographically meaningful pattern of clustering appeared.

In a further effort to determine whether the grouping of proximal sites into central, eastern, and western samples was statistically meaningful, a series of analyses of variance was conducted. None of the seven characters examined showed significant variation as a result of classification of samples according to their location in the peninsula. No probability values were less than 0.28. Because the number of characters included in the model exceeded the number of available samples, no multivariate tests could be conducted. However, a series of univariate ANOVA's were run and showed no correspondence between variation in each character and geographic clustering.

Variation between Recent interglacial samples. Significant variation was found between central, eastern, and western samples of Recent Geomys pinetis for each of the four sex/age classes. Probability values for three multivariate statistics (Hotelling-Lawley and Pillai's traces, Wilks' criterion) ranged from 0.0001 to 0.0418 (Table 18). In each of the four analyses only four or fewer characters varied significantly (Table 18). IOC was significantly different in each analysis, whereas six other characters (WROST, LWNAS, GWNAS, LUDIAST, WUINC, LMNDTR) were significantly different in one or two analyses (Table 18).

#### Chronological Variation

Variation in Florida geomyines over a period of nearly two million years was examined by analysis of major fossil samples from ten sites. Geographic location of samples as a source of variation

Table 18.--Results of MANOVA's testing for differences between central (Gainesville, Alachua Co.), eastern (Brevard Co.), and western (Pinellas Co.) samples of Recent Geomys pinetis using 16 cranial characters.

Parameter	MALES		FEMALES	
	Age 1	Age 2	Age 1	Age 2
Hotelling-Lawley Trace	1.5289	1.9872	0.6960	2.6807
$\underline{F}$	2.01	1.86	1.83	3.02
$\underline{d.f.}$	32,84	32,60	32,168	32,72
Prob > $\underline{F}$	0.0060	0.0188	0.0079	0.0001
Pillai's Trace	0.7900	0.9087	0.5057	1.0720
$\underline{F}$	1.80	1.67	1.82	2.74
$\underline{d.f.}$	32,88	32,64	32,172	32,76
Prob > $\underline{F}$	0.0169	0.0418	0.0082	0.0002
Wilks' Criterion	0.3429	0.2737	0.5543	0.1983
$\underline{F}$	1.90	1.77	1.82	2.88
$\underline{d.f.}$	32,86	32,62	32,170	32,74
Prob > $\underline{F}$	0.0100	0.0278	0.0080	0.0001
Roy's Maximum Root Criterion	1.2081	1.5600	0.4619	1.9985
$\underline{F}$	35.03	35.88	23.10	51.96
$\underline{d.f.}$	2,58	2,46	2,100	2,52
Characters significantly different at $\underline{P} < 0.05$	IOC LWNAS LUDIAST	WROST IOC GWNAS WUINC	IOC LMNDTR	IOC LWNAS WUINC LMNDTR
Sample Size				
Central	85	34	85	37
Eastern	5	6	5	4
Western	13	9	14	14
Total	103	49	104	55

was minimized by including only those samples from the central peninsula. Five time intervals are represented by these samples: early Irvingtonian (Inglis IA), late Irvingtonian (Coleman), Sangamonian (Arredondo, several Haile sites, Kendrick, Reddick), Wisconsinan (Haile XIV, Ichetucknee River), and Recent (Gainesville reference sample).

A second analysis was conducted using an eight-site subset of the previous set. It differed only in the exclusion of the Inglis sample, thereby deleting representation of the early Irvingtonian. Although inclusion of Inglis is desirable because it extends chronological coverage, it was deleted in this second analysis because of its location near the periphery of the peninsula. The Inglis population might have experienced an isolation event during various of the interglacials during which divergence from central peninsular populations could have occurred. These reservations against including Inglis are probably overly cautious because the Inglis material was clearly deposited during a glacial stage. Furthermore, there is direct faunal evidence that grassland savannas dotted with xeric hammocks characterized the Inglis area. Such habitats probably extended inland, providing continuity between the Inglis populations and those in the central peninsula (Klein, 1971; Meylan, 1980). Nevertheless, this second analysis was produced as a precautionary test of this paleoecological hypothesis.

Evaluation of temporal variation entailed two series of analyses. The first includes multivariate analyses and associated analyses of variance. The other set of analyses examines trends in individual character variation using regression analysis.

### Multivariate Analyses

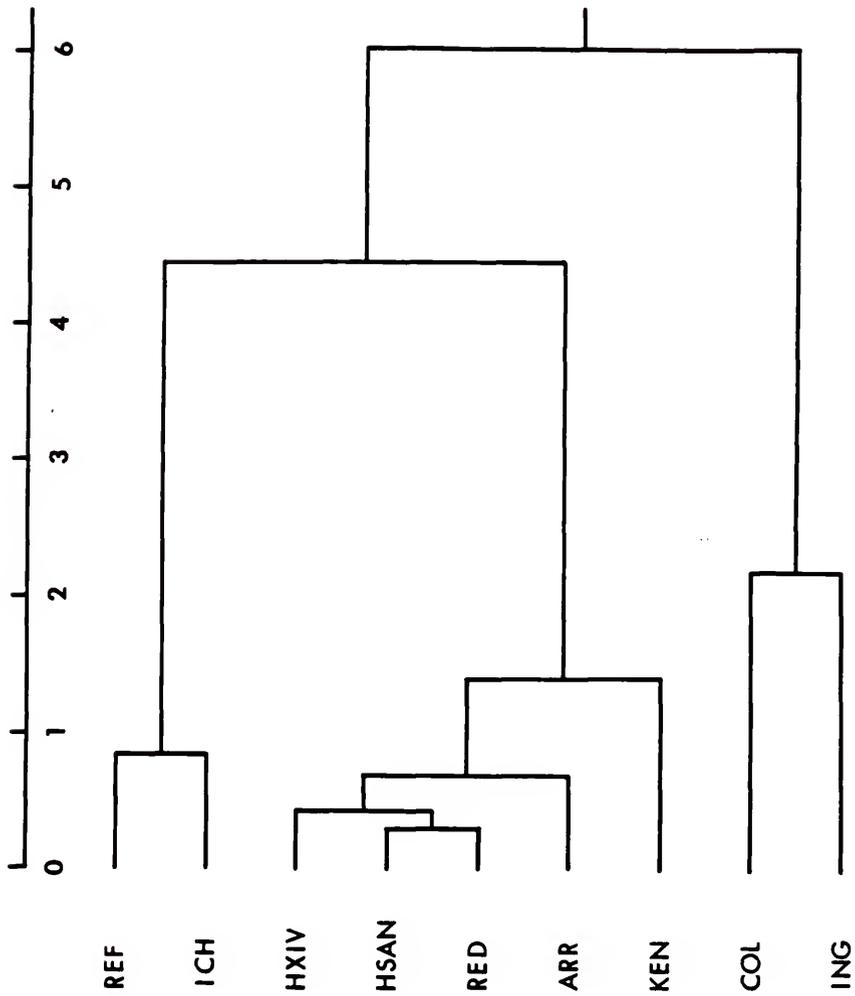
Eight characters comprised input data for multivariate analyses: LRMF, WRMF, DRMF, LP4, LANTP4, WANTP4, WPOSTP4, and WML. Clustering of the data set including Inglis yielded a dendrogram having two major clusters (Fig. 17). The smaller cluster includes the two Irvingtonian samples (Inglis and Coleman). The second major cluster is comprised of two subclusters. The four Sangamonian samples (Arredondo, several Haile sites, Kendrick, Reddick) unite with Haile XIV, a Wisconsinan site. The other Wisconsinan material (Ichetucknee River) joins the Recent reference sample (Gainesville) to form the other subcluster. The second dendrogram (not figured) that resulted from analysis of the nine-site data set (excluding Inglis) demonstrates the same relationships.

Multivariate analyses of variance examined differences between character means for the five represented time intervals (early Irvingtonian to Recent). Singularity of error matrices precluded calculation of multivariate test statistics for either data set. ANOVA's showed two of eight characters to be significantly different (at  $P < 0.05$ ) for both data sets. Probability values for LANTP4 and LP4 for the analyses including Inglis are 0.0102 and 0.0065, respectively; exclusion of Inglis results in significance values of 0.0155 (LANTP4) and 0.0102 (LP4) for the same two characters.

### Univariate Analyses

Analysis of temporal variation in individual characters was expanded to 12 characters, eight of which were used in the immediately preceding cluster analysis. Length of ml (LML), deleted

Fig. 17.--Dendrogram demonstrating relationships amongst nine central peninsular samples. Variation corresponds to geological age of samples: early Irvingtonian (ING, Inglis IA); late Irvingtonian (COL, Coleman); Sangamonian (ARR, Arredondo; HSAN, Sangamonian Haile sites; KEN, Kendrick; RED, Reddick); Wisconsinan (HXIV, Haile XIV; ICH, Ichetucknee River); Recent (REF, Recent reference sample). Scale indicates distance between samples in multivariate space.



earlier due to significant sexual variation (see section on non-geographic variation), was retrieved for computing the relative width of m1 ( $RWm1 = Wm1 \div LM1$ ). Relative widths of the anterior loph of p4 ( $RWANTP4 = WANTP4 \div LP4$ ) and posterior loph of p4 ( $RWPOSTP4 = WPOSTP4 \div LP4$ ) were computed as indicated. Means and 95% confidence intervals for these 12 characters are listed in Table 19.

Regression analyses are useful in elucidating the overall temporal trends in these characters. Conducting such analyses requires the independent variable (time) to be quantified. Mid-point ages of intervals were used for those intervals containing more than one sample; otherwise, single values were assigned to samples isolated in time. Approximate dates recognized here are: early Irvingtonian,  $1.8 \pm 0.1$  million years ago (mya); late Irvingtonian,  $1.0 \pm 0.25$  mya; Sangamonian,  $0.2 \pm 0.1$  mya; Wisconsinan,  $0.06 \pm 0.04$  mya; and Recent, 0 mya.

Results of regression analyses and analyses of variance are presented in Table 20. Although regression lines for all 12 characters had positive slopes, only those for five characters were significantly greater than zero ( $\underline{P} \leq 0.055$ ). Four of these characters assess absolute or relative tooth widths ( $WANTP4$ ,  $WPOSTP4$ ,  $Wm1$ , and  $RWANTP4$ ), while the fifth records length of the retromolar fossa ( $LRMF$ ). ANOVA's showed that means of only one of these five characters ( $Wm1$ ,  $\underline{P} = 0.0613$ ) differ significantly over the 1.8 million years represented.

Table 19.--Means and 95% confidence intervals for 12 dentary characters for central peninsular Florida *Geomys* samples used in analyses of chronological variation. Measurements in millimeters.

Character	Early Irvingtonian		Late Irvingtonian		Sangamonian	Wisconsinan	Recent
	Mean	95% CI	Mean	95% CI			
LRMF	3.65		4.17		4.23 3.72-4.73	4.94 3.96-5.91	4.83
WRMF	2.01		2.17		2.02 1.82-2.21	2.32 2.08-2.55	2.55
DRMF	1.45		1.98		1.78 1.31-2.24	2.05 1.36-2.74	3.14
LANTP4	1.66		1.49		1.67 1.63-1.70	1.67 1.53-1.80	1.62
LP4	2.85		2.61		2.90 2.85-2.95	2.89 2.74-3.04	2.74
LMI	1.23		1.16		1.27 1.18-1.36	1.27 1.15-1.39	1.17
WANTP4	1.52		1.54		1.80 1.68-1.92	1.72 1.44-1.99	1.81
WPOSTP4	2.09		2.17		2.24 2.15-2.33	2.24 2.05-2.42	2.35
WMI	2.12		2.19		2.35 2.27-2.43	2.33 2.20-2.46	2.46

Table 19.--Continued.

Character	Early Irvingtonian	Late Irvingtonian	Sangamonian	Wisconsinan	Recent
RWANTP4	0.53	0.59	0.62 0.49-0.71	0.59 0.43-0.75	0.66
RPOSTP4	0.73	0.83	0.77 0.67-0.88	0.77 0.63-0.91	0.86
RM1	1.73	1.89	1.84 1.63-2.04	1.84 1.57-2.11	2.10
Number of sites	1	1	4	2	1
Age of sample (mya)	1.8-0.1	1.0-0.25	0.2-0.1	0.6-0.04	0

Table 20.--Statistics for regression analyses of eight dentary characters against age of samples. ANOVA probability indicates significance of differences between character values for the five time intervals. Based on nine samples.

Character	Y Intercept	Slope	Correlation Coeff. (R)	Regression Prob.	ANOVA Probability
LRMF	4.6078	0.5511	0.6571	0.0545	0.1689
WRMF	2.2081	0.1217	0.3336	0.3804	0.1005
DRMF	2.1327	0.3802	0.4293	0.2488	0.1041
LANTP4	1.6531	0.0317	0.3144	0.4100	0.0155
LP4	2.8676	0.0587	0.3336	0.3803	0.0102
LM1	1.2550	0.0282	0.3479	0.3590	0.0175
WANTP4	1.7921	0.1690	0.7820	0.0128	0.1117
WPOSTP4	2.2686	0.1014	0.7434	0.0217	0.2027
WM1	2.3770	0.1540	0.8538	0.0034	0.0613
RWANTP4	0.6253	0.0473	0.7200	0.0287	0.1281
RWPOSTP4	0.7919	0.0191	0.2877	0.4528	0.0457
RWM1	1.8975	0.0845	0.4832	0.1876	0.0201

Five other characters varied significantly ( $P < 0.05$ ) through time; three of these reflect tooth lengths (LP4, LANTP4, LM1) whereas the other two (RWPOSTP4, RWML) indicate relative tooth widths. None of the remaining six characters changed significantly through time.

#### Patterns of Chronological Variation

The "best fit" approach of regression analyses is most useful in elucidating overall trends in character variation. However, damping and obscuring of oscillations to either side of the regression line can result in the loss of important information and, perhaps, erroneous interpretation of data. For this reason, patterns of temporal variation were examined separately for each of the 12 characters.

Variation in individual characters with geological age follows one of four general patterns (Figs. 18, 19, 20, and 21). Three of the patterns are variations on the theme of increasing means from Irvingtonian low values to Recent high values. The fourth pattern is comprised of great oscillations about a regression line of gently increasing slope. The four variation patterns apparently correspond to four functional suites of characters.

Values for tooth width characters (WANTP4, WPOSTP4, WML) increased rather smoothly from early Irvingtonian through late Irvingtonian and into the Sangamonian (Fig. 18). Wisconsinan values dropped slightly from Sangamonian levels and were followed by an abrupt increase to present levels.

Fig. 18.--Pleistocene to Recent variation in three tooth width characters in samples of Florida Geomys. A: width of anterior loph of lower premolar (WANTP<sup>4</sup>). B: width of posterior loph of lower premolar (WPOSTP<sup>4</sup>). C: width of first lower molar (WML). Measurements in millimeters; age in millions of years before present (MYA). Samples plotted for early Irvingtonian (EI = 1.8 mya), late Irvingtonian (LI = 1.0 mya), Sangamonian (S = 0.2 mya), Wisconsinan (W = 0.06 mya), and Recent (R = 0 mya). Dots are observed values (adjusted means for each site). Solid line connects means of observations for each time interval. Dashed line is best-fit regression line.

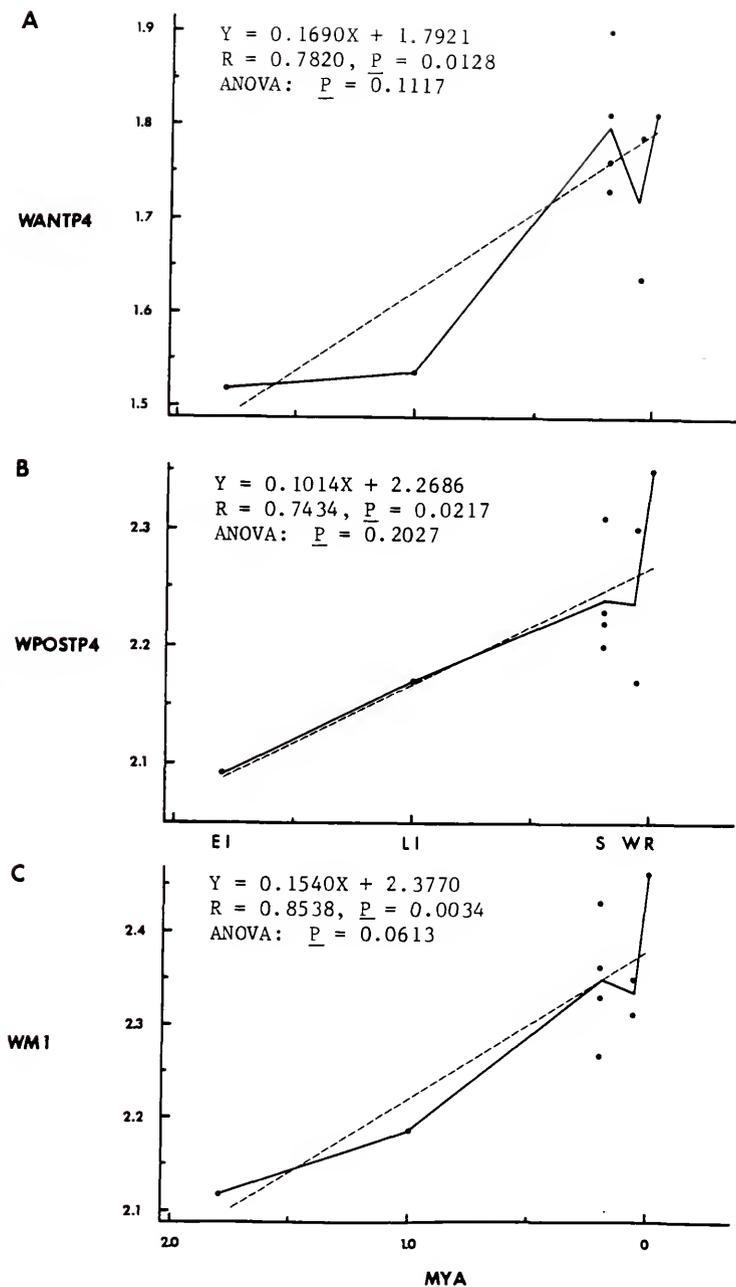


Fig. 19.--Pleistocene to Recent variation in three tooth length characters in samples of Florida Geomys. A: length of anterior loph of lower premolar (LANTP<sub>4</sub>). B: length of lower premolar (LP<sub>4</sub>). C: length of first lower molar (LM<sub>1</sub>). Further explanations as for Fig. 18.

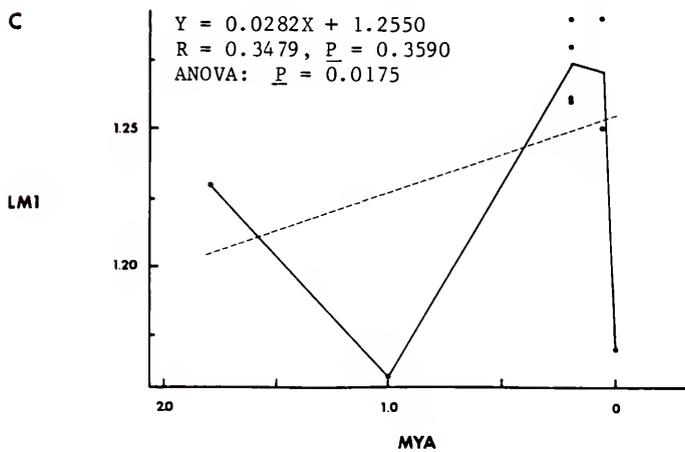
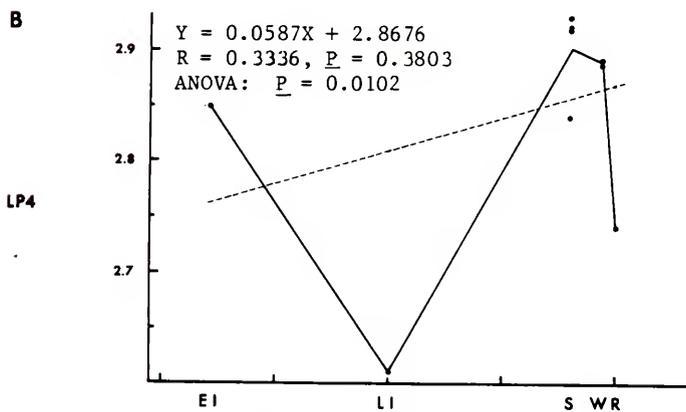
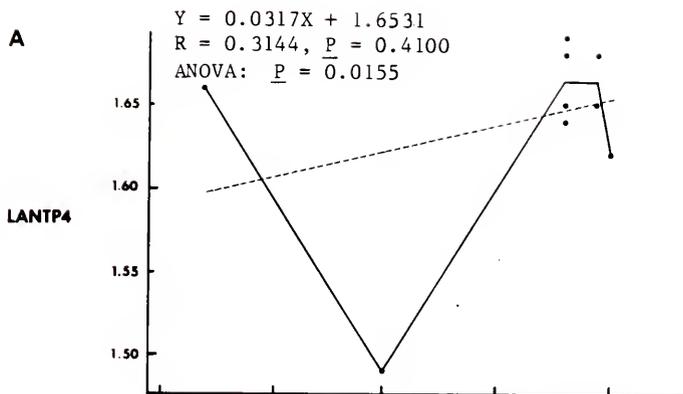


Fig. 20.--Pleistocene to Recent variation in three relative tooth width characters in samples of Florida Geomys. A: relative width of anterior loph of lower premolar (RWANTP4). B: relative width of posterior loph of lower premolar (RWPOSTP4). C: relative width of first lower molar (RWML). Further explanations as for Fig. 18.

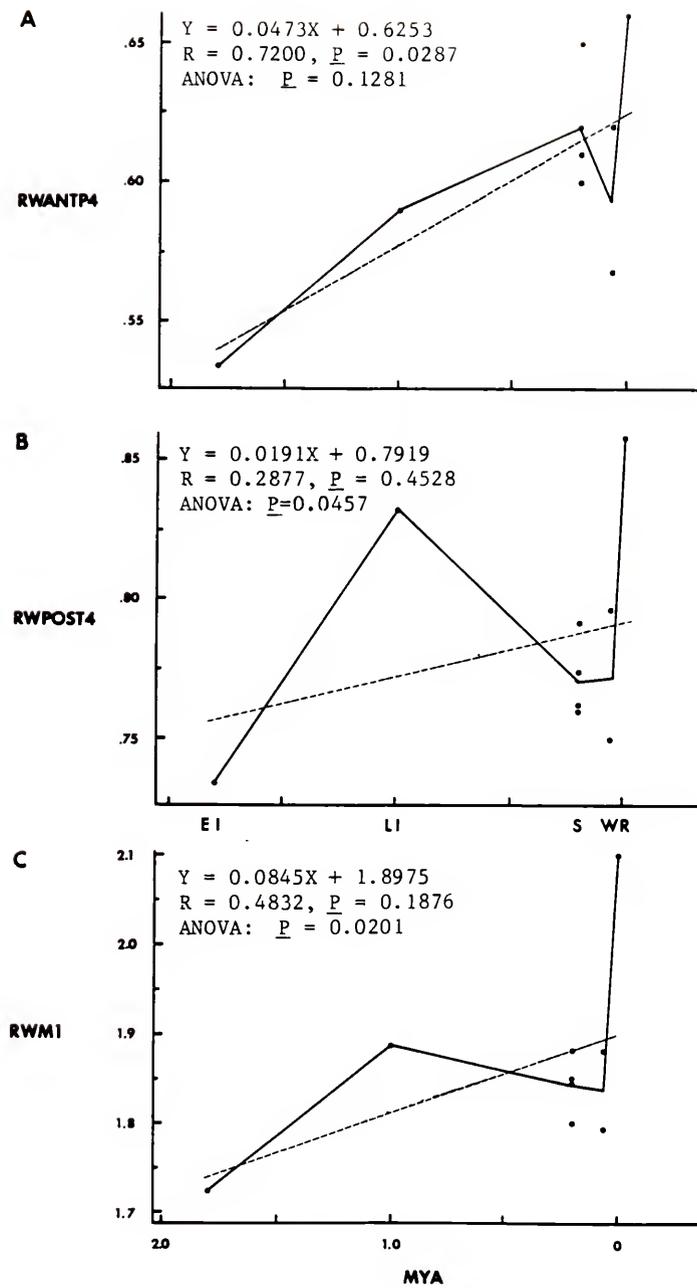
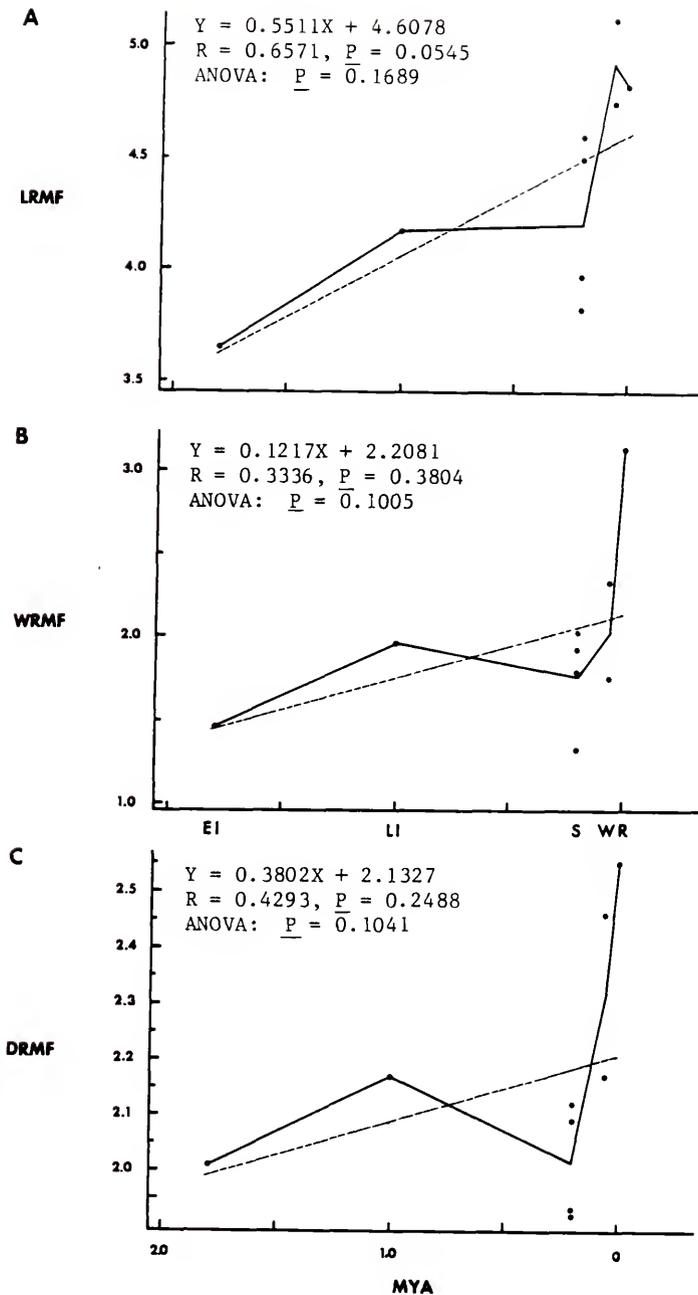


Fig. 21.--Pleistocene to Recent variation in three characters assessing dimensions of the retromolar fossa in samples of Florida Geomys. A: length (LRMF). B: width (WRMF). C: depth (DRMF). Further explanations as for Fig. 18.



Trends exhibited by the tooth length characters (LANTP4, LP4, LM1) oscillate broadly (Fig. 19). Early Irvingtonian values are intermediate to large, but late Irvingtonian values fall to the lowest level known. Sangamonian and Wisconsinan levels approximate each other, and represent maximum values. Recent values drop moderately or drastically from Wisconsinan levels.

Relative tooth width values (RWANTP4, RWPOSTP4, RWMI), calculated from measured tooth lengths and widths, showed a more or less common pattern (Fig. 20). Early Irvingtonian values were lowest. From an intermediate late Irvingtonian level, values either decreased (for RWPOSTP4, RWMI) or increased (for RWANTP4) to Sangamonian levels. Wisconsinan values (similar to Sangamonian values) abruptly increase to high levels in the Recent sample.

Chronological changes in characters assessing dimensions of the retromolar fossa generally followed a fourth pattern (Fig. 21). Low early Irvingtonian values increased to moderate late Irvingtonian values. These then decreased (or, for LRMF, slightly increased) in the Sangamonian material. All Sangamonian to Wisconsinan shifts were increases. For WRMF and DRMF, Recent values were much higher than Wisconsinan levels; LRMF decreased slightly from Wisconsinan to Recent.

#### Summary of Results

Morphometric investigations of dentary characters in Pleistocene and Recent geomyine material from Florida have addressed various aspects of non-geographic, geographic, and chronological variation. Analyses of the Gainesville reference sample have identified those

characters varying significantly by sex and those exhibiting high individual variation. Several of the characters with high coefficients of variation have previously been used in diagnosing species. Ontogenetic age was found to significantly affect all characters measured. Using width of the lower incisor (WLINC) as an age estimator, covariance analyses permitted direct comparisons of samples despite possible different ontogenetic age composition.

For Recent Geomys pinetis, significant geographic variation was found between samples from the east coastal, west coastal, and central regions of the peninsula. During Wisconsinan glacial time, however, samples from these same areas were not significantly different. The difference in these significance levels for the Recent and Wisconsinan stages is attributed to the role of sealevel. Presumably, glacial ages maximized the extent of favorable habitats and promoted genetic continuity among widespread populations. The Recent, on the other hand, exemplifies early interglacial conditions in which rising sealevels and increasing surface water promotes barriers to pocket gopher continuity and restricts their distributions.

Variation through geological time was examined for the central peninsular samples representing five time intervals spanning nearly two million years. Multivariate analyses generally indicated that samples of similar geological age were also most similar phenetically. Individual character analyses showed prevailing trends toward increasing size from the early Irvingtonian to the Recent. Evolution in several characters is towards increased efficiency of the masticatory apparatus.

## DISCUSSION

### Zoogeography

Geographic variation in cranial morphology of Geomys pinetis of any particular sex/age category is not so great that an unknown specimen may be assigned to a particular region of the state by visual inspection. Yet, when simultaneously evaluating multiple characters on the basis of samples of reasonable size, certain trends in geographic variability are evident. The pattern elucidated through use of an array of multivariate statistical techniques is that Florida consists of two major zoogeographic units: (1) the panhandle west of the Apalachicola River (area I), and (2) the remainder of the state, which may be further subdivided. The two areas east of the Apalachicola River are separated by the Suwannee River into the (1) peninsula (area III) and (2) eastern panhandle (area II). MANOVA and canonical variate analyses show slight to extensive overlap between samples from the peninsula and eastern panhandle, but no overlap of these with the western panhandle samples. Hence, the Apalachicola River comprises a more effective barrier to pocket gopher dispersal and gene flow than the Suwannee River. The following comparison of these two rivers and associated basins aids in explaining their apparent differential influence on pocket gopher zoogeography.

Comparison of the Apalachicola and Suwannee Rivers

Zoogeographic barrier effects

The Apalachicola River is unique among Florida river basins. Originating in the Appalachian mountains, it is the only Florida river with its headwaters located outside the southeastern United States coastal plain. Furthermore, it is the largest of all Florida rivers, and physical relief encountered in this basin is the greatest of all rivers in the state. At least two habitats are unique to the Apalachicola basin: steepheads and underground troglobite ecosystems. The Apalachicola River basin is renowned for the occurrence of disjunct northern habitats and associated taxa. Hence, many species (or relatives thereof) found more commonly in the northern United States occur in Florida only in these disjunct habitats. As a result of isolation from similar northern habitats, endemism is more common in the Apalachicola basin than in other areas in the Florida panhandle. Extensive studies of endemic plants, invertebrates, and vertebrates have been made (Neill, 1957; Means, 1976).

The effect of the Apalachicola River as a zoogeographic barrier has been widely recognized in a wide array of animals. Hubbell (1954) and Howden (1963) discussed the distributions of several species of flightless, burrowing beetles (Coleoptera: Scarabaeidae: Geotrupinae) with regard to the Apalachicola River (see also Udvardy, 1969:14-15). Although suitable sandy soils habitat exists west of this river in Florida and Alabama, Mycotrupes occurs in the southeastern United States coastal plains only east of this river. The genus Gronocarus is restricted to the west side

of the river (Howden, 1963:181-183). Hubbell (1954:47) viewed the effect of the Apalachicola River on these genera to be "as insurmountable an obstacle as the sea." As summarized by Neill (1957:186) from the original literature (Bailey et al., 1954), the larger streams of the panhandle (including the Apalachicola) 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 occurring east of the Apalachicola River. The existence of this pattern of variation in species so closely connected to pocket gophers supports the interpretation that the Apalachicola River has influenced gene flow between Florida Geomys populations.

Neill noted that "the Apalachicola proper appears to be an exceptionally important barrier to east-west distribution in many groups." This certainly seems to hold for Geomys pinetis whose eastern and western "forms" are separated by this river in Florida (Avisé et al., 1979; this study). Hall (1981:505), which went to press before the Williams and Genoways (1980) revision, figures the Apalachicola River as the division between a western subspecies (G. p. mobilensis) and two eastern subspecies (G. p. pinetis and G. p. floridanus). A survey of range maps in Hall (1981) of all

mammal species occurring in Florida revealed Neotoma floridana (p. 750) to be the only other mammal species with subspecies boundaries coinciding with the Apalachicola River. The entire range of Neofiber alleni lies east of the Apalachicola River. Excluding marine mammals, about 70 species of mammals occur in Florida (Stevenson, 1976). Of these, 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, in a recent study of geographic variation in 15 species of snakes occurring through Florida, Christman (1980) defined seven major patterns of geographic variation, none of which corresponded with the Apalachicola River.

Phenetic breaks in pocket gopher morphometrics also correspond to a second river--the Suwannee. Reviewing 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%, having subspecies limits approximating the Suwannee River. No Florida mammals have species boundaries coinciding with this river. One of the most important patterns of geographic variation observed in 15 species of Florida snakes (Christman, 1980), the Suwannee Straits Pattern, demonstrates the zoogeographic effect of the Suwannee River. The Suwannee Straits, a former salt water channel between the United States mainland and peninsular Florida that existed to various extents during various

interglacials, occupied that area now drained by the Suwannee River and its tributaries (Neill, 1957:188). During the Pleistocene interglacials, the Suwannee Straits apparently barred movement of many species between the mainland and "peninsula." Neill (1957: 189-194) argues that evidence for the effectiveness of these straits as a barrier is embodied in the lengthy list of subspecies and species of vertebrates and invertebrates presently restricted to peninsular Florida. The importance of the Suwannee Straits is also evident in the ranges of mainland species of mollusks not occurring south or east of the Suwannee River (Dall, 1890-1903, and Clench and Turner, 1956, both cited in Neill, 1957:192). Neill (1957:193) also remarked that cyprinid, sucker, and darter fish, groups which occur abundantly in the southeastern United States, are very poorly represented in the Florida peninsula.

Consideration of a wide range of invertebrate and vertebrate groups suggests that the Suwannee River is more influential zoogeographically than the Apalachicola River. Yet, the opposite appears true for pocket gophers. The explanation in regard to Geomys pinetis appears to hinge on a number of features associated with these rivers. The Apalachicola extends into the piedmont and mountains far north of the range of G. pinetis, whereas the entire Suwannee River basin is contained within the range of G. pinetis. Hence, without actually crossing the river channel, populations on opposite sides of the Suwannee are potentially in genetic communication (albeit indirectly) around the headwaters of the Suwannee system. Pocket gophers are distributed in most counties surrounding the

Okefenokee Swamp region (embedded in the Suwannee River system) which is centered in Charlton County, Georgia. Those surrounding counties from which specimens are known include Cook, Lanier, Ben Hill, Dodge, Pulaski, Telfair, Wheeler, Appling, Tattnall, Ware, and Wayne (Williams and Genoways, 1980).

#### Streamflow and swimming ability

Although pocket gophers are not naturally adapted to swimming, they are capable of doing so. Barrington (1940:15-16) investigated swimming ability of G. pinetis and reported that one female swam "dog fashion" at a pace covering about 23 m in 8 minutes. Other studies have shown other geomyid species capable of swimming (e.g., G. bursarius in Kennerly, 1963). The actual value of swimming ability in aiding dispersal surely would depend on the width, flow rates, and other features of the barrier rivers and to local distribution of suitable habitats.

Streamflow information available from United States and Florida geological surveys (Heath and Wimberly, 1971:466, 531) demonstrates differences between the Apalachicola and Suwannee rivers. Average discharge of the Suwannee at Branford (Suwannee County) is 192 cubic meters per second (cms) in contrast to the mean discharge of 709 cms for the Apalachicola at Blountstown (Calhoun County). Recorded maximum and minimum discharges (and associated gage water heights) for the Suwannee and Apalachicola rivers, respectively, are 2,374 cms (10.38 m) and 43 cms (0.60 m), and 2,773 cms (6.77 m) and 152 cms (0.73 m). Clearly, the Apalachicola is the larger river, with consistently greater flow volumes than the Suwannee, although both are

subject to vast fluctuations in water height and discharge. On the basis of water flow alone the Apalachicola can be viewed as a more formidable barrier to a terrestrial animal than the Suwannee.

During droughts average water flow rates are not necessarily indicative of the effectiveness of a channel as a barrier. At low water extremes, presumably a pocket gopher could swim or, perhaps, even walk across either river channels that otherwise could not normally be crossed. However, for such low water dispersal to occur, pocket gophers must already occur nearby. The Apalachicola and Suwannee rivers differ in regard to proximity of established pocket gopher populations (as indicated by specimen or sight records or by distribution of suitable habitats). Almost the entire length of the Suwannee (and other associated rivers) corridor in Florida is lined by preferred sandhill habitat and associated friable sandy soils (Davis, 1980; see also Fig. 3). In places (e.g., Branford vicinity, Suwannee and Lafayette counties), pocket gophers occur in the Suwannee floodplain as little as 100 m from the water's edge on both sides of the river (pers. obs.). In most such areas, a swamp hardwood forest (unsuitable for pocket gophers) is absent from the floodplain or at most forms a very narrow fringe at the water's edge. In contrast, the Apalachicola River is continuously bounded by a low floodplain having extensive swamp hardwood forests. These forests are very broad (several km) in Gulf and Franklin counties and southern parts of Calhoun and Liberty counties. Sandhill habitat suitable for pocket gophers approaches the river within as little as 2 or 3 km only in northwestern Liberty and

western Gadsen counties, but here, too, the swamp forest separates the sandhill habitat from the river. In May 1980, I observed pocket gopher diggings within 8 to 10 km of the Apalachicola River along Highway 271 and in adjacent slash pine plantations about 2 to 4 km north of its intersection with Highway 12; the soil there was coarse and granular and contained some red clay. My survey (May 1980) of surrounding Liberty and Gadsen counties revealed very little pocket gopher activity although appropriate soils and habitats are present. Unlike those in the areas surrounding the Suwannee River, populations near the Apalachicola River do not appear to be thriving.

#### Topography of river valleys

The Apalachicola and Suwannee rivers may be further contrasted by the nature of the topographic relief of their river valleys and relative elevations of habitats suitable and unsuitable to pocket gophers. In the more northern portion of its run through Florida, the Apalachicola has cut a deep river valley. Surrounding bluffs tower over the river by as much as 60 m at the Palisades just north of Bristol (Liberty Co.). As another example, the elevation of the town of Rock Bluff in extreme northern Liberty Co. is about 120 m. Only 8 km to the west is the Apalachicola River at about 16 m. Suitable pocket gopher habitats occur only on the higher plateau, whereas the unsuitable swamp forests are restricted to the river valley. Because the Apalachicola basin populations of pocket gophers are distant from the river and because they do not occur in the floodplain valley, neither flooding, drought nor shifts of the river course are likely to effect dispersal and communication between gene pools of populations from opposite banks.

Terrain along most of the Suwannee River is gentle relative to that bounding the Apalachicola River. Because no extensive bluffs occur along the rivercourse, a wider valley is available for flooding and meandering. Oxbowing and meandering can serve to mix gene pools of formerly separated populations by annexing adjacent favorable habitat and resident fauna via shifts in the rivercourse (Honeycutt and Schmidly, 1979:5-6). Because of the proximity of pocket gophers to the edge of the Suwannee, flooding and droughts could result in dispersal of Geomys across the river. An observation made by Dr. Stephen R. Humphrey (pers. comm.) lends credence to these contentions. During the Spring 1973 flood of the Suwannee River, he observed a dead bloated pocket gopher floating in the floodwaters on the floodplain across the river from Branford (Suwannee Co.). Although this Geomys was not alive, this observation suggests that rafting and swimming might be feasible means available to pocket gophers for crossing rivers, particularly where suitable habitats and floodplains overlap.

#### Changes in Geographic Distribution of Habitats through Time

Comparisons of morphometric features of samples from central, eastern, and western areas of the Florida peninsula demonstrated the presence of significant geographic variation among Recent samples but the absence of significant geographic variation among Wisconsinan samples. These results may be interpreted in terms of continuity of gene flow between populations. Morphometric similarity of Wisconsinan (glacial) samples supports the hypothesis that gene flow was occurring throughout the peninsula. Conversely, morphometric

dissimilarity of present-day (interglacial) samples supports the hypothesis that populations from these distant areas are not now interbreeding. Furthermore, they have been isolated for a period (< 19,000 years) sufficient to allow detectable morphological divergence to occur.

The occurrence of dispersal barriers between these populations is the probable cause for interruption of gene flow. For example, the Brevard Co. population is (if not now extinct; see Humphrey, 1981) isolated from the Alachua Co. and Pinellas Co. populations by at least one major obstacle, the St. Johns River. Similarly, a combination of unsuitable habitat and aquatic barriers prevents gene flow between the Pinellas Co. pocket gophers and the nearby central peninsular conspecifics in Hillsborough Co. and Pasco Co. Extending from the Gulf of Mexico southeastward towards Tampa Bay, the barrier consists of the Anclote River, Salt Lake, Lake Tarpon, South Creek, Lake St. George, Possum Branch, Safety Harbor, and associated wet lowlands. It is probable that such barriers were absent or drastically reduced during the Wisconsinan and other glacial intervals.

Two related mechanisms seem to influence the relative extent and distribution of habitat suitable to pocket gophers and of intervening barriers. First, at low coastal sites, sealevel changes have affected pocket gopher distributions by directly altering regional hydrological conditions by submergence and emergence. Since the Wisconsinan full glacial at about 19,000 B.P. (Bloom et al., 1974), sealevel has been rising continuously, presumably en route

to a future full interglacial high sea stand (Scholl and Stuiver, 1967; Bloom et al., 1974). The barriers (e.g., intracoastal waterways and associated wetlands) presently affecting gene flow are now more effective than earlier in the present interglacial; with continuing increase of sealevel, these barriers will restrict gene flow even further. Conversely, with expansion of glaciers and concomitant lowering of sealevel during the Wisconsinan glacial, wider areas of suitable habitat became available as many former barriers ceased to exist. Pocket gopher populations then expanded and gene flow was thereby enhanced. Such enhancement of gene flow tended to decrease or swamp out whatever interpopulation differences had emerged as a result of isolation during an earlier high sea stand.

In upland areas farther from the sea, pocket gopher distributions are regulated through a somewhat less direct mechanism. Decreased rainfall, increased evapotranspiration, and in a longer time frame, lower piezometric surface (water table) all tend to decrease surface water and soil moisture content. These in turn affect (1) the physical suitability of soils to pocket gopher habitation and (2) the distribution of vegetation associations suitable to pocket gophers. The rainfall regime is probably the major determinant of soil moisture conditions.

Changes in sealevel and in climatic patterns seem inadequate as mechanisms for alterations of certain habitats. For example, pine flatwoods occur in depressed areas of sandy former marine terraces. These areas are moister than surrounding habitats

because of the presence of a hardpan that prevents deep percolation of water. Therefore, flatwoods should remain more or less in place even in times of drier climates or low stands of sealevel, or of lowered water tables. Similar problems apply to freshwater marshes and swamps and to marine estuaries. How is it, then, that these habitats may be converted into others?

One means of altering habitats on a grand scale is by total inundation by rising seas. Marine sands would be deposited over all types of habitats. Following regression of the sea, vast areas would undergo re-development of communities, presumably in a manner not influenced by the habitat distribution pattern prior to the transgression, but in a way influenced by new topographic relationships.

Processes acting on a smaller scale may be classified as erosional. A perched pine flatwoods might be invaded and subsequently drained by headwater or lateral erosion of streams. Subterranean collapse is common in karst topography; opening of a sinkhole in a flatwoods habitat would drain the area. Further modification or removal of these soils by oxidation or burning of organics and leaching could result in an edaphic situation suitable for pocket gophers. These events might not result in entire flatwoods situations being converted into ideal pocket gopher habitat. However, repeated occurrence through time and space might convert enough habitat to form dispersal corridors between larger tracts of preferred habitat.

Suitable pocket gopher habitats bordering the St. Johns River are patchily distributed. Interlying areas are unsuitably moist and are impassable. Therefore, communication between pocket gopher populations can occur only through changes in habitat distribution. A general reduction of excess soil moisture from interlying swamps or marshes would probably accompany lowering of sealevel. However, soil moisture of drained areas would still be too great for pocket gophers due to water-holding capacity of organic soil components. Removal of peat soil could occur through natural fires and leaching. Unfavorable moisture regimes would preclude regeneration of swamp vegetation. The ground surface denuded of vegetation would be subject to erosion, which would remove additional organics. A vegetation association characteristic of drier situations (e.g., longleaf pine flatwoods) might then invade. Pocket gophers would probably follow this development. The intersection of such mobile parcels of suitable habitats would provide the opportunity for enhanced gene flow between pocket gopher populations.

It is unknown whether such habitat shifts have occurred through general radial expansion from refugia or through elevational shifts of habitat parcels that track the changing soil moisture regimes. Either mechanism would facilitate invasion of new areas by pocket gophers. The more likely model would be the one which (1) results in the overall more widespread distribution of upland habitat and (2) results in longer-duration contacts between previously isolated populations. Expanding the habitat distribution might require that once an area changes into upland habitat, it

must persist as hydrological regimes continue to change rather than passing into an even drier habitat (e.g., sandhill or sand scrub). Intuitively the general expansion approach seems to better meet the requirements; the elevational shift model seems associated with relatively ephemeral contact over a geographically smaller area. Research directed towards identifying the mechanism(s) involved will certainly be difficult because such habitat changes are slow and little historical evidence is available.

Degree of Variability in Florida *Geomys pinetis*

Two groups of investigators (John Avise, Joshua Laerm et al., University of Georgia and Steve Williams and Hugh Genoways, Carnegie Museum) have recently undertaken comprehensive revisions of pocket gophers in the southeastern United States. Both teams agree that the *Geomys pinetis* species complex, formerly including three peripherally-located nominal species (*G. fontanelus*, *G. colonus*, and *G. cumberlandius*), actually comprises the single species, *G. pinetis*. This species is viewed as consisting of two subspecies by Williams and Genoways and of three subspecies by Laerm.

On the basis of morphology, Williams and Genoways (1980) recognize the restricted (and probably extinct) population near Savannah, Georgia, as the subspecies *G. p. fontanelus*; all remaining southeastern United States pocket gophers comprise *G. p. pinetis*. Avise et al. (1979:6695) and Laerm (pers. comm.), using electrophoretic, karyological, and mitochondrial DNA techniques as well as cranial morphometrics, recognize the Apalachicola River, which courses through the central panhandle of Florida and comprises parts

of the Georgia-Alabama boundary, as the geographic feature dividing the eastern and western "forms." They, too, recognize the extinct G. p. fontanelus. Over the entire range of G. pinetis, no gross karyotypic differences between populations have been demonstrated (Williams and Genoways, 1975; Avise et al., 1979).

Despite the disagreement of these two teams of investigators on subspecific boundaries, one point is clear. Populations of pocket gophers in the southeastern United States are much more homogeneous chromosomally, biochemically, and morphometrically than those of any other geomyid of comparable distributional extent yet examined. Why is Geomys pinetis characterized by such a lack of variability? A comparison of this species with its nearest relative, Geomys bursarius, is instructive. Geomys bursarius is represented by 21 subspecies (Hall, 1981:502). Recent and ongoing work by David J. Schmidly and students demonstrates that geographic variability in chromosomal characters in G. bursarius is common along river courses in areas as small as a few hectares. Their work in southeastern Texas further shows that different chromosomal races (= subspecies) may not be separated on the basis of the soils in which they presently occur (e.g., Honeycutt and Schmidly, 1979; Tucker and Schmidly, 1981). Parameters considered in this study include diversity of habitats and associated soils inhabited, elevations of areas inhabited by these species and effects thereon of sealevel changes, and presence of interspecific competition.

### Habitats and soils

In terms of general soil and diet requirements, the needs of G. pinetis and G. bursarius (of the North American Great Plains) differ very little. Both species require friable soils (usually sandy or loamy, but rarely clayey) supporting growths of herbaceous vegetation in areas where groundwater levels are not too near ( $\leq 1.5$  m) the surface (Downhower and Hall, 1966; Lowrey, 1974:47, 207; Honeycutt and Schmidly, 1979:34-37). However, more types of suitable habitat and soils are available to, and are occupied by, G. bursarius than G. pinetis. These include sandy portions of mesquite plains in northwestern Texas (Blair, 1954:245), pine-oak forest, oak-hickory forest and coastal prairie vegetation types of east Texas (McCarley, 1959:402), and grasslands of eastern Colorado (Armstrong, 1972:163). In the oak-hickory forest vegetation type in north-central Texas (e.g., in Arlington, Tarrant Co.), G. bursarius is abundant in heavier reddish soils of relatively high clay content (pers. obs.). In northern Missouri, G. bursarius prefers windblown loess soils (Schwartz and Schwartz, 1959:158). Only one close analogue of a habitat occupied by Florida G. pinetis also occurs west of the Mississippi River in Louisiana and Texas within the range of G. bursarius. This shared habitat is the sandy, longleaf pine forest with an understory of post oak (Quercus stellata) and blackjack oak (Q. marilandica) substituting for the turkey oak found in Florida longleaf pine forests (McCarley, 1959: 387-389). Xeric hammocks, pine flatwoods, and sand scrub, the other three Florida habitats occupied by pocket gophers, are less preferred than the longleaf pine-turkey oak sandhill association.

Elevation and sealevel changes

In addition to differences in the diversity of habitats occupied, the ranges of Geomys pinetis and G. bursarius differ markedly in another crucial physiognomic character--elevation. In Florida, whose greatest elevation is 105 m above sealevel (in Walton Co.), G. pinetis occupies ground ranging from just above sealevel in Walton Co. (and others) to about 75 m in Gadsden Co. G. pinetis occurs in Georgia at elevations up to about 160 to 230 m, the approximate zone of contact between the lower, more suitable coastal plains habitats and the higher, less suitable habitat of the Piedmont (Brantly, 1916:1-2; LaForge et al., 1925; Golley, 1962:106). Extensions of pocket gophers into the Piedmont regions (e.g., Harris Co., Ga., Golley, 1962:106) are generally restricted to the sandy alluvial soils associated with river valleys.

Elevation per se probably has little or no bearing on the distribution of these species. However, through geological time, habitats lying at different elevations have experienced different events. The events of interest in this scenario pertain to the cycles of transgressions and retreats of the seas during the interglacial-glacial periods of the Pleistocene. Land areas comprising the current ranges of G. bursarius and G. pinetis were affected quite differently by late Cenozoic sealevel changes.

It was suggested above (Introduction) that the degree of isolation between populations of Florida pocket gophers is directly proportional to the height of sealevel, and that morphological divergence between populations is related to sealevel as well.

Hence, with expansion of pocket gopher ranges during low seas, panmixia among peninsular populations was more nearly approached and whatever divergence was attained during previous isolations was probably swamped. It follows, then, that any variability in present-day Florida G. pinetis has occurred as a result of isolation and subsequent divergence due to melting of the Wisconsinan glacier after about 19,000 B.P. In actuality, however, the time available for differentiation is certainly even less than 19,000 years. Because sealevel has been rising that entire time, many populations presently isolated may have been in contact within the last few centuries or millenia. Because sealevel changes can directly affect water table levels, especially in coastal areas, the length of time two populations have been isolated could conceivably be determined by knowing the elevation of the intervening area and the rate of sealevel rise.

Unlike G. pinetis, only a small portion of the range of G. bursarius was subjected to periodic inundation and emergence during the Neogene glacial cycles noted previously. The highest sea stand in Florida, represented by the Coharie marine terrace (Cooke, 1945), reached an elevation of 70 m. Assuming tectonic stability of the Gulf Coastal plains in Texas and Louisiana during the Neogene (although surely subsidence has been extensive), present contours of about 70 m should minimally identify the portions of G. bursarius range inundated during that (Aftonian?) interglacial. The distance from the current Texas Gulf Coast to a roughly-approximated 70 m contour line averages about 120 km. This 120 km swath of land along

the Texas coast represents a very small proportion of the current range of G. bursarius, which includes much of the North American Great Plains. This same interglacial inundation covered almost the entire land mass of the Florida peninsula. Subsequent transgressions were less severe and had even lesser impact on the range of G. bursarius.

Proximity of competitive geomyids

G. bursarius is parapatric, and in at least a few localities, sympatric with other geomyids. An example of proximal allopatry was recently reported in western Texas (Thornton and Creel, 1975) where ranges of Thomomys bottae, Pappogeomys castanops, and Geomys bursarius approach each other in a four county area. Although there is currently no sympatric occurrence of these species, it might have existed previously or could in the future. In Manitoba, G. bursarius and Thomomys talpoides have been collected within one mile of each other at five localities (Wrigley and Dubois, 1973). The authors interpret this situation in Manitoba as parapatry, although on a broader scale, it could be viewed as sympatry. In the Hill Country of central Texas, G. bursarius and T. bottae are currently allopatric. On the basis of three post-Wisconsinan cave deposits, however, as recently as 4,000 B.P. both species "lived within the hunting radius of individual barn owls" in Edwards Co. (Dalquest and Kilpatrick, 1973:5). G. bursarius and Pappogeomys castanops occur sympatrically in Hamilton Co. in western Kansas where the two species have been taken together in a roadside ditch (Birney et al., 1971:368-369). As is evident from the above examples,

the possibility for interspecific competition between G. bursarius and various contrageners and congeners (e.g., G. personatus in south Texas) clearly exists. Inasmuch as G. pinetis is the only geomyid rodent species occurring in the southeastern United States, it seems doubtful that interspecific competition has played much of a role in its evolutionary history. This statement should be qualified, however, by acknowledging Simpson's (1928:6-7) description of a Pleistocene species, Thomomys orientalis, from Sabertooth Cave, Citrus Co., Florida.

Summary of comparison of Geomys pinetis and G. bursarius

The preceding comparison of Geomys pinetis and Geomys bursarius with regard to diversity of soils, habitats, and elevations and with regard to amounts of interspecific competition encountered may be summarized in light of an argument presented by Smith and Patton (1980:692-695) and James L. Patton (pers. comm.). They (quite reasonably) assert that the external morphology of pocket gophers is subject to extensive selection pressures of local environments. Therefore, variation between populations of the same species may more likely represent phenotypic than genotypic variation. These selection pressures may take the form of (1) soils of different hardness, (2) soils supporting vegetation of variable nutritive qualities, or (3) interspecific competition. Their argument implies (p. 693) that results of morphometric studies assessing phylogenetic relationships between conspecific populations of pocket gophers (e.g., this study) may be suspect because phenotypic similarities and differences may be non-genetic. Features not directly in contact

with (or influenced by) the external environment should comprise more conservative and reliable lines of evidence in evaluating inter-population relatedness. Karyological and other biochemical approaches are capable of evaluating such protected, internal data bases. In addressing this problem, it should be recalled that the geographic relationships of G. pinetis demonstrated in this study solely via cranial morphometrics concur with the relationships Avise et al. (1979) obtained via electrophoretic and mitochondrial DNA studies.

Numerous factors acting in concert, then, appear to underlie the lack of extensive morphological variability of G. pinetis in Florida. Because sealevel has been rising since the late Wisconsinan, the isolation of populations seen in the present mosaic distribution is so recent that insufficient time has been available for differentiation of isolated populations. The four habitats in which pocket gophers occur in Florida have rather similar soils, at least in terms of mechanical suitability to pocket gophers. Additionally, G. pinetis is free from competition with other geomyids. Hence, selective pressures favoring adaptation and divergence of pocket gopher populations as per Smith and Patton (1980) appear to have been absent from G. pinetis but present for G. bursarius which occurs in a greater diversity of habitats having a relatively wider range of soil types. G. bursarius ranges over a broad range of elevations; sufficient time for divergence has been available because sealevel changes have not obliterated divergent characters of most inland populations. Furthermore, G. bursarius is and/or has been subject to interspecific and intergeneric competition.

### Phylogenetic Trends: Anatomical Considerations

Despite the general lack of mathematical significance in temporal variation of nine measured dentary characters, the observed trends (particularly in the three computed ratios) are still biologically meaningful and instructive in understanding the evolution of geomyines. A more detailed examination of the two suites of characters concerning relative tooth widths and dimensions of the basitemporal fossa is presented below. From these trends, the possible pressures driving evolution can be addressed and rates of evolution can be calculated.

#### Relative Widths of Teeth

Considered separately, the five characters pertaining to lengths and widths of teeth are not particularly useful in understanding Geomys evolution. When employed in calculating ratios expressing changes in the relative widths of occlusal surfaces, however, these characters are instructive. Fig. 20 shows the general trend of increasing breadth of the three examined surfaces. Changes in breadth of m1 and the anterior loph of p4 express a more smoothly increasing trend than seen in the more erratically increasing pattern for the posterior loph of p4. Despite the lack of desired levels of statistical significance for many parameters (Table 20), general trends of change towards greater tooth widths are apparent.

From early Irvingtonian time to present, width of m1 has increased from 1.72 times the length of m1 to 2.1 times its length; relative width of m1 has increased by 22% over about 1.8 million years. Increase in width of posterior loph of p4 has similarly

outpaced gain in length. During the early Irvingtonian, the WPOSTP4 was 73.3% of LP4, whereas WPOSTP4 is 85.8% of LP4 in modern populations; the proportion increase for RWPOSTP4 is 17%. For the same time interval, the relative width of the anterior loph of p4 has increased from 53.3% to 66.1% of LP4, a change of 24%.

The relative amounts of change in these three characters may reflect the relative importances of these occlusal surfaces in chewing and, hence, the relative intensity of selection pressures on each surface. Geomys pinetis is known to chew propalinally (Wilkins and Woods, unpub. data). Food sectioning occurs as anteriorly-concave lower enamel blades pass oppositely-oriented enamel blades on the upper molars. There are four transversely-oriented lower enamel bands, namely on the posterior edges of the three molars and of the posterior loph of p4. In the lower cheekteeth, the only enamel on an anterior tooth surface occurs on p4; the labial and lingual re-entrant angles separating the prisms are also invested with enamel. The loss of enamel on the anterior faces of the lower molar occurred in the unknown geomyine ancestral form [collateral with Pliogeomys, which showed no enamel reduction during the late Hemphillian-early Blancan (mid to late Pliocene)], presumably as its function was lost (Russell, 1968).

The degree of usage of each enamel band is indicated by the amount and type of wear it exhibits. The more heavily used teeth are those with well-worn bands having numerous striations (indicating direction of passage of abrasive particles) and those with shorter crowns (i.e., those with occlusal surfaces situated closer to the

alveolar level). The following description characterizes the molars, and to a lesser extent, the posterior loph of p4. The tallest of the lower cheekteeth is p4, with its anterior loph projecting above the posterior one. Wear on the anteriormost enamel band of p4 is more often in the form of the loss of large chips of enamel rather than the regular pattern of tooth scars for the molars or for posterior p4. Furthermore, examination of the relative positions of upper and lower teeth through the power and recovery stroke cycle shows that even in the jaw's most retracted position the anterior p4 enamel band fails to solidly occlude with any of the upper dentition. In many cases, anteriormost lower p4 remains anterior to the anteriormost portion of upper p4, thereby altogether failing to occlude.

From the foregoing, it is apparent that p4 plays a lesser role in chewing than does m1. Presumably selection will be more intense on characters more directly involved in such vital functions as in mastication. Because of the greater involvement of m1 and the posterior loph of p4 in chewing, the actions of selection should be more evident in the widths of m1 and the posterior part of p4 than in the anterior part of p4. Greater efficiency in propalinal chewers may be achieved by broadening the occlusal surface perpendicular to the direction of the power stroke, thereby increasing the length of the surface (e.g., enamel band) available for shearing food (Rensberger, 1975). This trend of increasing tooth breadth is evident for all three surfaces investigated herein, with the greatest broadening seen for m1 and the least for the anterior loph of p4. These changes represent morphological responses to selection pressures that have resulted in increased chewing efficiency.

Dimensions of Retromolar Fossa

Another trend involved in strengthening the dental battery of Geomys pertains to increases in the size of the retromolar fossa. This fossa is the site of insertion for the deeper fibers of the temporalis muscle. The temporalis, which originates from the superior nuchal line, the sagittal or temporal ridge, and the greater part of the temporal fossa (Hill, 1937:104), holds the occlusal surface of the lower molariform dentition firmly against the upper teeth during mastication (Russell, 1968:481). Since its first appearance in late Pliocene geomyines, this fossa has enlarged, thereby increasing the surface area available for attachment of the temporalis. Increasing depth of this fossa has resulted in increasing length of the muscle as well. The force generated by a muscle is proportional to its cross-sectional area and to its shortening distance (Brunnstrom, 1981:32). Therefore, an evolutionary trend towards increasing strength of the temporalis is evident.

In this study, these trends are corroborated by three characters assessing size of the retromolar fossa. Although regression line slopes did not significantly increase (at  $P \leq 0.05$ ), this fossa has increased in length, width, and depth over the 1.8 million years of geomyine history recorded in Florida. Likewise, changes in mean values of LRMF, WRMF, and DRMF were not statistically significant; yet the absolute and proportional changes in these three characters were all positive from the early Irvingtonian to present as follows: LRMF, 3.65 mm to 4.83 mm (a 32% increase); WRMF, 2.01 mm to 2.55 mm (a 26% increase); and DRMF, 1.45 mm to 3.14 mm (a 116% increase).

These data show that evolution in geomyines in the southeastern United States is following a course comparable to that previously demonstrated for other geomyine lineages (Russell, 1968:481). Russell remarked that enlargement of the retromolar fossa was probably an adaptation for diets of coarser foods. Such changes in this fossa probably represent responses to the same selective pressures as the broadening of cheekteeth.

Factors responsible for chronological trends. Patterns of chronological variation seen for relative tooth widths and for retromolar fossa dimensions share a common temporary deviation from their generally increasing trend. A notable decrease occurs in each of six characters (RWANTP4, RWPOSTP4, RWMI, LRMF, WRMF, and DRMF) during the Sangamonian to Wisconsinan interval (Figs. 20 and 21). These decreases each represent shifts towards more primitive character states. These character state reversals offer independent lines of evidence assessing the response of the masticatory apparatus to selection pressures. Presumably the three relative tooth width characters and also the three retromolar fossa dimension characters are related to abrasiveness of diet (Russell, 1968). Each of these changes thus suggests reduced selection for powerful mastication and thus a temporary return to a less abrasive diet.

Decreased dental abrasion could be achieved in various ways. Diets could shift from plants with greater to those with lesser silica content, that is, from grasses to forbs and other non-grasses. At present, palynological data do not extend far enough back in time to allow determination of herbaceous community composition during

pre-Wisconsinan time intervals. Another alternative is that diets of pocket gophers have changed little through this period, but silica content of grasses and other food items has fluctuated. A third possibility pertains to abrasiveness of soils. It is possible that, through time, pocket gophers have shifted soil type preferences.

The preceding possible explanations regarded the Sangamonian to Wisconsinan shift as a unique deviation from a unidirectional trend. It is worth considering the possibility that this observed deviation represents only one segment of a recurring cyclic pattern characterizing Florida geomyine phylogeny during the Pleistocene. Direct correlation with glacial-interglacial stages seems untenable because values for samples during various glacials are rather dissimilar for various characters (e.g., WRMF, LRMF, RWANTP4, RWPOSTP4, RWM1). Likewise, samples of the Sangamonian and Recent interglacials differ widely in all six characters. Furthermore, samples from various glacials and interglacials often have similar values (e.g., LRMF, RWPOSTP4, RWM1). Another problem lies in the observation that the direction of change from an interglacial to a glacial (Sangamonian to Wisconsinan) or from an interglacial to a glacial (Wisconsinan to Recent) is not the same for all (or even most) characters. Thus, it seems preferable to regard the Sangamonian to Wisconsinan shift as an important but unique evolutionary burst.

Another possible causative factor for the observed trends could be in the types of habitats formerly surrounding the fossil sites. Glacial-interglacial cycles are known to be correlated with shifts in climate and, therefore, with vegetation associations (Watts,

1980). However, variation in habitats (with or without an interaction with glacial cycles) is also an unlikely source of the observed character trends. Ecological conditions during the represented early (Inglis) and late Irvingtonian (Coleman) are adequately understood. Both the mammalian and herpetofaunas of Inglis suggest surrounding habitats to have been ecotonal situations between scrub and grassland savanna. Klein (1971) more specifically considered the ecological conditions of Inglis IA times to have been similar to those in the present-day Yucatan Peninsula (Mexico); Meylan (1980) constructs a situation of mixed longleaf pine with xeric hammocks (some of which were seasonally wet) interspersed. Similar ecological conditions characterized the Illinoian Coleman area, with habitat being more open and more xeric than at present (Martin, 1974). Pocket gophers inhabit rather similar vegetation associations today, a time falling into the post-Wisconsinan interglacial. Therefore, habitat preferences seem not to correspond with glacial-interglacial stages. Presumably continuing adaptation to these habitats provides the best explanation for the trends in morphological changes in Florida Pleistocene Geomys.

#### Summary of Discussion

The discussion of the findings of this study has focussed on factors that have influenced the extent of geographic variation in Recent Florida Geomys pinetis and those responsible for observed patterns of geographic and chronological variation in Florida Geomys from the early Irvingtonian to present. Study findings are consistent

with the proposed hypotheses. To summarize:

(1) Differences in the Apalachicola and Suwannee Rivers with regard to various physical parameters correspond to their relative effectiveness in inhibiting pocket gopher dispersal. These features include distance between suitable pocket gopher habitats on opposite sides of the river, suitability of habitats for pocket gophers around the headwaters of the river, size (i.e., width, depth) of the waterway, flow rates and volumes, and seasonality of flow rates.

(2) A survey of the influence of the Apalachicola and Suwannee Rivers on other vertebrate and invertebrate species was presented. The Apalachicola River corresponds to generic boundaries of flightless, burrowing beetles (Scarabaeidae: Geotrupinae), to species boundaries of pocket gopher lice (Mallophaga: Trichodectidae), and to subspecies boundaries of the eastern woodrat (Neotoma floridana). The zoogeographic importance of the Suwannee River is evident in more taxa than the Apalachicola River. Animal groups whose dispersal is apparently influenced by the Suwannee River include mollusks, fishes, snakes, and at least five species of mammals.

(3) Changes in pocket gopher distribution are thought to correspond closely with variation (through time and space) of the distribution of suitable habitats. Habitat distribution may be influenced directly through sealevel changes or less directly through changes in soil moisture and climatic regimes. Means of altering soil characteristics so as to allow changes in habitats were considered.

(4) On the basis of variability in other geomyids of comparable distributional extent, the amount of geographic variation in Geomys

pinetis is unexpectedly low. Efforts towards explaining this apparent anomaly entailed a comparison of Geomys pinetis with its congener G. bursarius. The diversity of habitats and soils inhabited by G. pinetis is less than that inhabited by G. bursarius. Sealevel changes have repeatedly affected vast portions of the range of G. pinetis, but only minute portions of the range of G. bursarius. G. pinetis has been less influenced by interspecific competition than has G. bursarius.

(5) Phylogenetic trends in four suites of dental characters were interpreted as adaptations towards chewing efficiency. The several explanations offered for observed trends variously pertain to dietary changes, shifts in soil or habitat preferences, or correspondence with glacial-interglacial cycles.

Closing comment. It is hoped that this study will be viewed as a contribution, not only towards understanding Florida geomyine zoogeography, but also in regard to a general methodological approach. The most common approach to systematic paleontology studies has been typological. In such studies, attributes of a single (or few) specimen(s) form the basis for systematic decisions and phylogenetic discussions. Granted, the nature of fossil material oftentimes necessitates such an approach. Indeed, this has been the case even for certain geomyid taxa. However, for groups where large samples are available (e.g., Floridian and many other geomyines), a population level approach is more desirable than is the typological method. Large samples allow understanding of non-geographic variability in the form of sex, age, and individual variation. In this study, for

example, ontogenetic age was generally a greater source of character variation than was time or geography. Had ontogenetic variation not been eliminated (via covariance analysis) early in the study, many comparisons and statistical decisions would surely have been fallacious. My review of the pocket gopher literature indicates that certain taxa are recognized on the basis of characters whose variation may well emanate from ontogenetic rather than phylogenetic sources. A review of features diagnosing pocket gopher taxa is in order.

The completion of this dissertation should not imply that all questions regarding zoogeography and systematics of Florida geomyines have been addressed. The next step in my studies of Florida pocket gopher material is to determine whether the Inglis IA sample contains material referable to Orthogeomys, a Central American geomyid genus as yet unknown in the United States; my observations do not support this contention. Other efforts will involve scrutiny of Florida pocket gopher material purportedly belonging to the genus Thomomys.

LITERATURE CITED

- Akersten, W. A. 1973. Evolution of geomyine rodents with rooted cheek teeth. Ph.D. dissert., Univ. Michigan, Ann Arbor, 236 pp.
- Alt, D., and H. K. Brooks. 1965. Age of Florida marine terraces. *J. Geol.*, 73:406-411.
- Anderson, S. 1966. Taxonomy of gophers, especially Thomomys in Chihuahua, Mexico. *Syst. Zool.*, 15:189-198.
- Armstrong, D. M. 1972. Distribution of mammals in Colorado. Univ. Kans., Mus. Nat. Hist., Monograph No. 3, 415 pp.
- Auffenburg, W. 1957. A note on an unusually complete specimen of Dasypus bellus (Simpson) from Florida. *Quar. J. Florida Acad. Sci.*, 20:233-237.
- \_\_\_\_\_. 1958. Fossil turtles of the genus Terrapene in Florida. *Bull. Florida State Mus.*, 3:53-92.
- \_\_\_\_\_. 1963. The fossil snakes of Florida. *Tulane Studies Zool.*, 10:131-216.
- Avise, J. C., C. Giblin-Davidson, J. Laerm, J. C. Patton, and R. A. Lansman. 1979. Mitochondrial DNA clones and matriarchal phylogeny within and among geographic populations of the pocket gopher, Geomys pinetis. *Proc. Natl. Acad. Sci.*, 76:6694-6698.
- Bailey, R. M., H. E. Winn, and C. L. Smith. 1954. Fishes from the Escambia River, Alabama and Florida, with ecologic and taxonomic notes. *Proc. Acad. Nat. Sci., Philadelphia*, 106:109-164.
- Bangs, O. 1898. The land mammals of peninsular Florida and the coast region of Georgia. *Proc. Boston Soc. Nat. Hist.*, 28: 157-235.
- Barrington, B. A. 1940. The natural history of pocket gophers. M. S. thesis, Univ. Florida, Gainesville, 49 pp.
- Baumgardner, G. D., and D. J. Schmidly. 1981. Systematics of the southern races of two species of kangaroo rats (Dipodomys compactus and D. ordii). *Occas. Papers Mus., Texas Tech Univ.*, 73:1-27.

- Bender, M. L., R. G. Fairbanks, F. W. Taylor, R. K. Matthews, J. G. Goddard, and W. S. Broecker. 1979. Uranium-series dating of the Pleistocene reef tracts of Barbados, West Indies. *Geol. Soc. Amer. Bull.*, 90:577-594.
- Birney, E. C., J. K. Jones, and D. M. Mortimer. 1971. The yellow-faced pocket gopher, *Pappogeomys castanops*, in Kansas. *Trans. Kansas Acad. Sci.*, 73:368-375.
- Blackith, R. E., and R. A. Reyment. 1971. *Multivariate morphometrics*. Academic Press, New York, 412 pp.
- Blackwelder, B. W., O. H. Pilkey, and J. D. Howard. 1979. Late Wisconsin sea levels on the southeast U.S. Atlantic shelf on in-place shoreline indicators. *Science*, 204:618-620.
- Blair, W. F. 1954. Mammals of the mesquite plains biotic district in Texas and Oklahoma. *Texas J. Sci.*, 6:235-264.
- Bloom, A. L. 1970. Holocene submergence in Micronesia as the standard for eustatic sea-level changes. *Quaternaria*, 12: 145-154.
- \_\_\_\_\_, W. S. Broecker, J. M. A. Chappell, R. K. Matthews, and K. J. Mesolella. 1974. Quaternary sea level fluctuations on a tectonic coast:  $^{230}\text{Th}/^{234}\text{U}$  dates from the Huon Peninsula, New Guinea. *Quaternary Res.*, 4:185-205.
- Brantly, J. E. 1916. A report on the limestones and marls of the coastal plain of Georgia. *Bull. Geol. Survey Georgia*, 21:1-300.
- Broecker, W. S., and D. L. Thurber. 1965. Uranium-series dating of corals and oolites from Bahaman and Florida Key limestones. *Science*, 149:58-60.
- \_\_\_\_\_, \_\_\_\_\_, J. Goddard, T. Ku, R. K. Matthews, and K. J. Mesolella. 1968. Milankovitch hypothesis supported by precise dating of coral reefs and deep-sea sediments. *Science*, 159:297-300.
- Brunnstron, S. 1981. *Clinical kinesiology*. Third ed. F. A. Davis Co., Philadelphia, 392 pp.
- Bryant, E. H., and C. R. Turner. 1979. Comparative morphometric adaptation of the house fly and the face fly in the United States. *Evolution*, 33:759-770.
- Cant, R. V. 1972. Jamaica's Pleistocene reef terraces. *Jamaica J., Geol. Soc.*, 12:13-17.

- Chappell, J. 1974. Geology of coral terraces, Huon Peninsula, New Guinea: a study of Quaternary tectonic movement and sea-level changes. Geol. Soc. Amer. Bull., 85:553-570.
- \_\_\_\_\_, and H. A. Polach. 1976. Holocene sealevel changes and coral reef growth at Huon Peninsula, Papua New Guinea. Geol. Soc. Amer. Bull., 87:235-239.
- Christman, S. P. 1980. Patterns of geographic variation in Florida snakes. Bull. Florida State Mus., 25:157-256.
- Clench, W. J., and R. D. Turner. 1956. Freshwater mollusks of Alabama, Georgia, and Florida from the Escambia to the Suwannee River. Bull. Florida State Mus., 1:97-239.
- Clifford, H. T., and W. Stephenson. 1975. An introduction to numerical classification. Academic Press, New York, 229 pp.
- Cooke, C. W. 1939. Scenery in Florida interpreted by a geologist. Bull. Florida Geol. Survey, 17:1-118.
- \_\_\_\_\_. 1945. Geology of Florida. Bull. Florida Geol. Survey, 29:1-339.
- Dall, W. H. 1890-1903. Tertiary mollusks of Florida. Trans. Wagner Free Inst. Sci., Philadelphia, 3:1-1654.
- Dalquest, W. W., and C. W. Kilpatrick. 1973. Dynamics of pocket gopher distribution on the Edwards Plateau of Texas. South-western Nat., 18:1-9.
- Davis, J. H. 1980. General map of natural vegetation of Florida. Inst. Food and Agric. Sci., Univ. Florida, Circ. S-178.
- Downhower, J. F., and E. R. Hall. 1966. The pocket gopher in Kansas. Misc. Publ. Mus. Nat. Hist., Univ. Kansas, 44:1-32.
- Dunnigan, P. B. 1967. Pocket gophers of the genus Thomomys of the Mexican state of Sinaloa. Radford Rev., 21:139-168.
- Ehrhart, L. M. 1978. Goff's pocket gopher. Pp. 6-7 in Rare and endangered biota of Florida. Vol. 1. Mammals (J. N. Layne, ed.). Univ. Presses Florida, Gainesville, 52 pp.
- Florida Agricultural Experiment Station. 1962. General soils map of Florida. Gainesville: Inst. Food and Agric. Sci., Univ. Florida.
- Gillette, D. D. 1976. Late Quaternary mammals from the St. Marks River, Wakulla County, Florida. Florida Sci., 39:120-122.

- ✓Golley, F. B. 1962. Mammals of Georgia: a study of their distribution and functional role in the ecosystem. Univ. Georgia Press, Athens, 218 pp.
- ✓Hall, E. R. 1981. The mammals of North America. John Wiley and Sons, New York, 1:1-600 + 90.
- Hamilton, W. J., Jr., and J. O. Whitaker. 1979. Mammals of the eastern United States. Second ed. Cornell Univ. Press, Ithaca, New York. 346 pp.
- Harmon, R. S., H. P. Schwarcz, and D. C. Ford. 1978. Late Pleistocene sea level history of Bermuda. Quaternary Res., 9:205-218.
- Harper, F. 1927. The mammals of the Okefinokee Swamp region of Georgia. Proc. Boston Soc. Nat. Hist., 38:191-396.
- Harris, R. J. 1975. A primer of multivariate statistics. Academic Press, New York, 332 pp.
- Healy, H. F. 1975. Terraces and shorelines of Florida. Florida Dept. Nat. Resources, Bur. Geol., Map Series No. 71.
- Heath, R. C., and E. T. Wimberly. 1971. Selected flow characteristics of Florida streams and canals. Florida Bur. Geol., Inf. Circ. No. 69, 595 pp.
- Helwig, J. T., and K. A. Council. 1979. SAS user's guide. SAS Inst., Raleigh, 494 pp.
- Hill, J. E. 1937. Morphology of the pocket gopher mammalian genus Thomomys. Univ. California Publ. Zool., 42:81-171.
- Hoffmeister, D. F. 1969. The species problem in the Thomomys bottae-Thomomys umbrinus complex of pocket gophers in Arizona. Misc. Publ. Mus. Nat. Hist., Univ. Kansas, 51:75-91.
- Honeycutt, R. L., and D. J. Schmidly. 1979. Chromosomal and morphological variation in the plains pocket gopher, Geomys bursarius, in Texas and adjacent states. Occas. Papers Mus., Texas Tech. Univ., 58:1-54.
- Howden, H. F. 1963. Speculations on some beetles, barriers, and climates during the Pleistocene and pre-Pleistocene periods in some non-glaciated portions of North America. Syst. Zool., 12:178-201.

- Hubbell, T. H. 1954. Relationships and distribution of Mycotrupes (pt. 2). In A. L. Olson, T. H. Hubbell, and H. F. Howden. The burrowing beetles of the genus Mycotrupes (Coleoptera: Scarabaeidae: Geotrupinae). Misc. Publ. Mus. Zool., Univ. Michigan, 84:39-51.
- \_\_\_\_\_, and C. C. Goff. 1939. Florida pocket-gopher burrows and their arthropod inhabitants. Proc. Florida Acad. Sci., 4:127-166.
- ✓ Humphrey, S. R. 1981. Goff's pocket gopher (Geomys pinetis goffi) is extinct. Florida Sci., 44:250-252.
- Kennerly, T. E., Jr. 1954. Local differentiation in the pocket gopher (Geomys personatus) in southern Texas. Texas J. Sci., 6:297-329.
- \_\_\_\_\_. 1963. Gene flow pattern and swimming ability of the pocket gopher. Southwestern Nat., 8:85-88.
- Klein, J. G. 1971. The ferungulates of the Inglis IA local fauna, early Pleistocene of Florida. M.S. thesis, Univ. Florida, Gainesville, 115 pp.
- Ku, T. L., M. A. Kimmel, W. H. Easton, and T. J. O'Neill. 1974. Eustatic sea level 120,000 years ago in Oahu, Hawaii. Science, 183:959-962.
- Kurten, B., and E. Anderson. 1980. Pleistocene mammals of North America. Columbia Univ. Press, New York, 442 pp.
- LaForge, L., W. Cooke, A. Keith, and M. R. Campbell. 1925. Physical geography of Georgia. Bull. Geol. Survey Georgia, 42:1-189.
- Lee, M. R., and F. F. B. Elder. 1980. Yeast stimulation of bone marrow mitosis for cytogenetic investigations. Cytogenet. Cell Genet., 29:36-40.
- Lowrey, G. H., Jr. 1974. The mammals of Louisiana and its adjacent waters. Louisiana State Univ. Press, Baton Rouge, 565 pp.
- MacNeil, F. S. 1950. Pleistocene shorelines in Florida and Georgia. U.S. Geol. Survey, Prof. Paper 221-F:95-106.
- Marshall, J. F., and J. Launay. 1978. Uplift rates of the Loyalty Islands as determined by  $^{230}\text{Th}/^{234}\text{U}$  dating of raised coral terraces. Quaternary Res., 9:186-192.
- Martin, R. A. 1969. Taxonomy of the giant Pleistocene beaver Castoroides from Florida. J. Paleo., 43:1033-1041.

- \_\_\_\_\_. 1975. Giant Pleistocene beavers and the Waccasassa River, Levy County, Florida. Bull. New Jersey Acad. Sci., 20:29-30.
- McCarley, H. 1959. The mammals of eastern Texas. Texas J. Sci., 11:385-426.
- Means, D. B. 1976. Aspects of the significance to terrestrial vertebrates of the Apalachicola River drainage basin, Florida. Florida Marine Research Publ., 26:37-67.
- Merriam, C. H. 1895. Monographic revision of the pocket gophers, family Geomyidae (exclusive of the species of Thomomys). N. Amer. Fauna, 8:1-258.
- Mesolella, K. J., R. K. Matthews, W. S. Broecker, and D. L. Thurber. 1969. The astronomical theory of climatic change: Barbados data. J. Geol., 77:250-274.
- Meylan, P. A. 1980. The squamate reptiles of the Inglis IA fauna (Irvingtonian: Citrus County, Florida). M.S. thesis, Univ. Florida, Gainesville, 154 pp.
- Monk, C. D. 1968. Successional and environmental relationships of the forest vegetation of north central Florida. Amer. Midland Nat., 79:441-457.
- Neff, N. A., and L. F. Marcus. 1980. A survey of multivariate methods for systematics. Privately published, New York, 243 pp.
- Neill, W. T. 1957. Historical biogeography of present-day Florida. Bull. Florida State Mus., 2:175-220.
- Neumann, A. C., and W. S. Moore. 1975. Sea level events and Pleistocene coral ages in the northern Bahamas. Quaternary Res., 5:215-224.
- Nevo, E. 1979. Adaptive convergence and divergence of subterranean mammals. Ann. Rev. Ecol. Syst., 10:269-308.
- Osmond, J. K., J. R. Carpenter, and H. L. Windom. 1965. Th<sup>230</sup>/U<sup>234</sup> age of the Pleistocene corals and oolites of Florida. J. Geophysical Res., 70:1843-1847.
- Patton, J. L. 1967. Chromosomal studies of certain pocket mice, genus Perognathus (Rodentia: Heteromyidae). J. Mamm., 48:27-37.

- \_\_\_\_\_, and R. E. Dingman. 1970. Chromosome studies of pocket gophers, genus Thomomys II. Variation in T. bottae in the American southwest. *Cytogenetics*, 9:139-151.
- \_\_\_\_\_, R. K. Selander, and M. H. Smith. 1972. Genic variation in hybridizing populations of gophers (genus Thomomys). *Syst. Zool.*, 21:263-270.
- ✓ Pembleton, E. F., and S. L. Williams. 1978. Geomys pinetis. *Mamm. Species*, 86:1-3.
- Quarterman, E., and C. Keever. 1962. Southern mixed hardwood forest: climax in the southeastern coastal plain, U.S.A. *Ecol. Monogr.*, 32:167-185.
- Quay, W. B. 1949. Notes on mammals of Thomas County, Georgia, with two state records. *J. Mamm.*, 30:66-68.
- Rensberger, J. M. 1975. Function in the cheek tooth evolution of some hypsodont geomyoid rodents. *J. Paleo.*, 49:10-22.
- Ross, J. P. 1976. Seasonal energy budgets of a fossorial rodent, Geomys pinetis. Ph.D. dissert., Univ. Florida, Gainesville, 153 pp.
- Russell, R. J. 1968. Evolution and classification of the pocket gophers of the subfamily Geomyinae. *Univ. Kans. Publ., Mus. Nat. Hist.*, 16:473-579.
- Scholl, D. W., and M. Stuiver. 1967. Recent submergence of southern Florida: a comparison with adjacent coasts and other eustatic data. *Bull. Geol. Soc. Amer.*, 78:437-454.
- Schwartz, C. W., and E. R. Schwartz. 1959. The wild mammals of Missouri. Univ. Missouri Press, Columbia, 341 pp.
- Shackleton, N. J., and N. D. Opdyke. 1973. Oxygen isotope and palaeomagnetic stratigraphy of equatorial Pacific core V28-238: Oxygen isotope temperatures and ice volumes on a  $10^5$  year and  $10^6$  year scale. *Quaternary Res.*, 3:39-55.
- Simpson, G. G. 1928. Pleistocene mammals from a cave in Citrus County, Florida. *Amer. Mus. Novitates*, 328:1-16.
- Smith, M. F., and J. L. Patton. 1980. Relationships of pocket gopher (Thomomys bottae) populations of the lower Colorado River. *J. Mamm.*, 61:681-696.

- Steel, R. G. D., and J. H. Torrie. 1960. Principles and procedures of statistics with special reference to the biological sciences. McGraw-Hill Book Co., New York, 481 pp.
- Stevenson, H. M. 1976. Vertebrates of Florida. Univ. Presses Florida, Gainesville, 607 pp.
- Thaeler, C. S., Jr. 1968a. Karyotypes of sixteen populations of the Thomomys talpoides complex of pocket gophers (Rodentia-Geomyidae). *Chromosoma*, 25:172-183.
- \_\_\_\_\_. 1968b. An analysis of three hybrid populations of pocket gophers (Genus Thomomys). *Evolution*, 22:543-555.
- Thornton, W. A., and G. C. Creel. 1975. Distribution of gophers (Geomyidae) in western Texas. *Southwestern Nat.*, 20:271-287.
- Tucker, P. K., and D. J. Schmidly. 1981. Studies of a contact zone among three chromosomal races of Geomys bursarius in east Texas. *J. Mamm.*, 62:258-272.
- Udvardy, M. D. F. 1969. Dynamic zoogeography with special reference to land animals. Van Nostrand Reinhold Co., New York, 445 pp.
- Veno, P. A. 1976. Successional relationships of five Florida plant communities. *Ecology*, 57:498-508.
- Vernon, R. O. 1951. Geology of Citrus and Levy counties, Florida. *Bull. Florida State Geol. Survey*, 33:1-256.
- Ward, J. H., Jr. 1963. Hierarchical grouping to optimize an objective function. *J. Amer. Stat. Assn.*, 58:236-244.
- Watts, W. A. 1980. The late Quaternary vegetation history of the southeastern United States. *Ann. Rev. Ecol. Syst.*, 11:387-409.
- \_\_\_\_\_, and M. Stuiver. 1980. Late Wisconsin climate of northern Florida and the origin of species-rich deciduous forests. *Science*, 210:325-327.
- Webb, S. D., ed. 1974. Pleistocene mammals of Florida. Univ. Presses Florida, Gainesville, 270 pp.
- White, W. A. 1970. The geomorphology of the Florida peninsula. *Geological Bull., Florida Bur. Geol.*, 51:1-164.
- Williams, S. L., and H. H. Genoways. 1975. Karyotype of Geomys pinetis with a discussion of the chromosomal relationships within the genus. *Experientia*, 31:1141-1142.

\_\_\_\_\_, and \_\_\_\_\_. 1977. Morphometric variation in the tropical pocket gopher (Geomys tropicalis). Ann. Carnegie Mus., 46:245-264.

\_\_\_\_\_, and \_\_\_\_\_. 1980. Morphological variation in the southeastern pocket gopher, Geomys pinetis (Mammalia: Rodentia). Ann. Carnegie Mus., 49:405-453.

Winchester, B. H., and R. S. DeLotelle. 1978. The current status of the colonial pocket gopher. Oriole, 43:33-35.

Wishart, D. 1975. CLUSTAN 1C user manual. CLUSTAN Project, Univ. College, London, 124 pp.

Wright, S. 1943. Isolation by distance. Genetics, 28:114-138.

Wrigley, R. E., and J. E. Dubois. 1973. Distribution of the pocket gophers Geomys bursarius and Thomomys talpoides in Manitoba. Canadian Field-Nat., 87:167-169.

APPENDIX A  
STANDARD UNIVARIATE STATISTICS BY REGION  
FOR CRANIAL CHARACTERS IN RECENT DATA SET

Table A-1.--Standard univariate statistics by region for cranial characters in Recent data set for age class 1 males. Included statistics are: sample size (N), mean ( $\bar{X}$ ), extreme values, standard deviation (SD), standard error (SE), and coefficient of variation (CV, as percent). Measurements in millimeters. Maximally non-significant subsets, as determined by Duncan's multiple range tests, indicated in right column; means of samples connected by vertical bar are not significantly different ( $P \leq 0.05$ ).

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
GLS	D	7	49.61	47.4-51.5	1.42	0.54	2.87	
	J	106	49.21	44.0-54.8	2.29	0.23	4.45	
	L	6	49.13	47.3-52.4	2.14	0.96	4.36	
	M	18	49.07	45.1-52.2	2.09	0.54	4.27	
	K	34	48.16	42.8-51.2	1.88	0.34	3.92	
	C	4	47.83	46.4-49.2	1.54	0.89	3.24	
	G	4	47.28	46.3-48.4	0.92	0.46	1.95	
	A	1	46.90					
	I	1	46.90					
	F	8	46.40	43.1-49.3	2.07	0.84	4.48	
E	1	44.30						
ZYGO	M	17	30.12	26.5-39.4	5.70	1.52	8.85	
	A	1	29.90					
	J	106	29.48	25.6-38.3	1.88	0.19	6.39	
	L	6	28.78	27.5-30.8	1.31	0.58	4.54	
	K	34	28.77	26.5-31.4	1.30	0.24	4.51	
	C	4	28.56	27.0-29.0	1.10	0.64	3.90	
	D	7	28.54	26.3-30.7	1.41	0.53	4.95	
	G	4	28.00	27.5-28.5	0.48	0.24	1.70	
	F	8	27.56	26.2-29.5	1.19	0.49	4.35	
	I	1	27.50					
E	1	26.90						
WMAST	L	6	25.67	24.9-28.0	1.32	0.59	5.13	
	K	34	25.62	24.0-27.9	0.96	0.18	3.75	
	J	106	25.59	22.6-28.8	2.27	0.23	8.86	
	M	18	25.16	23.6-26.7	0.99	0.26	3.97	
	G	4	25.15	24.4-25.9	0.62	0.31	2.48	
	A	1	25.10					
	C	4	25.10	24.6-25.6	0.53	0.31	2.12	
	F	8	25.01	23.9-26.9	1.11	0.45	4.47	
	D	7	24.86	24.0-26.5	0.86	0.33	3.47	
	I	1	24.40					
E	1	24.10						

Table A-1.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
DCRAN	J	106	14.94	13.6-16.0	1.10	0.11	7.32	
	M	18	14.82	14.1-15.6	0.48	0.12	3.25	
	L	6	14.82	14.4-15.4	0.43	0.19	2.91	
	K	34	14.71	10.4-16.2	0.94	0.17	6.36	
	F	8	14.68	13.9-15.8	0.71	0.29	4.87	
	G	4	14.65	14.2-15.0	0.34	0.17	2.33	
	I	1	14.50					
	D	7	14.37	13.8-14.7	0.31	0.12	2.19	
	E	1	14.30					
	C	4	14.18	14.0-14.4	0.23	0.13	1.62	
A	1	13.90						
DROST	J	106	7.33	6.2- 9.0	0.47	0.05	6.49	
	M	18	7.10	6.3- 7.8	0.49	0.13	6.90	
	D	7	7.09	6.7- 7.7	0.33	0.12	4.64	
	K	34	7.09	6.2- 7.7	0.34	0.06	4.72	
	L	6	6.98	6.6- 7.6	0.40	0.18	5.80	
	G	4	6.95	6.8- 7.0	0.10	0.05	1.44	
	A	1	6.90					
	I	1	6.90					
	C	4	6.68	6.5- 7.0	0.26	0.15	3.95	
	E	1	6.60					
F	8	6.53	6.0- 7.0	0.41	0.17	6.39		
WROST	J	106	10.58	9.1-11.8	0.60	0.06	5.72	
	M	18	10.48	9.4-11.4	0.65	0.17	6.26	
	A	1	10.40					
	C	4	10.33	10.3-10.4	0.06	0.03	0.56	
	K	34	10.31	9.3-11.6	0.54	0.10	5.24	
	D	7	10.21	9.3-10.9	0.66	0.25	6.43	
	L	6	10.18	9.3-11.0	0.70	0.32	7.06	
	I	1	10.10					
	G	4	10.08	9.7-10.7	0.45	0.23	4.47	
	F	8	9.85	9.4-10.4	0.44	0.18	4.40	
E	1	8.70						

Table A-1.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
IOC	A	1	7.70					
	C	4	7.33	7.2-7.6	0.21	0.12	2.83	
	D	7	7.24	6.7-8.2	0.51	0.19	7.08	
	I	1	7.10					
	M	18	7.06	6.6-7.8	0.37	0.09	5.13	
	G	4	7.05	6.8-7.3	0.24	0.12	3.38	
	J	106	7.02	6.2-8.1	0.37	0.04	5.34	
	K	34	6.89	5.9-7.5	0.37	0.07	5.44	
	L	6	6.87	6.7-7.1	0.16	0.07	2.29	
	F	8	6.70	6.5-6.8	0.16	0.07	2.47	
E	1	6.10						
TEMP	E	1	6.10					
	I	1	6.10					
	G	4	4.33	3.7-5.0	0.54	0.27	12.43	
	J	106	4.25	1.7-9.1	1.26	0.13	29.40	
	M	18	4.04	1.9-5.9	1.02	0.27	24.50	
	L	6	4.00	2.7-5.4	0.96	0.43	23.91	
	K	34	3.97	2.0-7.0	1.19	0.22	29.49	
	D	7	3.41	2.2-4.8	1.05	0.40	30.69	
	F	8	2.80	2.8-4.6	0.66	0.27	18.75	
	A	1	2.80					
C	4	2.70	2.4-4.1	0.91	0.52	29.59		
AWINT	E	1	2.70					
	G	4	2.70	2.0-3.3	0.57	0.29	21.17	
	M	18	2.67	1.0-3.8	0.79	0.20	29.82	
	L	6	2.67	1.8-3.5	0.70	0.31	26.64	
	F	8	2.56	1.7-3.4	0.55	0.22	20.63	
	J	106	2.39	0.1-6.1	1.00	0.10	41.93	
	K	34	2.17	0.5-3.6	0.82	0.15	37.98	
	A	1	2.00					
	D	7	1.69	0.7-2.4	0.58	0.22	34.32	
	I	1	1.20					
C	4	1.08	0.6-1.9	0.65	0.38	51.37		

Table A-1.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
PWINT	D	7	6.46	5.2-7.5	0.78	0.29	12.06	
	I	1	6.20					
	J	106	5.95	2.0-8.0	0.99	0.10	16.53	
	E	1	5.90					
	G	4	5.88	4.8-6.8	0.87	0.43	14.80	
	M	18	5.83	4.4-8.2	0.98	0.25	16.97	
	K	34	5.77	3.8-6.6	0.69	0.13	12.06	
	A	1	5.70					
	L	6	5.68	4.5-7.0	0.96	0.43	17.39	
	F	8	5.46	4.8-6.3	0.56	0.23	10.23	
C	4	5.10	4.8-5.1	0.15	0.09	3.10		
LINT	I	1	7.90					
	D	7	6.07	5.4-6.5	0.34	0.13	5.52	
	M	18	5.87	4.0-12.4	2.29	0.59	38.28	
	K	34	5.47	3.9-7.7	1.07	0.20	19.30	
	L	6	5.30	4.7-6.1	0.58	0.26	11.00	
	C	4	5.23	4.6-5.7	0.61	0.35	11.48	
	J	106	4.93	3.5-8.3	0.83	0.08	16.68	
	E	1	4.80					
	F	8	4.59	4.1-4.9	0.32	0.13	7.05	
	A	1	4.50					
G	4	4.40	3.5-5.3	0.77	0.39	17.60		
LWNAS	A	1	2.70					
	J	106	2.34	1.3-4.2	0.39	0.04	16.43	
	K	34	2.33	1.8-3.2	0.34	0.06	14.54	
	I	1	2.30					
	G	4	2.18	1.5-2.6	0.48	0.24	22.01	
	M	18	2.17	1.6-2.7	0.30	0.08	13.54	
	C	4	1.98	1.7-2.5	0.46	0.27	23.49	
	F	8	1.95	1.7-2.1	0.16	0.07	8.43	
	L	6	1.95	1.6-2.2	0.29	0.13	15.36	
	D	7	1.86	1.5-2.1	0.20	0.08	10.71	
E	1	1.70						

Table A-1.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
GWNAS	A	1	3.60					
	G	4	2.95	2.2- 3.7	0.81	0.41	27.47	
	J	106	2.90	2.1- 3.6	0.38	0.04	12.96	
	K	34	2.88	1.8- 3.8	0.45	0.08	15.58	
	C	4	2.85	2.5- 3.3	0.44	0.25	15.57	
	E	1	2.70					
	D	7	2.70	2.4- 3.2	0.29	0.11	10.90	
	M	18	2.64	2.3- 3.1	0.23	0.06	8.69	
	I	1	2.60					
	F	8	2.41	2.2- 2.7	0.23	0.09	9.59	
L	6	2.33	1.8- 2.4	0.25	0.11	11.22		
PMEXT	I	1	4.60					
	F	8	3.69	3.3- 4.0	0.30	0.12	8.24	
	M	18	3.46	2.5- 5.3	0.84	0.22	24.25	
	D	7	3.17	2.1- 4.1	0.70	0.26	21.98	
	L	6	3.15	1.8- 3.9	0.91	0.41	30.65	
	K	34	3.15	1.9- 4.7	0.73	0.13	23.95	
	J	106	3.14	1.4- 5.1	0.74	0.07	23.52	
	E	1	3.10					
	C	4	3.03	2.4- 3.5	0.55	0.32	18.78	
	A	1	2.70					
G	4	2.68	1.6- 4.1	1.07	0.53	39.96		
LUDIAST	D	7	19.77	17.4-21.0	1.18	0.45	5.98	
	J	106	19.13	15.5-22.7	1.48	0.15	7.75	
	M	18	19.01	17.3-20.5	1.07	0.28	5.66	
	L	6	18.83	17.7-20.4	1.09	0.49	5.80	
	C	4	18.83	18.0-19.2	0.64	0.37	3.48	
	K	34	18.55	15.6-20.4	1.16	0.21	6.25	
	A	1	18.00					
	G	4	17.75	17.2-18.1	0.40	0.20	2.28	
	F	8	17.34	15.0-18.5	1.22	0.50	7.13	
	I	1	16.90					
E	1	15.80						

Table A-1.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
LMXTR	A	1	10.50					
	I	1	10.10					
	J	106	10.06	8.9-11.6	0.50	0.05	5.00	
	M	18	9.96	9.0-10.6	0.40	0.10	4.08	
	L	6	9.90	9.1-11.0	0.70	0.31	7.04	
	K	34	9.77	9.0-11.0	0.39	0.07	4.05	
	G	4	9.68	9.2-10.0	0.36	0.18	3.72	
	D	7	9.60	8.9-10.2	0.38	0.14	3.99	
	C	4	9.43	8.8- 9.7	0.47	0.27	5.06	
	F	8	9.19	8.4- 9.5	0.39	0.16	4.25	
E	1	8.80						
WUINC	M	18	2.35	2.0- 2.6	0.19	0.05	8.20	
	J	106	2.32	1.9- 3.0	0.21	0.02	9.18	
	L	6	2.32	2.1- 2.5	0.16	0.07	7.21	
	K	34	2.29	2.0- 2.6	0.15	0.03	6.79	
	D	7	2.27	2.1- 2.6	0.18	0.07	7.92	
	C	4	2.23	2.1- 2.3	0.12	0.07	5.17	
	G	4	2.18	2.1- 2.3	0.10	0.05	4.40	
	F	8	2.11	1.9- 2.2	0.12	0.05	5.97	
	A	1	2.10					
	E	1	2.00					
I	1	2.00						
LLDIAST	D	7	12.56	11.0-13.5	0.95	0.36	7.58	
	C	4	12.00	10.8-11.9	0.56	0.32	4.88	
	J	106	11.78	7.2-14.9	1.17	0.12	9.98	
	L	6	11.37	10.6-12.3	0.71	0.32	6.26	
	M	18	11.31	8.2-12.9	1.41	0.36	12.84	
	K	34	11.27	9.1-12.6	0.82	0.15	7.34	
	A	1	10.90					
	G	4	10.78	10.5-11.3	0.36	0.18	3.34	
	F	8	10.75	9.9-11.5	0.57	0.23	5.39	
	I	1	10.10					
E	1	9.70						

Table A-1.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
LMNDTR	I	1	9.20					
	L	6	8.98	8.4-9.2	0.30	0.14	3.45	
	M	18	8.97	8.2-9.5	0.37	0.10	4.16	
	A	1	8.80					
	J	106	8.79	7.6-9.8	0.42	0.04	4.78	
	K	34	8.72	7.7-9.6	0.40	0.07	4.55	
	D	7	8.67	8.2-8.9	0.30	0.11	3.44	
	G	4	8.63	8.0-9.1	0.49	0.24	5.63	
	C	4	8.50	8.4-8.7	0.15	0.09	1.79	
	F	8	8.34	7.9-8.6	0.27	0.11	3.32	
E	1	7.90						
WLINC	L	6	2.22	2.1-2.4	0.14	0.06	6.43	
	M	18	2.17	1.9-2.6	0.20	0.05	9.04	
	J	106	2.15	1.7-2.9	0.20	0.02	9.06	
	K	34	2.12	1.8-2.3	0.14	0.03	6.51	
	D	7	2.04	1.9-2.2	0.10	0.04	4.78	
	C	4	2.03	1.9-2.1	0.10	0.06	5.00	
	I	1	2.00					
	G	4	2.00	1.9-2.1	0.08	0.04	4.08	
	F	8	1.95	1.7-2.2	0.17	0.07	8.99	
	A	1	1.90					
E	1	1.80						

Table A-2.--Standard univariate statistics by region for cranial characters in Recent data set for age class 2 males. Included statistics are: sample size (N), mean ( $\bar{X}$ ), extreme values, standard deviation (SD), standard error (SE), and coefficient of variation (CV, as percent). Measurements in millimeters. Maximally non-significant subsets, as determined by Duncan's multiple range tests, indicated in right column; means of samples connected by vertical bar are not significantly different ( $P \leq 0.05$ ).

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
GLS	L	6	53.95	54.9-57.1	1.14	0.66	2.04	
	B	1	53.40					
	C	6	52.63	49.5-55.8	2.67	1.19	5.05	
	J	95	52.43	47.6-60.0	2.03	0.22	3.86	
	F	8	52.43	51.0-53.7	1.02	0.42	1.95	
	K	27	52.40	49.4-57.2	2.24	0.45	4.24	
	M	23	52.10	47.6-57.3	2.01	0.44	3.85	
	D	5	51.50	50.5-51.6	0.47	0.23	0.91	
	G	2	50.35	49.9-50.8	0.64	0.45	1.26	
E	1	49.60						
ZYGO	D	5	33.30	31.0-39.2	3.88	1.94	11.61	
	B	1	33.00					
	L	6	32.37	31.7-34.4	1.46	0.84	4.37	
	K	27	32.19	29.2-37.4	1.89	0.38	5.87	
	F	8	32.00	30.8-33.9	1.08	0.44	3.41	
	C	6	31.90	27.9-35.6	2.35	1.05	7.32	
	J	94	31.70	27.3-36.2	1.64	0.18	5.17	
	M	23	31.53	28.3-34.4	1.55	0.34	4.91	
	G	2	30.80	30.3-31.3	0.71	0.50	2.30	
E	1	30.50						
WMAST	L	6	28.17	27.5-29.9	1.20	0.69	4.18	
	K	26	28.00	25.7-31.5	1.49	0.30	5.32	
	B	1	27.60					
	F	8	27.58	25.7-29.2	1.14	0.47	4.16	
	J	95	27.28	20.1-30.1	1.27	0.14	4.68	
	C	6	27.17	25.1-29.3	1.81	0.81	6.63	
	G	2	26.90	26.1-27.7	1.13	0.80	4.21	
	M	23	26.85	25.4-28.5	0.72	0.16	2.69	
	E	1	26.80					
	D	5	26.22	25.0-26.6	0.67	0.33	2.58	

Table A-2.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
DCRAN	F	8	15.68	15.2-16.7	0.61	0.25	3.82	-----   -----
	K	27	15.49	13.9-17.2	0.72	0.14	4.67	
	M	23	15.42	14.8-16.5	0.43	0.09	2.76	
	G	2	15.40	14.7-16.1	0.99	0.70	6.43	
	L	6	15.37	15.6-15.9	0.15	0.09	0.97	
	J	95	15.32	14.2-17.0	0.55	0.06	3.56	
	B	1	15.10					
	E	1	15.10					
	C	6	14.93	14.2-16.1	0.80	0.36	5.29	
	D	5	14.52	14.0-14.8	0.39	0.19	2.68	
DROST	J	95	7.83	6.6- 9.1	0.47	0.05	6.06	-----   -----
	K	27	7.82	6.8- 8.8	0.54	0.11	6.86	
	L	6	7.72	7.9- 8.1	0.10	0.06	1.25	
	B	1	7.70					
	E	1	7.70					
	M	23	7.67	7.1- 8.5	0.42	0.09	5.52	
	F	8	7.58	7.1- 8.0	0.31	0.13	4.08	
	C	6	7.57	6.9- 8.1	0.48	0.21	6.20	
	D	5	7.44	7.1- 7.4	0.15	0.08	2.05	
G	2	6.85	6.7- 7.0	0.21	0.15	3.10		
WROST	M	23	11.46	10.4-13.0	0.58	0.13	5.01	-----   -----
	B	1	11.40					
	K	27	11.22	10.5-12.9	0.56	0.11	4.98	
	J	95	11.17	9.7-12.3	0.56	0.06	5.04	
	C	6	11.13	10.4-12.2	0.75	0.34	6.68	
	F	8	10.90	10.4-11.5	0.40	0.16	3.72	
	D	5	10.86	10.2-11.0	0.34	0.17	3.21	
	E	1	10.70					
	L	6	10.12	7.2-11.4	2.34	1.35	23.67	
G	2	9.60	9.3- 9.9	0.42	0.30	4.42		

Table A-2.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
IOC	C	6	7.68	7.3-8.3	0.38	0.17	4.95	               
	B	1	7.60					
	D	5	7.48	7.1-7.7	0.26	0.13	3.49	
	M	23	7.35	6.5-8.5	0.53	0.11	7.12	
	F	8	7.29	6.9-7.5	0.23	0.10	3.26	
	J	95	6.98	5.9-8.3	0.47	0.05	6.81	
	G	2	6.95	6.8-7.1	0.21	0.15	3.05	
	L	6	6.92	7.1-7.7	0.30	0.17	4.05	
	K	27	6.91	5.3-8.1	0.65	0.13	9.32	
E	1	6.60						
TEMP	G	2	3.55	3.3-3.8	0.35	0.25	9.96	             
	J	95	2.54	0.3-7.6	1.42	0.15	55.59	
	M	23	2.38	0.3-4.9	1.42	0.31	58.46	
	K	27	2.04	0.1-4.3	1.17	0.23	55.97	
	D	5	1.66	0.3-0.9	0.28	0.14	47.89	
	L	6	1.48	0.7-2.1	0.74	0.43	48.07	
	E	1	1.40					
	F	8	1.31	0.6-1.9	0.52	0.21	39.44	
C	6	0.97	0.4-1.7	0.55	0.25	54.77		
B	1	0.40						
AWINT	G	2	2.80	2.3-3.3	0.71	0.50	25.25	               
	J	95	1.29	0.2-3.2	0.75	0.08	57.74	
	M	23	1.25	0.3-2.9	0.86	0.19	66.69	
	K	27	1.19	0.1-2.9	0.77	0.15	62.75	
	L	6	0.90	0.5-1.1	0.31	0.18	36.67	
	F	8	0.80	0.1-1.1	0.37	0.15	50.78	
	E	1	0.60					
	C	6	0.50	0.2-0.9	0.35	0.16	64.95	
	D	5	0.32	0.1-0.5	0.17	0.09	62.10	
B	1	0.10						

Table A-2.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
PWINT	G	2	6.50	6.3-6.7	0.28	0.20	4.35	I
	L	6	5.80	4.6-7.1	1.26	0.73	21.21	
	J	95	5.66	3.5-7.7	0.80	0.09	14.23	
	M	23	5.64	3.6-7.5	0.77	0.17	13.57	
	K	27	5.39	2.4-8.7	1.44	0.29	27.19	
	C	6	4.98	3.4-5.5	0.84	0.38	17.59	
	F	8	4.96	3.7-5.6	0.69	0.28	14.33	
	D	5	4.74	2.2-5.8	1.47	0.74	36.37	
	E	1	4.30					
B	1	1.30					I	
LINT	M	23	5.84	3.7-10.3	1.58	0.34	27.08	I
	K	27	5.60	2.1-8.0	1.35	0.27	24.14	
	J	95	5.28	3.1-8.8	0.97	0.10	18.33	
	L	6	5.07	2.6-7.4	2.46	1.42	46.33	
	G	2	4.65	4.6-4.7	0.07	0.05	1.52	
	F	8	4.59	3.8-5.5	0.81	0.33	17.66	
	C	6	4.32	2.2-5.4	1.47	0.66	36.00	
	D	5	4.20	2.2-7.3	2.17	1.09	49.08	
	E	1	3.90					
B	1	1.30					I	
LWNAS	E	1	2.60					I
	K	27	2.39	1.6-2.8	0.28	0.06	11.98	
	J	95	2.35	1.4-4.2	0.41	0.04	17.44	
	M	23	2.21	1.4-2.7	0.33	0.07	14.67	
	C	6	2.17	1.6-2.5	0.36	0.16	16.72	
	F	8	2.14	1.0-3.0	0.68	0.28	32.44	
	L	6	2.10	1.8-2.2	0.21	0.12	10.24	
	G	2	1.95	1.8-2.1	0.21	0.15	10.88	
	D	5	1.72	1.2-2.0	0.34	0.17	20.70	
B	1	1.70						

Table A-2.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
GWNAS	C	6	3.37	2.8- 3.8	0.40	0.18	11.77	
	E	1	3.20					
	K	27	2.99	2.4- 3.6	0.34	0.07	11.37	
	J	95	2.93	1.9- 3.8	0.42	0.05	14.43	
	D	5	2.88	2.5- 3.0	0.24	0.12	8.75	
	M	23	2.86	1.9- 3.4	0.37	0.08	12.68	
	F	8	2.61	1.7- 3.5	0.68	0.28	26.97	
	B	1	2.60					
	L	6	2.55	1.9- 3.1	0.60	0.35	24.00	
G	2	2.35	2.3- 2.4	0.07	0.05	3.01		
PMEXT	G	2	5.10	4.7- 5.5	0.57	0.40	11.09	
	L	6	4.03	4.2- 4.7	0.26	0.15	6.01	
	B	1	3.90					
	F	8	3.78	3.2- 4.6	0.49	0.20	12.67	
	E	1	3.50					
	J	95	3.39	1.4- 5.3	0.77	0.08	23.17	
	M	23	3.34	1.7- 5.4	0.90	0.20	27.48	
	K	27	3.30	1.4- 3.4	0.79	0.16	23.90	
	D	5	3.18	2.6- 3.6	0.41	0.21	13.52	
C	6	3.15	2.8- 3.8	0.43	0.19	13.44		
LUDIAST	C	6	23.00	20.9-25.7	1.81	0.81	7.73	
	B	1	22.70					
	L	6	21.77	22.2-23.6	0.74	0.43	3.20	
	D	5	21.46	20.7-21.5	0.36	0.18	1.70	
	K	27	21.43	19.0-27.0	1.78	0.36	8.32	
	F	8	21.13	19.7-22.2	0.87	0.36	4.17	
	J	95	21.09	18.6-25.2	1.20	0.13	5.70	
	M	23	20.63	18.8-22.7	1.00	0.22	4.86	
	G	2	20.25	19.6-20.9	0.92	0.65	4.54	
E	1	19.40						

Table A-2.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
LMXTR	L	6	10.87	10.8-11.7	0.47	0.27	4.23	
	K	27	10.60	9.5-20.6	2.13	0.43	20.09	
	M	23	10.40	9.7-11.4	0.42	0.09	4.02	
	F	8	10.36	10.1-10.7	0.23	0.09	2.18	
	J	95	10.33	9.0-11.7	0.52	0.06	5.06	
	D	5	10.22	9.8-10.3	0.22	0.11	2.14	
	B	1	10.20					
	E	1	10.20					
	C	6	9.87	9.5-10.1	0.23	0.10	2.34	
	G	2	9.50	9.3- 9.7	0.28	0.20	2.98	
WUINC	D	5	2.62	2.5- 2.8	0.13	0.06	4.79	
	M	23	2.57	2.3- 2.8	0.19	0.04	7.41	
	K	27	2.50	2.2- 3.0	0.21	0.04	8.26	
	E	1	2.50					
	J	95	2.47	2.1- 2.9	0.17	0.02	6.88	
	F	8	2.45	2.3- 2.5	0.08	0.03	3.36	
	L	6	2.43	2.5- 2.7	0.12	0.07	4.39	
	C	6	2.38	2.2- 2.6	0.15	0.07	6.23	
	B	1	2.30					
	G	2	2.25	2.2- 2.3	0.07	0.05	3.14	
LLDIAS	C	6	14.52	13.3-15.9	1.04	0.47	7.20	
	B	1	14.20					
	D	5	14.06	13.0-14.2	0.57	0.29	4.24	
	L	6	13.78	14.0-14.6	0.35	0.20	2.44	
	F	8	13.56	12.2-14.5	0.81	0.33	6.09	
	J	95	13.13	10.7-16.8	1.12	0.12	8.59	
	K	27	13.09	11.4-16.1	1.16	0.23	8.90	
	G	2	12.75	12.5-13.0	0.35	0.25	2.77	
	M	23	12.63	10.5-14.8	1.10	0.24	8.78	
	E	1	12.20					

Table A-2.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
LMNDTR	M	23	9.40	8.9-10.7	0.48	0.10	5.08	
	L	6	9.38	9.4- 9.8	0.21	0.12	2.18	
	K	27	9.27	8.5-10.0	0.44	0.09	4.69	
	F	8	9.21	9.0- 9.7	0.27	0.11	2.88	
	J	95	9.11	4.1-10.2	0.70	0.07	7.71	
	B	1	9.10					
	C	6	9.02	8.4- 9.8	0.60	0.27	6.67	
	E	1	9.00					
	D	5	8.94	8.3- 9.5	0.53	0.27	5.96	
G	2	8.70	8.5- 8.9	0.28	0.20	3.25		
WLINC	M	23	2.34	2.0- 2.6	0.17	0.04	7.07	
	K	27	2.32	2.0- 2.9	0.24	0.05	10.40	
	L	6	2.32	2.3- 2.6	0.15	0.09	6.19	
	E	1	2.30					
	J	94	2.27	1.7- 2.9	0.27	0.03	11.71	
	D	5	2.24	2.2- 2.3	0.05	0.03	2.25	
	B	1	2.20					
	G	2	2.20	2.2	0	0	0	
	F	8	2.19	2.1- 2.3	0.08	0.03	3.45	
C	6	2.12	2.2- 2.3	0.11	0.05	5.17		

Table A-3.--Standard univariate statistics by region for cranial characters in Recent data set for age class 1 females. Included statistics are: sample size (N), mean ( $\bar{X}$ ), extreme values, standard deviation (SD), standard error (SE), and coefficient of variation (CV, as percent). Measurements in millimeters. Maximally non-significant subsets, as determined by Duncan's multiple range tests, indicated in right column; means of samples connected by vertical bar are not significantly different ( $P \leq 0.05$ ).

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
GLS	L	11	44.98	43.4-47.2	1.42	0.54	3.12	
	M	28	44.82	42.9-48.4	1.44	0.29	3.20	
	J	162	44.58	40.0-51.6	1.77	0.14	3.97	
	C	15	44.35	42.4-45.8	0.86	0.22	1.93	
	B	2	44.30	43.8-44.8	0.71	0.05	1.60	
	A	1	44.20					
	K	40	44.10	26.2-47.0	3.21	0.52	7.29	
	F	12	44.04	40.8-47.2	1.59	0.46	3.62	
	G	5	43.86	42.7-44.9	0.86	0.39	1.97	
	D	24	43.85	39.5-46.5	1.90	0.42	4.33	
	H	3	43.23	42.3-44.5	1.14	0.66	2.63	
E	1	41.50						
ZYGO	M	28	26.63	24.0-30.8	1.43	0.29	5.37	
	K	39	26.46	24.7-28.9	0.99	0.16	3.74	
	G	5	26.42	25.0-27.2	0.89	0.40	3.38	
	J	162	26.27	23.5-30.4	1.27	0.10	4.83	
	A	1	26.20					
	L	11	26.12	24.6-28.2	1.38	0.52	5.28	
	B	2	26.05	25.9-26.2	0.21	0.15	0.81	
	F	12	25.99	23.2-27.4	1.09	0.31	4.18	
	C	15	25.97	24.8-27.0	0.55	0.14	2.11	
	D	24	25.33	23.1-27.4	1.21	0.27	4.79	
	E	1	25.20					
H	3	25.17	24.8-25.8	0.55	0.32	2.19		
WMAST	G	5	23.98	23.4-24.5	0.47	0.20	1.94	
	K	40	23.87	22.7-25.8	0.66	0.11	2.78	
	M	27	23.82	22.3-27.9	1.22	0.25	5.10	
	J	162	23.70	14.5-28.9	1.27	0.10	5.36	
	L	11	23.62	22.2-24.8	0.88	0.33	3.71	
	F	12	23.47	20.6-24.9	1.11	0.32	4.73	
	B	2	23.20	22.6-23.8	0.85	0.60	3.66	
	H	3	23.13	22.8-23.6	0.42	0.24	1.80	
	C	15	23.12	22.6-23.8	0.35	0.09	1.50	
	D	24	22.60	21.2-24.3	1.03	0.22	4.56	
	A	1	22.40					
E	1	22.10						

Table A-3.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
DCRAN	M	28	14.35	13.3-15.2	0.45	0.09	3.16	I                   
	K	40	14.09	13.2-15.0	0.44	0.07	3.13	
	J	162	14.01	12.6-16.6	0.51	0.03	3.62	
	L	11	13.98	13.5-14.6	0.39	0.15	2.73	
	G	5	13.96	13.5-14.7	0.44	0.20	3.19	
	F	12	13.90	13.1-14.5	0.47	0.14	3.42	
	H	3	13.80	13.6-14.0	0.20	0.12	1.45	
	C	15	13.67	13.3-14.1	0.24	0.06	1.72	
	D	24	13.53	12.6-14.0	0.40	0.09	2.97	
	E	1	13.50					
	A	1	13.30					
B	2	13.15	13.1-13.2	0.07	0.05	0.54		
DROST	A	1	6.6					I                   
	H	3	6.60	6.2- 7.1	0.46	0.26	6.94	
	J	162	6.59	5.7- 7.8	0.40	0.03	6.08	
	M	28	6.57	5.9- 7.4	0.35	0.07	5.29	
	B	2	6.50	6.50	0	0	0	
	C	15	6.41	5.8- 7.1	0.33	0.08	5.09	
	K	40	6.37	5.6- 7.1	0.39	0.06	6.18	
	G	5	6.36	6.0- 6.6	0.26	0.12	4.10	
	L	11	6.31	6.0- 7.1	0.41	0.16	6.40	
	D	24	6.26	5.7- 6.9	0.34	0.07	5.38	
	F	12	6.21	5.7- 7.0	0.35	0.10	5.60	
E	1	6.00						
WROST	M	28	9.73	8.8-10.8	0.42	0.18	4.30	I                   
	J	161	9.57	8.2-10.9	0.52	0.04	5.41	
	C	15	9.51	9.3- 9.8	0.20	0.05	2.08	
	K	39	9.58	8.3-10.5	0.50	0.08	5.26	
	G	5	9.38	9.2- 9.6	0.18	0.08	1.91	
	L	11	9.36	8.5- 9.8	0.49	0.18	5.24	
	F	12	9.26	7.9-10.0	0.59	0.17	6.41	
	B	2	9.25	9.1- 9.4	0.21	0.15	2.29	
	D	24	9.18	8.1-10.1	0.42	0.09	4.62	
	H	3	9.13	8.9- 9.5	0.32	0.19	3.52	
	A	1	9.10					
E	1	9.10						

Table A-3.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
IOC	A	1	7.50					
	C	15	7.27	6.6-7.7	0.30	0.08	4.12	
	D	24	7.16	6.7-7.8	0.27	0.06	3.84	
	H	3	6.97	6.7-7.2	0.25	0.15	3.61	
	B	2	6.95	6.7-7.2	0.35	0.25	5.09	
	M	28	6.92	6.2-7.7	0.30	0.06	4.34	
	J	162	6.83	6.1-7.7	0.33	0.03	4.82	
	L	11	6.83	6.4-7.1	0.28	0.08	4.07	
	K	40	6.67	5.7-7.8	0.37	0.06	5.58	
	E	1	6.60					
	G	5	6.60	6.1-7.5	0.53	0.24	8.02	
	F	12	6.55	6.1-7.1	0.21	0.08	4.19	
TEMP	H	3	6.37	5.0-7.2	1.19	0.69	18.74	
	E	1	6.10					
	J	162	5.65	1.4-12.4	1.30	0.11	23.06	
	F	12	5.38	4.0-6.3	0.76	0.22	14.03	
	L	11	5.31	3.8-7.2	1.11	0.42	21.05	
	G	5	5.28	4.0-6.0	0.52	0.23	9.79	
	M	28	5.23	2.6-7.1	1.36	0.27	25.89	
	K	40	4.92	3.5-7.1	0.92	0.15	18.69	
	A	1	4.80					
	D	24	4.74	2.8-7.7	1.32	0.29	28.10	
	C	15	4.51	3.4-6.4	0.79	0.20	17.58	
	B	2	3.00	2.9-3.1	0.14	0.10	4.71	
AWINT	E	1	4.40					
	H	3	3.67	2.9-4.5	0.80	0.46	21.88	
	F	12	3.54	2.8-4.0	0.36	0.10	10.18	
	J	162	3.51	0.9-8.6	1.02	0.08	29.10	
	M	28	3.21	1.4-4.9	0.96	0.19	30.31	
	L	11	3.15	2.0-4.0	0.77	0.29	26.73	
	K	40	2.99	0.6-4.7	0.73	0.12	24.79	
	G	5	2.90	2.5-3.7	0.48	0.22	16.72	
	D	24	2.75	1.4-3.9	0.72	0.16	27.12	
	A	1	2.60					
	C	15	2.27	1.6-3.3	0.56	0.14	24.46	
	B	2	1.85	1.8-1.9	0.07	0.15	3.82	

Table A-3.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
PWINT	E	1	7.40					I
	J	162	6.17	4.0-8.2	0.66	0.05	10.63	
	D	24	6.06	4.6-7.0	0.73	0.16	12.26	
	M	28	5.98	4.8-6.7	0.52	0.10	8.71	
	H	3	5.93	5.1-6.4	0.72	0.42	12.19	
	K	40	5.90	4.5-8.2	0.76	0.12	13.00	
	L	11	5.87	4.8-7.1	0.85	0.32	14.31	
	F	12	5.87	4.4-7.0	0.74	0.21	12.55	
	C	15	5.77	4.6-7.4	0.77	0.20	13.33	
	G	5	5.52	4.9-6.1	0.48	0.21	8.63	
	A	1	5.10					
B	2	5.05	4.9-5.2	0.21	0.15	4.20		
LINT	M	28	5.69	4.0-8.1	1.05	0.21	18.61	I
	K	40	5.29	3.7-7.8	0.98	0.16	18.54	
	L	11	5.25	4.0-7.2	1.05	0.40	19.76	
	C	15	5.24	4.5-6.5	0.52	0.13	9.91	
	D	24	4.98	4.2-6.6	0.50	0.11	9.83	
	J	162	4.76	3.0-7.5	0.73	0.06	15.34	
	F	12	4.73	3.9-5.3	0.40	0.11	8.42	
	H	3	4.70	4.4-5.1	0.36	0.21	7.67	
	B	2	4.65	4.6-4.7	0.07	0.05	1.52	
	G	5	4.42	3.8-5.1	0.50	0.22	11.24	
	E	1	4.30					
A	1	4.20						
LWNAS	E	1	2.40					I
	H	3	2.37	2.0-2.8	0.40	0.23	17.08	
	C	15	2.31	1.9-2.8	0.27	0.07	11.54	
	A	1	2.30					
	B	2	2.25	2.2-2.3	0.07	0.05	3.14	
	J	162	2.22	1.5-2.9	0.28	0.02	12.45	
	K	40	2.22	1.4-2.9	0.31	0.05	14.14	
	M	28	2.14	1.6-2.1	0.31	0.06	14.51	
	G	5	2.12	1.5-2.7	0.48	0.21	22.47	
	F	12	2.08	1.6-2.7	0.28	0.08	13.40	
	L	11	2.01	1.9-2.3	0.14	0.05	6.80	
	D	24	2.00	1.6-2.6	0.25	0.06	12.44	

Table A-3.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
GWNAS	A	1	3.10					
	E	1	3.00					
	H	3	2.97	2.7- 3.1	0.23	0.13	7.78	
	C	15	2.96	2.5- 3.9	0.33	0.09	11.19	
	B	2	2.85	2.8- 2.9	0.07	0.05	2.48	
	D	24	2.75	2.4- 3.2	0.26	0.06	9.56	
	K	40	2.74	2.0- 3.3	0.38	0.06	13.81	
	J	162	2.71	2.0- 3.6	0.31	0.02	11.26	
	G	5	2.66	2.0- 3.3	0.58	0.26	21.70	
	F	12	2.55	1.9- 3.3	0.38	0.11	14.72	
	M	28	2.46	1.6- 3.3	0.36	0.07	14.51	
L	11	2.35	2.1- 2.8	0.24	0.09	9.98		
PMEXT	H	3	3.43	2.7- 4.0	0.67	0.38	19.39	
	G	5	3.38	2.7- 3.9	0.52	0.23	15.43	
	F	12	3.22	1.9- 4.8	0.79	0.23	24.69	
	M	28	3.15	1.7- 5.0	0.82	0.16	26.89	
	B	2	3.10	2.7- 3.5	0.57	0.40	18.25	
	K	40	3.00	0.4- 5.0	0.77	0.13	26.09	
	D	24	2.95	1.9- 3.6	0.45	0.10	15.56	
	J	162	2.88	1.1- 5.2	0.69	0.06	24.14	
	L	11	2.82	2.3- 3.6	0.45	0.17	15.31	
	C	15	2.70	1.5- 3.2	0.50	0.13	18.47	
	A	1	2.50					
E	1	2.30						
LUDIAST	C	15	16.98	15.2-23.0	1.76	0.45	10.36	
	M	28	16.59	14.6-20.7	1.27	0.25	7.67	
	A	1	16.50					
	B	2	16.50	16.4-16.6	0.14	0.10	0.86	
	K	40	16.40	14.8-18.1	0.87	0.14	5.32	
	L	11	16.38	16.0-17.6	0.58	0.22	3.46	
	J	162	16.37	10.2-20.1	1.12	0.09	6.85	
	D	24	16.20	13.4-18.1	1.33	0.29	8.15	
	G	5	16.20	15.8-16.6	0.32	0.14	1.95	
	F	12	16.01	13.9-17.7	0.97	0.28	6.04	
	H	3	15.67	14.9-16.3	0.71	0.41	4.53	
E	1	15.00						

Table A-3.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
LMXTR	L	11	9.82	8.8-10.2	0.49	0.18	5.04	
	M	28	9.62	9.0-10.4	0.34	0.07	3.55	
	J	162	9.61	5.2-11.6	0.62	0.05	6.46	
	F	12	9.53	8.8-10.1	0.43	0.13	4.55	
	A	1	9.50					
	K	40	9.44	8.8-10.6	0.39	0.06	4.15	
	D	24	9.43	8.8-10.1	0.34	0.07	3.61	
	B	2	9.30	9.30	0	0	0	
	C	15	9.25	8.8- 9.8	0.27	0.07	2.92	
	H	3	9.10	8.8- 9.4	0.30	0.17	3.30	
	G	5	9.06	8.7- 9.6	0.34	0.15	3.71	
E	1	8.60						
WUINC	K	40	2.15	1.9- 2.5	0.15	0.02	7.07	
	J	162	2.14	1.8- 2.6	0.15	0.01	6.87	
	M	28	2.13	1.9- 2.4	0.13	0.03	6.18	
	L	11	2.12	2.1- 2.2	0.05	0.02	2.29	
	B	2	2.10	2.10	0	0	0	
	C	15	2.03	1.9- 2.1	0.07	0.02	3.47	
	F	12	2.03	1.9- 2.2	0.11	0.03	5.62	
	G	5	2.02	2.0- 2.1	0.04	0.02	2.21	
	A	1	2.00					
	H	3	2.00	1.9- 2.1	0.10	0.06	5.00	
	D	24	1.97	1.7- 2.1	0.13	0.03	6.58	
E	1	1.80						
LLDIAS	D	23	10.68	8.0-12.0	1.00	0.21	9.72	
	M	28	10.33	9.0-13.8	0.93	0.19	9.13	
	L	11	10.26	9.7-10.9	0.44	0.17	4.27	
	J	162	10.21	8.1-13.2	0.79	0.06	7.74	
	C	15	10.11	8.5-11.0	0.69	0.18	6.87	
	G	5	10.06	9.7-10.7	0.43	0.19	4.25	
	K	40	10.04	8.8-11.1	0.65	0.11	6.52	
	F	12	9.83	9.0-11.1	0.56	0.16	5.69	
	A	1	9.80					
	B	2	9.80	9.7- 9.9	0.14	0.10	1.44	
	H	3	9.47	9.1- 9.9	0.40	0.23	4.27	
E	1	8.60						

Table A-3.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
LMNDTR	A	1	8.90					
	L	11	8.67	8.4-9.0	0.26	0.10	3.00	
	M	28	8.67	8.0-9.3	0.31	0.06	3.59	
	G	5	8.44	8.0-9.0	0.38	0.02	4.48	
	J	162	8.39	6.1-9.5	0.46	0.04	5.52	
	K	40	8.38	7.6-9.2	0.33	0.05	3.95	
	B	2	8.35	8.3-8.4	0.07	0.05	0.85	
	C	15	8.35	7.8-8.8	0.29	0.08	3.50	
	D	24	8.31	7.6-9.0	0.31	0.07	3.69	
	F	12	8.28	7.2-9.2	0.51	0.15	6.17	
H	3	7.83	7.4-8.1	0.38	0.22	4.83		
E	1	7.80						
WLINC	L	11	2.03	1.9-2.1	0.08	0.03	4.08	
	K	40	2.01	1.7-2.4	0.16	0.03	8.08	
	M	28	2.00	1.8-2.2	0.11	0.02	5.29	
	J	162	1.97	1.7-3.0	0.17	0.01	8.37	
	A	1	1.90					
	B	2	1.85	1.8-1.9	0.07	0.05	3.82	
	C	15	1.85	1.7-2.1	0.10	0.03	5.36	
	F	12	1.84	1.7-2.0	0.09	0.03	4.89	
	G	5	1.84	1.8-1.9	0.38	0.17	4.48	
	E	1	1.80					
	D	24	1.78	1.6-2.0	0.13	0.03	7.15	
	H	3	1.73	1.6-1.8	0.12	0.07	6.66	

Table A-4.--Standard univariate statistics by region for cranial characters in Recent data set for age class 2 females. Included statistics are: sample size (N), mean ( $\bar{X}$ ), extreme values, standard deviation (SD), standard error (SE), and coefficient of variation (CV, as percent). Measurements in millimeters. Maximally non-significant subsets, as determined by Duncan's multiple range tests, indicated in right column; means of samples connected by vertical bar are not significantly different ( $P \leq 0.05$ ).

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
GLS	G	1	48.60					
	C	5	46.86	45.7-49.7	1.70	0.85	3.59	
	M	27	46.62	43.8-51.0	1.83	0.39	3.90	
	D	3	46.50	45.5-48.0	1.32	0.76	2.85	
	K	35	46.19	42.3-49.2	1.61	0.28	3.49	
	F	7	46.17	43.4-50.6	2.66	1.09	5.66	
	J	94	46.08	40.1-55.1	2.20	0.24	4.76	
	A	3	45.60	44.8-46.0	0.69	0.40	1.52	
	L	3	45.60	45.0-46.1	0.56	0.32	1.22	
E	5	45.30	43.0-49.8	3.76	2.17	8.28		
B	1	44.10						
ZYGO	G	1	28.40					
	C	5	28.12	27.6-30.0	1.09	0.50	3.83	
	K	33	28.05	25.7-39.8	2.41	0.43	8.59	
	F	7	27.97	25.7-33.4	2.82	1.15	9.91	
	M	25	27.92	26.3-31.0	1.08	0.24	3.86	
	D	3	27.77	26.7-29.1	1.22	0.71	4.40	
	L	3	27.73	26.7-28.5	0.93	0.54	3.35	
	J	94	27.56	25.1-34.3	1.46	0.16	5.28	
	A	3	27.10	25.7-28.1	1.25	0.72	4.61	
E	5	26.54	24.6-27.5	1.53	0.88	5.94		
B	1	26.10						
WMAST	G	1	25.90					
	F	7	24.90	23.06-26.6	1.17	0.48	4.63	
	K	35	24.75	22.5-26.0	0.78	0.14	3.14	
	J	94	24.66	22.3-28.9	1.11	0.12	4.48	
	M	27	24.64	22.9-27.6	1.14	0.24	4.63	
	C	5	24.52	23.7-25.4	0.79	0.39	3.20	
	D	3	23.96	23.5-24.9	0.81	0.47	3.37	
	A	3	23.90	23.7-24.3	0.35	0.20	1.45	
	L	3	23.73	23.7-23.8	0.06	0.03	0.24	
E	5	23.68	22.7-26.2	1.92	1.11	7.98		
B	1	23.10						

Table A-4.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
DCRAN	M	27	14.62	14.0-15.5	0.40	0.09	2.75	                 
	F	7	14.51	13.8-15.6	0.62	0.25	4.24	
	K	35	14.50	13.4-17.9	0.72	0.13	4.99	
	J	94	14.31	13.4-16.2	0.49	0.05	3.44	
	C	5	14.26	13.9-14.9	0.46	0.23	3.18	
	G	1	14.20					
	A	3	14.00	13.7-14.5	0.44	0.25	3.11	
	E	5	13.98	13.7-14.9	0.62	0.36	3.40	
	D	3	13.97	13.6-14.5	0.47	0.27	3.38	
	L	3	13.87	13.7-14.2	0.29	0.17	2.08	
B	1	13.00						
DROST	J	93	6.83	6.1- 8.2	0.43	0.05	6.20	                 
	B	1	6.80					
	G	1	6.80					
	M	27	6.78	6.1- 7.6	0.41	0.09	6.06	
	C	5	6.78	6.4- 7.3	0.40	0.20	5.86	
	K	35	6.76	6.1- 7.4	0.36	0.06	5.31	
	A	3	6.73	6.6- 6.9	0.15	0.09	2.27	
	D	3	6.67	6.5- 6.9	0.21	0.12	3.12	
	F	7	6.63	6.1- 7.3	0.45	0.19	6.75	
	E	5	6.58	6.2- 7.9	0.74	0.33	11.24	
L	3	6.43	6.1- 6.7	0.31	0.18	4.75		
WROST	M	27	10.22	9.3-11.2	0.43	0.09	4.24	                 
	D	3	10.17	9.8-10.8	0.55	0.32	5.42	
	F	7	9.97	9.5-10.9	0.55	0.23	5.50	
	C	5	9.94	9.3-10.5	0.54	0.27	5.42	
	J	94	9.93	9.0-11.4	0.63	0.07	6.31	
	K	35	9.86	9.3-10.8	1.10	0.19	11.25	
	E	5	9.82	9.4-10.7	0.70	0.40	7.07	
	L	3	9.63	9.0-10.7	0.93	0.54	9.65	
	B	1	9.60					
	G	1	9.60					
A	3	9.50	9.1-10.0	0.46	0.26	4.82		

Table A-4.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
IOC	A	3	7.50	7.3-7.7	0.20	0.12	2.67	
	C	5	7.30	7.2-7.3	0.06	0.03	0.80	
	B	1	7.10					
	M	27	7.05	6.3-7.7	0.39	0.08	5.46	
	D	3	7.03	6.3-7.4	0.64	0.37	9.03	
	G	1	7.00					
	E	5	7.00	6.7-7.3	0.22	0.10	3.19	
	K	35	6.89	6.2-7.7	0.42	0.07	6.07	
	F	7	6.87	6.4-7.6	0.45	0.19	6.56	
	J	94	6.85	6.2-7.7	0.33	0.04	4.76	
L	3	6.73	6.5-6.9	0.21	0.12	3.09		
TEMP	G	1	5.00					
	J	94	4.55	1.6-8.9	1.41	0.16	31.53	
	E	5	4.42	3.1-5.2	1.12	0.64	25.54	
	L	3	4.13	3.5-4.5	0.55	0.32	13.33	
	A	3	4.00	3.3-5.3	1.13	0.65	28.17	
	M	27	3.83	1.6-6.5	1.26	0.27	32.81	
	K	35	3.81	1.9-5.6	0.99	0.18	26.16	
	F	7	3.33	1.7-4.5	1.04	0.42	33.61	
	D	3	2.90	1.8-3.7	0.98	0.57	33.96	
	C	5	2.80	1.3-2.8	0.69	0.35	29.88	
B	1	2.70						
AWINT	G	1	3.50					
	E	5	2.88	2.0-3.3	0.53	0.24	18.28	
	J	94	2.84	0.6-6.3	1.01	0.11	36.31	
	L	3	2.77	2.0-3.8	0.93	0.54	33.58	
	K	35	2.69	0.9-7.5	1.21	0.21	45.21	
	M	27	2.52	0.6-3.9	0.93	0.20	36.44	
	F	7	2.50	0.8-3.3	0.93	0.38	39.13	
	A	3	2.23	2.0-2.5	0.25	0.15	11.27	
	B	1	2.00					
	D	3	1.47	1.0-2.2	0.64	0.37	43.84	
C	5	1.22	0.7-1.4	0.30	0.15	26.54		

Table A-4.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
PWINT	E	5	6.80	6.2-7.5	0.49	0.22	7.28	
	L	3	6.07	5.7-6.5	0.40	0.23	6.66	
	K	35	5.94	3.9-6.9	0.68	0.12	11.59	
	F	7	5.84	5.0-7.4	0.87	0.35	15.29	
	C	5	5.76	4.6-6.9	1.06	0.53	17.88	
	J	93	5.75	3.3-7.5	0.80	0.09	13.97	
	M	27	5.74	1.9-7.7	1.10	0.23	19.29	
	A	3	5.27	5.0-5.6	0.31	0.18	5.80	
	D	3	5.27	4.4-6.5	1.10	0.63	20.83	
	G	1	5.20					
B	1	5.10						
LINT	M	27	5.40	3.7-9.5	1.26	0.27	23.32	
	C	5	5.38	5.0-6.3	0.66	0.33	11.82	
	L	3	5.37	5.2-5.6	0.21	0.12	3.91	
	A	3	5.20	5.1-5.4	0.17	0.10	3.33	
	K	35	5.13	3.7-7.3	0.82	0.15	16.06	
	D	3	4.90	4.6-5.2	0.30	0.17	6.12	
	J	93	4.81	3.3-8.8	0.89	0.10	18.46	
	G	1	4.70					
	E	5	4.60	4.5-4.7	0.10	0.06	2.17	
	B	1	4.50					
F	7	4.50	3.6-5.4	0.58	0.24	12.68		
LWNAS	B	1	2.50					
	A	3	2.40	2.2-2.7	0.27	0.15	11.02	
	K	35	2.33	1.8-2.8	0.27	0.05	11.72	
	J	93	2.29	1.6-2.2	0.62	0.07	6.80	
	M	27	2.26	1.8-2.7	0.24	0.05	11.05	
	G	1	2.20					
	C	5	2.20	1.9-2.6	0.33	0.17	15.43	
	E	5	2.20	2.1-2.3	0.12	0.07	5.17	
	L	3	2.17	1.9-2.4	0.25	0.15	11.62	
	D	3	2.07	1.8-2.3	0.25	0.15	12.18	
F	7	2.00	1.7-2.2	0.19	0.08	9.79		

Table A-4.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
GWNAS	B	1	3.30					
	C	5	3.04	2.9- 3.1	0.12	0.06	3.85	
	A	3	3.00	2.6- 3.3	0.36	0.21	12.02	
	G	1	2.90					
	J	94	2.86	2.0- 3.6	0.62	0.07	11.50	
	D	3	2.77	2.7- 2.9	0.12	0.07	4.17	
	K	35	2.73	1.9- 3.3	0.33	0.06	12.09	
	E	5	2.64	2.6- 2.7	0.06	0.03	2.17	
	L	3	2.63	2.6- 2.7	0.06	0.03	2.19	
	M	27	2.59	1.9- 3.5	0.36	0.08	14.33	
F	7	2.59	2.1- 3.2	0.46	0.18	18.05		
PMEXT	F	7	3.76	3.2- 4.7	0.49	0.20	12.25	
	E	5	3.52	2.8- 4.4	0.61	0.27	17.44	
	G	1	3.50					
	D	3	3.27	2.9- 3.9	0.55	0.32	16.86	
	M	27	3.25	1.8- 4.7	0.88	0.19	26.53	
	K	35	3.15	1.7- 4.3	0.59	0.11	18.90	
	L	3	3.10	2.6- 4.0	0.78	0.45	25.19	
	J	94	3.01	1.2- 5.4	0.64	0.07	21.36	
	A	3	2.97	2.9- 3.1	0.12	0.07	3.89	
	C	5	2.88	2.2- 3.1	0.43	0.21	15.12	
B	1	2.80						
LUDIAST	G	1	19.50					
	D	3	18.53	17.7-19.9	1.19	0.69	6.44	
	C	5	18.38	17.7-20.2	1.06	0.53	5.61	
	J	94	17.49	15.3-23.2	1.21	0.13	6.90	
	A	3	17.47	17.0-17.9	0.45	0.26	2.58	
	F	7	17.40	15.2-20.7	1.96	0.80	10.96	
	K	35	17.39	15.6-19.4	1.01	0.18	5.82	
	M	27	17.31	12.9-20.5	1.37	0.29	7.88	
	L	3	16.77	16.5-17.0	0.25	0.15	1.50	
	E	5	16.54	15.0-20.4	2.26	1.01	13.67	
B	1	16.20						

Table A-4.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
LMXTR	M	27	10.01	9.0-10.9	0.45	0.10	4.44	
	E	5	9.90	9.6-10.1	0.21	0.09	2.14	
	J	94	9.85	8.8-11.6	0.47	0.05	4.77	
	L	3	9.83	9.6-10.2	0.32	0.19	3.27	
	F	7	9.69	9.3-10.0	0.27	0.11	2.77	
	K	35	9.67	8.8-10.9	0.54	0.09	5.53	
	B	1	9.60					
	G	1	9.60					
	C	5	9.48	9.1-10.0	0.42	0.21	4.40	
	D	3	9.33	9.0- 9.5	0.29	0.17	3.09	
A	3	9.30	9.0- 9.6	0.30	0.17	3.23		
WUINC	M	27	2.28	2.0- 2.6	0.17	0.04	7.35	
	K	35	2.24	1.9- 2.5	0.13	0.02	5.97	
	J	94	2.18	1.8- 2.6	0.16	0.02	7.18	
	F	7	2.17	1.9- 2.5	0.24	0.10	10.76	
	C	5	2.16	2.0- 2.4	0.17	0.09	7.85	
	D	3	2.13	2.0- 2.3	0.15	0.09	7.16	
	G	1	2.10					
	L	3	2.10	2.1	0	0	0	
	E	5	2.08	1.7- 2.5	0.29	0.13	14.18	
	A	3	2.07	1.9- 2.2	0.15	0.09	7.39	
B	1	2.00						
LLDIAS	G	1	13.20					
	D	3	12.13	11.5-13.0	0.78	0.45	6.40	
	C	5	11.46	11.1-12.9	0.84	0.42	7.20	
	A	3	10.97	10.9-11.1	0.12	0.07	1.05	
	J	94	10.96	7.9-14.5	0.94	0.10	8.58	
	M	27	10.77	9.6-12.4	0.78	0.17	7.38	
	K	35	10.75	9.4-12.3	0.81	0.14	7.58	
	F	7	10.66	9.4-12.2	1.03	0.42	9.43	
	L	3	10.63	10.5-10.8	0.15	0.09	1.44	
	E	5	10.60	9.2-13.0	1.54	0.69	14.57	
B	1	10.10						

Table A-4.--Continued.

Character	Region	N	$\bar{X}$	Extremes	SD	SE	CV	Subsets
LMNDTR	M	27	9.10	8.7-10.2	0.38	0.08	4.11	
	E	5	8.74	8.5-8.9	0.23	0.13	2.68	
	A	3	8.73	8.6-8.8	0.12	0.07	1.32	
	D	3	8.70	8.4-8.9	0.26	0.15	3.04	
	K	35	8.69	8.0-9.4	0.34	0.06	3.93	
	J	94	8.66	7.7-9.9	0.42	0.05	4.87	
	C	5	8.64	8.5-8.8	0.14	0.07	1.63	
	L	3	8.63	8.4-8.8	0.21	0.12	2.41	
	F	7	8.59	8.0-8.8	0.31	0.13	3.63	
	G	1	8.50					
B	1	8.40						
WLINC	M	27	2.10	1.9-2.3	0.13	0.03	6.05	
	K	35	2.04	1.8-2.3	0.12	0.02	6.08	
	L	3	2.03	2.0-2.1	0.06	0.03	2.84	
	J	94	2.02	1.6-2.6	0.17	0.02	8.32	
	F	7	1.99	1.8-2.3	0.21	0.09	10.49	
	D	3	1.93	1.9-2.0	0.06	0.03	2.99	
	C	5	1.92	1.7-2.2	0.24	0.12	12.89	
	G	1	1.90					
	A	3	1.87	1.8-1.9	0.06	0.03	3.09	
	E	5	1.84	1.5-2.2	0.25	0.11	13.64	
B	1	1.80						

APPENDIX B  
RECENT SPECIMENS EXAMINED

The 1,123 Recent specimens of Geomys pinetis examined in this study are listed below by natural region. Parenthetically enclosed following each locality are indicated the number of specimens and the museum in which they are deposited for each locality. The code to collection acronyms is 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, Museum of Natural History (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 (UM); 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, USNM); 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). Gadsden 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 SRD 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, USNM); 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, UM; 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, UM); 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 National 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); Winterpark (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); Mahaw (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, UM); 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.: Belleaire (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 UM); Safety Harbor (2, UF); St. Petersburg (4, MCZ; 1, USNM); Tarpon Springs (4, AMNH; 1, UM; 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, UM); Welaka (7, UF); Welaka, Univ. Conservation Reserve (2, UF). St. Johns Co.: 13 mi N Bunnell (2, AMNH); 14 mi N Bunnell (1, AMNH); Cartersville (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 Smyrna (1, DMNH); Pierson city limits, US 17 (4, UGA); S of Seville, US 17 (1, UGA).

APPENDIX C  
FOSSIL MATERIAL EXAMINED AND ANALYZED

All specimens listed below are left or right mandibles with or without cheekteeth; essentially all specimens contain at least a portion of the lower incisor. The list is presented in an alphabetical scheme arranged in a chronological framework. All material is housed in the Vertebrate Paleontology Collection of the Florida State Museum, University of Florida (UF) unless otherwise noted. USNM refers to material borrowed from the United States National Museum. The total number of dentary specimens examined for a site is indicated after the site name. Oftentimes, one catalogue number identifies a series of specimens; much of the material is uncatalogued.

IRVINGTONIAN--Coleman II (16 specimens): 11660-11664, 11666-11675, 15001. Inglis IA (231 specimens): uncatalogued.

RANCHOLABREAN (Sangamonian)--Arredondo IA, IB, IIA, IIB (28 specimens): 12632, 12633, 12666, 12667; others uncatalogued. Haile VIIIA, XIB, XIII A, XIII B, XIV, XX (36 specimens): 3271, 3272, 12754, 13041, 13074, 13083, others uncatalogued. Kendrick IA (4 specimens): 2658. Reddick IA, IIC (68 specimens): 2534, others uncatalogued.

RANCHOLABREAN (Wisconsin)--Haile XIV (3 specimens): 13078, 16142, 16144. Ichetucknee River (17 specimens): 1619, 13940, V-4886, others uncatalogued. Melbourne 2 (4 specimens):

2 uncatalogued (UF), 91826 (USNM), 1 uncatalogued (USNM). Seminole Field (4 specimens): V-4020, V-4020A, 2 uncatalogued. Vero 2 (1 specimen): W 545. Waccasassa River (3 specimens): 16349, 1 uncatalogued.

RANCHOLABREAN (Holocene)--Devil's Den (11 specimens): 12885, 12888-12890, 13431, 16792.

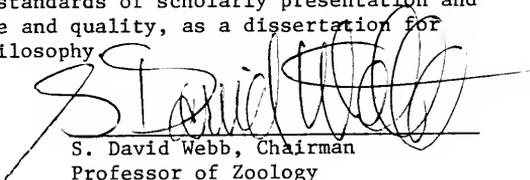
RANCHOLABREAN (stage uncertain)--Eichelberger Cave (1 specimen): 2504. Maximo Moorings (3 specimens): uncatalogued. St. Petersburg (5 specimens): uncatalogued. Wade's Cave (1 specimen): 10320.

RECENT (Holocene)--Vero 3 (1 specimen): W 444.

#### BIOGRAPHICAL SKETCH

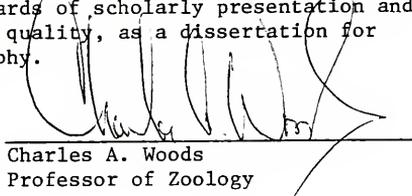
Kenneth T. Wilkins was born to Roy Allen and Gwendolyn Browne Wilkins on 28 August 1953 in Baton Rouge, Louisiana. He and Christine Nasie were married on 17 November 1979 in Gainesville, Florida. He took the Bachelor of Science degree in general biology in December 1974 at the University of Texas at Arlington where he was elected a member of Alphi Chi National Honor Scholastic Society. He earned the Master of Science degree in wildlife and fisheries sciences at Texas A&M University in August 1977 where he was elected to the honor societies Phi Kappa Phi and Phi Sigma. He has worked towards the Doctor of Philosophy degree in zoology since September 1977 at the University of Florida where he was elected member of Sigma Xi, the scientific research society. His permanent mailing address is 806 Red Oak Lane, Arlington, Texas 76012.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy



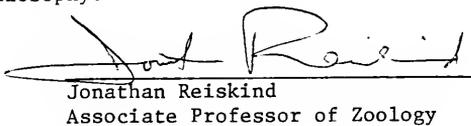
S. David Webb, Chairman  
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



Charles A. Woods  
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



Jonathan Reiskind  
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
\_\_\_\_\_  
Stephen R. Humphrey  
Associate Professor of Forest  
Resources and Conservation

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

May 1982

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Dean for Graduate Studies and  
Research

UNIVERSITY OF FLORIDA



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