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SYSTEMATICS OF SCALOPUS AQUATICUS (LINNAEUS) IN TEXAS AND ADJACENT STATES

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Moles of the family Talpidae are represented in Texas and surrounding states (Oklahoma, Arkansas, Kansas, Missouri, and Louisiana) by the species *Scalopus aquaticus* (Hall and Kelson, 1959). Two additional species, *S. montanus* and *S. inflatus*, are known from northern México on the basis of single specimens collected in Coahuila and Tamaulipas, respectively.

All moles of the genus *Scalopus* are highly specialized for fossorial life (Slonaker, 1920; Campbell, 1939; Reed, 1954; Lowery, 1974), and their eyes are useless except for light detection (Slonaker, 1902). Hall and Kelson (1959) estimated that 99 per cent of a mole's life is spent underground, a habit which has made acquisition of study specimens, especially live ones, difficult.

True (1896), Jackson (1915), and Davis (1942) made considerable use of morphological characters to separate subspecies, although no statistical analyses of geographic variation were made. Hall and Kelson (1952) and Eadie (1954) found color to be of little taxonomic value. The uncertain systematic status in which Jackson (1915) left the moles of Texas was addressed by Davis (1942), who pointed out that the number of specimens available was insufficient for a comprehensive taxonomic review.

Taxonomic History

The first mole to be described from Texas was *Scalops argentatus texanus* from Presidio County (Allen, 1891). After examination of a series of moles from Rockport, Aransas County, Texas, Allen (1893) elevated *Scalops argentatus texanus* to specific status. True (1896) reduced *Scalops argentatus* to subspecific rank in the species *Scalops aquaticus*, and, believing Allen's *Scalops argentatus texanus* to have come from Rockport, Aransas County, Texas, not Presidio County, assigned *texanus* to *Scalops aquaticus* as a subspecies. Palmer (1904) pointed out that *Scalopus* É. Geoffroy St.-Hilaire had priority over *Scalops* Cuvier, a *nomen nudum.* Jackson (1915) recognized two additional subspecies in Texas: *Scalopus a. pulcher* Jackson, 1914, from eastern Texas, and *S. a. intermedius* Elliot, 1899, from northern Texas.

To this list, Davis (1942) added two of his own, *S. a. cryptus* and *S. a. nanus.* According to Davis (1942), *pulcher* occupies the extreme eastern and northeastern parts of Texas from Denton County southeastward to Hardin County; *cryptus* occurs generally in the drainage basins of the Brazos and Colorado rivers; *nanus* is restricted to a small area between the ranges of *cryptus* and *pulcher* in Leon, Trinity, and Walker counties; *intermedius* occurs from the northern part of the Texas Panhandle southward to Mason County on the Edward's Plateau; and *texanus* ranges from Brownsville north to San Antonio, thence southeastward to Austwell, Refugio County.

According to Baker (1951), Presidio County is the type locality for *Scalopus aquaticus texanus,* not Aransas County, as True (1896) believed; the name *Scalopus aquaticus alleni* Baker, 1951, was applied to populations from Aransas County and southern Texas.

The name *Scalopus aquaticus aereus* (Bangs, 1896) was based on a single specimen with unusual coloration from Stilwell, Adair County, Oklahoma. Jackson (1915) accorded specific rank to *aereus,* but Hall and Kelson (1952), after examination of the holotype, found no difference other than color between *S. aereus* and specimens of *S. aquaticus pulcher* from the same locality. Thus, they referred all individuals formerly known as *S. a. pulcher* and *S. aereus* to *S. aquaticus aereus.*

METHODS AND MATERIALS

Museum study specimens of the eastern mole and live individuals from Texas were examined. In order to understand better the nature of geographic variation in Texas populations of *S. aquaticus,* it was necessary to examine material from adjacent areas in the United States and México. Specimens examined are listed in the accounts of subspecies, the number in parentheses being the total for that taxon. States and counties are arranged alphabetically; the number of specimens from each locality is given, and the institutions housing these specimens are identified by the following abbreviations (after Choate and Genoways, 1975).

AMNH—American Museum of Natural History, New York City
ANSP—Academy of Natural Sciences of Philadelphia, Philadelphia
DMNHT—Dallas Museum of Natural History, Dallas, Texas
FMNH—Field Museum of Natural History, Chicago
KU—Museum of Natural History, University of Kansas, Lawrence
LSUMZ—Museum of Zoology, Louisiana State University, Baton Rouge
MSUMC—Department of Biology, Murray State University, Murray, Kentucky
MVZ—Museum of Vertebrate Zoology, University of California, Berkeley
MWU—Department of Biology, Midwestern University, Wichita Falls, Texas
OSU—Museum of Natural and Cultural History, Oklahoma State University, Stillwater
SFA—Department of Biology, Stephen F. Austin State University, Nacogdoches, Texas
SRSU—Department of Biology, Sul Ross State University, Alpine, Texas
TAIU—Biology Department, Texas A&I University, Kingsville
TCWC—Texas Cooperative Wildlife Collection, Texas A&M University, College Station
TNHC—Texas Natural History Collection, Texas Memorial Museum, The University of Texas, Austin.
TTU—The Museum, Texas Tech University, Lubbock
UIMNH—Museum of Natural History, University of Illinois, Urbana
UMMZ—Museum of Zoology, The University of Michigan, Ann Arbor
USLBM—Department of Biology, University of Southwestern Louisiana, Lafayette
USNM—National Museum of Natural History, Washington, D.C.

All cranial measurements (as detailed in Fig. 1) as well as width and length of forepaws were taken to the nearest 0.1 millimeter with dial calipers. Total, tail, and hind foot lengths were taken directly from the museum specimen tags.

Specimens were collected by means of Victor harpoon and choker-loop traps from many areas in Texas where specimens were not already on deposit in museums. They were prepared as standard skin and skull study specimens and deposited in the Texas Cooperative Wildlife Collection.

A modification of a trap described by Moore (1940) was used to obtain live specimens. The basic spring and trigger mechanism was supplied by a Victor harpoon variety kill trap equipped with a steel plate with spikes at one-half inch intervals on both ends. The plate was a piece of 1/8-inch thick steel, 16 1/2-inches by 4 inches. The spikes were made by cutting 3/16-inch electric weldrods into 5-inch sections and threading one end. This was then mounted on top of a rectangular, open-ended, sheet-metal box, 4-inches square and 18-inches long. Holes were cut on top of the box to allow entrance of the trigger and weldrods. The box was then filled with dirt and placed in a straight section of a mole's surface runway. Problems with animals missing the trap were avoided by packing dirt firmly on all sides and

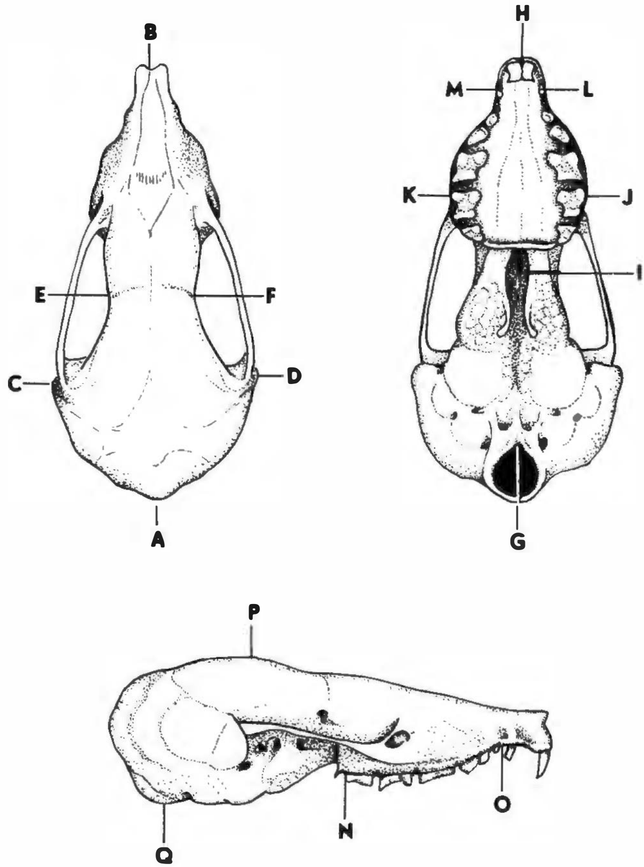

FIG. 1.—Dorsal, ventral, and lateral view of skull of *Scalopus aquaticus cryptus* TCWC 2853, showing points between which cranial measurements were taken: greatest length of skull, A-B; mastoidal breadth, C-D; inter-orbital breadth (least), E-F; basilar length (from anterior edge of alveolus of incisor), G-H; length of palate, I-H; width across M2-M2, J-K; width across canines, L-M; length of maxillary toothrow (alveolar length), N-O; depth of skull, P-Q.

leaving it loose in the trap. Dirt also was packed directly under the trigger mechanism to insure proper action.

Individual, age, and secondary sexual variation were analyzed with the statistical analysis system (SAS) designed and implemented by Barr and Goodnight (Service, 1972). All specimens were assigned to one of three age classes (juvenile, subadult, and adult). Means were calculated for each character and a one-way analysis of variance was used to test for differences among age classes and between sexes.

Coefficients of variation (CV) were calculated to determine the extent of variability for each character.

Geographic variation was analyzed by means of univariate (mean, standard deviation, and standard error) and multivariate statistics. Multivariate analysis consisted of clustering and ordination techniques. Cluster analysis utilized the UPGMA option (arithmetic averages used with unweighted pair-group method) on correlation and distance matrices generated from the NT-SYS programs developed by Rohlf and Kishpaugh (1972). Only distance phenograms were illustrated from the cluster analysis because they yielded a higher cophenetic correlation value than did correlation phenograms.

To assess the degree of divergence among samples, a multivariate analysis of variance (MANOVA) and canonical analysis program in SAS were used. Canonical analysis of the data aims at providing weighted combinations of the measurements, which maximize the distinction between groups. This program extracts characteristic roots and vectors and computes mean canonical variates for each locality. New orthogonal axes, termed canonical variates, were constructed to extract the next best combination of characters and emphasized those characters with the least within-sample and the greatest between-sample variation. This provided the next best combination of characters to discriminate among samples. Each eigenvalue and its corresponding canonical variate (characteristic root) represented an identifiable fraction of the total variation. Sample means and individuals were plotted on those canonical variates that accounted for the greater fractions of total variation. The relative importance of each original variable to a particular canonical variate was computed by multiplying the vector variable coefficient by the median value of the dependent variable, summing all variable values for a particular vector, and then computing the per cent relative importance of each variable per vector.

NONGEOGRAPHIC VARIATION

Three types of nongeographic variation (secondary sexual, age, and individual) are discussed in this section. To our knowledge, information of this type is not available in the literature for *Scalopus aquaticus*.

Secondary sexual variation.—Analysis of variance was used to test each of 14 external and cranial characters for significant differences between males and females in samples from Conroe and Rockport, Texas (Table 1). Significant differences between sexes were found for all but two measurements (tail length, interorbital breadth) in the

TABLE 1.—*Results of analysis of variance between males and females for two samples of* Scalopus aquaticus. *A single asterisk indicates a probability level of 0.10; a double asterisk, 0.05; a triple asterisk, 0.01.*

	Conroe						Rockport					
	Males		*Females*				*Males*		*Females*			
Variate	*N*	Mean	*N*	Mean	CV	*F*	*N*	Mean	*N*	Mean	CV	*F*
Total length	19	151.8	12	140.2	3.9	30.7***	8	140.0	10	131.0	4.1	11.8***
Tail length	19	24.4	12	23.2	12.4	1.1	8	24.2	10	21.6	6.9	12.5***
Hind foot length	19	19.5	12	18.5	5.5	7.1***	10	17.6	10	16.3	5.9	7.8***
Width of forepaw	19	16.3	12	14.9	7.8	9.8***	10	14.8	12	13.4	6.1	13.3***
Length of forepaw	19	21.1	12	19.6	4.1	25.8***	10	18.4	12	17.9	5.0	1.2
Greatest length of skull	19	32.8	12	31.7	2.1	20.2***	10	31.0	12	30.3	2.1	6.3**
Basilar length	19	27.3	12	26.3	2.4	16.3***	10	25.9	12	24.8	2.3	17.3***
Mastoidal breath	19	17.3	12	16.8	2.3	10.3***	10	16.6	12	16.2	1.7	10.7***
Interorbital breadth	19	7.1	12	7.0	3.4	0.8	10	6.8	12	6.6	3.3	2.0
Length of maxillary toothrow	19	10.1	12	9.7	2.7	16.5***	10	10.2	12	9.8	3.2	9.0***
Length of palate	19	14.2	12	13.7	2.8	11.7***	10	14.1	12	13.5	3.9	6.2**
Width across M2-M2	19	8.9	12	8.6	3.5	11.3***	10	9.6	12	8.7	4.1	3.9*
Width across canines	19	3.8	12	3.7	3.7	3.6*	10	3.8	12	3.6	6.8	3.9*
Depth of skull	19	9.8	12	9.4	2.0	22.4***	10	9.2	12	9.2	4.1	0.1

TABLE 2.—*Results of analysis of variance between age classes I and II in Montgomery County sample. Values under box headings Age I and Age II are means. A significant difference at the 0.05 level is indicated by an asterisk.*

	Males				Females			
Variate	Age I (N=7)	Age II (N=12)	CV	F	Age I (N=5)	Age II (N=7)	CV	F
Total length	155.6	149.7	3.4	5.7*	140.6	139.9	4.1	0.05
Length of hind foot	20.1	19.2	5.1	4.3*	18.4	18.6	5.6	0.08
Width of forepaw	17.0	15.9	8.6	2.9	14.6	15.1	4.2	1.90
Length of forepaw	21.6	20.9	3.9	3.4	19.6	19.5	4.1	0.06
Greatest length of skull	33.3	32.5	1.9	7.2*	31.8	31.6	1.8	0.30
Basilar length	27.7	27.1	2.6	2.8	26.6	26.1	1.7	2.30
Mastoidal breadth	17.6	17.1	2.4	5.2*	16.9	16.7	1.4	1.00
Interorbital breadth	7.2	7.0	3.3	5.6*	7.0	7.0	3.0	0.01
Length of maxillary toothrow	10.2	10.1	2.4	2.3	9.8	9.6	3.1	0.90
Length of palate	14.5	14.1	2.8	3.7	13.9	13.6	2.5	1.30
Width across M2-M2	9.0	8.9	3.9	0.0	8.9	8.6	2.9	0.05
Width across canines	3.8	3.7	3.5	3.3	4.0	3.6	3.8	0.20
Depth of skull	9.8	9.7	2.1	0.1	9.4	9.5	2.0	0.50

Conroe sample, and for all but three measurements (length of forepaw, interorbital breadth, depth of skull) in the sample from Rockport. Males averaged larger than females in all measurements.

The sexual differences noted were those of size. Because the multivariate portion of this study deals with measurements of size, the sexes were considered separately in all subsequent analyses.

Age variation.—All specimens were assigned originally to one of three age classes defined as follows:

Class I (adults). External roots of last two upper molars and all upper premolars not exposed through maxillary bones; upper molars and premolars showing evidence of wear.

Class II (subadults). External roots of last two upper molars frequently exposed through maxillary bones; little, if any, evidence of wear on upper molars and premolars.

Class III (juveniles). External roots of all upper molars, and frequently the third premolars, exposed through maxillary bones; upper molars and premolars showing no evidence of wear. Inasmuch as few juvenile specimens were available for study, they were excluded from further analyses.

Analysis of variance was used to test each of 14 external and cranial measurements for significant differences between age classes I and II from the Montgomery County sample (Table 2). Due to pronounced secondary sexual variation, sexes were considered separately.

Significant differences ($P \leq 0.05$) between age classes I and II were not noted for any measurement in females. However, males exhibited significant differences between classes in total length, hind foot length, greatest length of skull, mastoidal breadth, and interorbital breadth.

There are several possible explanations for the lack of significant size differences between adult and subadult female moles. First, the sample of females was small and sampling error could account for the failure to discriminate between the two age classes. Second, and probably of greater importance, females appear to develop sexually at a slower rate than do males. Conaway (1959) found no indication that females breed during the year they are born whereas males supposedly do. Likewise, development of the maxillary bones appears to be slower in females than in males. Most females captured in Texas during November and December still had molar roots exposed on several teeth whereas males taken during the same time period from the same localities had few exposed. Thus, the probability of incorrectly classifying a female as a subadult during this period is quite high when in fact the specimen is mature in terms of size.

Individual variation.—As expected, cranial measurements were less variable than were external features (Table 1). This is due, in part, to the greater difficulty in accurately taking external measurements. Although external measurements showed greater variation than cranial measurements, only tail length exhibited a CV of 10 or greater. Simpson (1953) and Long (1968) observed that CV's of morphological structures for most organisms usually range from 2 to 8. Because the CV for tail length was 12.4, this character was considered too variable to be included in further univariate analyses.

In most characters, males tended to be more variable than females. The average CV for males, considering all measurements, was 4.45; that for females, 3.53. As expected, the amount of difference was less when only cranial measurements were considered; males exhibited an average CV of 2.88; females, 2.44. These data support Long's (1969) finding that variation is generally low in insectivorous mammals.

Of the cranial measurements, depth of skull in the Conroe sample and mastoidal breadth in the Rockport sample, were the least variable. With the exception of width across the canines and depth of skull in the Rockport sample, all cranial measurements had CV's less than 4.0. The CV's for the external measurements ranged from a low of 3.88 for total length to a high of 12.42 for tail length.

Inasmuch as no quantitative measure of pelage color was used, no attempt was made to analyze statistically individual color variation. In examining samples of moles from Texas and adjacent states, however, we observed considerable variation in color within populations. Because much has been written concerning pelage coloration in *Scalopus* (Allen, 1891, 1893; Bangs, 1896; True, 1896; Scheffer, 1911; Jackson, 1914, 1915; Davis, 1942; Eadie, 1954; Stallcup, 1956) only a brief discussion is necessary here.

The occurrence of brown, yellow, orange, and olivaceous tints on the snout, chin, wrist, and other parts of the body of moles has led many authors to characterize, partially or completely, various subspecific and specific forms using these chromatic variations. Both Jackson (1915) and Eadie (1954) found such conditions common, not only in *Scalopus* but in *Parascalops* and *Condylura* as well. We found similar variations occurring throughout populations of moles in Texas and adjacent states. With the exception of occasional white spots and lines, which Jackson (1915) referred to as "partial albinism," these occurrences appear to be due to the activity of skin glands and not to genetic variations in pigmentation. These variations were especially noticeable during the breeding season and more pronounced in males than in females. Eadie (1954) regarded chromatic variations as temporary stains produced by suboriferous and perineal glands and possibly correlated with age and breeding condition. These observations led us to regard color to be of little value in assessing patterns of geographic variation in moles.

Geographic Variation

Analysis of geographic variation was based on examination of 804 specimens of *Scalopus aquaticus* from approximately 200 localities throughout Texas, Louisiana, Arkansas, Oklahoma, Kansas, and southwestern Missouri. The holotypes of *S. montanus* (from Coahuila, Mêxico) and *S. inflatus* (from Tamaulipas, Mêxico) also were examined. Only adults were included in the analysis, and the sexes were considered separately; however, only males were used in the final analysis of geographic variation because they were available in much larger numbers. Only adults are listed as specimens examined. Most specimens examined were pooled geographically into 45 grouped localities (Fig. 2) as follows (localities are taken to the nearest town of reference): *area 1*—KANSAS (Kingsdown, Meade, Liberal); *area 2*—KANSAS (Stafford, Little Salt Marsh, Atena, Sharon); *area 4*—MISSOURI (Columbia, Washburn, Camp Crowder) and KANSAS (Manhattan); *area 5*—OKLAHOMA (Alva, Fort Supply, Canton, Canton Reservoir) and TEXAS (Lipscomb, Stinnett, Canadian, Mobeetie); *area 6*—OKLAHOMA (Red Rock); *area 7*—OKLAHOMA (Pawnee, Stillwater, Guthrie); *area 8*—OKLAHOMA (Chandler, Norman, Mid-

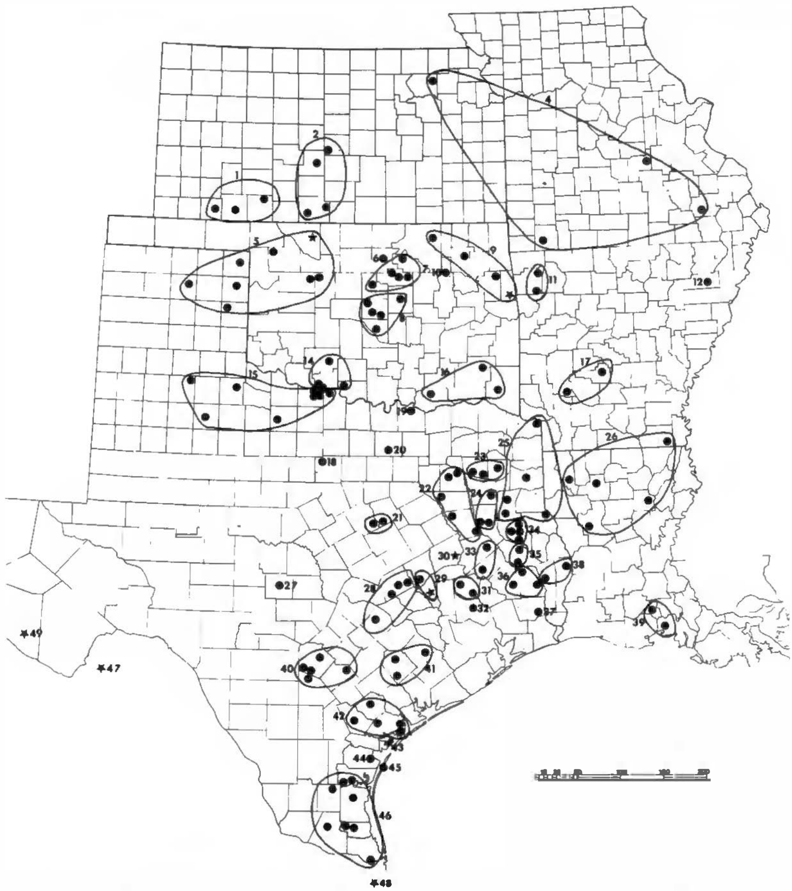

FIG. 2.—Geographic localities of samples included in the 45 areas of grouped samples of *Scalopus aquaticus*. See text for localities included in each area.

west City, Oklahoma City, Edmond); *area 9*—OKLAHOMA (Pawhuska, Garnett, Lowery, Stilwell); *area 10*—OKLAHOMA (Tulsa); *area 11*—ARKANSAS (Winslow, Fayetteville); *area 12*—ARKANSAS (Lake City); *area 14*—OKLAHOMA (Mt. Scott, Byers, Burkburnett, E Hwy. 281 on Red River); *area 15*—TEXAS (Burkburnett, Perkins Reservation, Paducah, Quitaque, Dickens, Seymour, Bomarton, Petrolia, Thornberry, Charlie); *area 16*—OKLAHOMA (Nashoba, Glover, Blue); *area 17*—ARKANSAS (Malvern, Delight); *area 18*—TEXAS (Possum Kingdom Lake); *area 19*—TEXAS (Sherman); *area 20*—TEXAS (Lewisville); *area 21*—TEXAS (Waco, 5 mi. NW jct. Hwy. 933 and Hwy. 2114, Laguna Park); *area 22*—TEXAS (Grand Saline, Canton, Cedar Creek Lake, Athens, Palestine, Slown); *area 23*—TEXAS

(Gilmer, Hawkins, Winnsboro, Mineola); *area 24*—TEXAS (Tyler, Rusk, Maydelle); *area 25*—TEXAS (Henderson, Hallsville, Joaquin, Texarkana); *area 26*—LOUISIANA (Bossier City, Bienville, Provencal, Columbia) and ARKANSAS (Wilmot); *area 27*—TEXAS (Mason); *area 28*—TEXAS (Gause, Milano, Rockdale, Bastrop); *area 29*—TEXAS (Hearne, Bryan, College Station); *area 30*—TEXAS (Centerville); *area 31*—TEXAS (Huntsville); *area 32*—TEXAS (Conroe); *area 33*—TEXAS (Ratcliff, Sebastopol); *area 34*—TEXAS (Nacogdoches); *area 35*—TEXAS (Huntington City, Lufkin, Dibol); *area 36*—TEXAS (Chester, Woodville, Spurger); *area 37*—TEXAS (Sour Lake); *area 38*—TEXAS (Jasper, Burkeville); *area 39*—LOUISIANA (Lafayette, Avery Island); *area 40*—TEXAS (Nixon, Lythe, Somerset, San Antonio); *area 41*—TEXAS (Eagle Lake, Victoria, Hallettsville); *area 42*—TEXAS (Goliad, Beeville, Woodsboro, Austwell, Aransas Wildlife Refuge); *area 43*—TEXAS (Rockport); *area 44*—TEXAS (Corpus Christi, Flour Bluff); *area 45*—TEXAS (Padre Island); *area 46*—TEXAS (Riviera, Falfurrias, Sarita, Raymondville, Linn, Brownsville); *area 47*—COAHUILA (Piedra Blanca); *area 48*—TAMAULIPAS (45 mi. S Brownsville); *area 49*—TEXAS (Presidio County).

Univariate analysis.—Standard statistics (mean, standard deviation, and standard error) were calculated for all external measurements used in this study. External measurements exhibited north-south and west-east clinal patterns of geographic variation. In general, moles were largest in the northern part of the study area, gradually decreased in size to the south, and reached a minimum size in southern Texas (Table 3). This pattern was well illustrated by mean total length for selected samples from south-central Kansas to southern Texas (areas 2, 14, 29, 43, and 46). Similar patterns of north-south clinal variation also occurred in length of tail and hind foot.

With the exception of areas 47 and 27, moles increased in size from central Texas to eastern Louisiana (areas 28, 36, 38, 26). Mean total lengths for samples from northern Coahuila, México, and Mason, Texas (areas 47 and 27) were larger than samples from east-central Texas. Although somewhat more erratic, the same pattern of variation existed for both length of tail and hind foot.

West-east clinal variation also existed from the Texas Panhandle to central Arkansas with moles being smaller in the west and gradually becoming larger to the east. Mean total length for selected samples from the Texas Panhandle east to central Arkansas exemplified this type of variation. Tail length also showed a west-east decrease.

The nine cranial measurements analyzed are discussed below in three groups: measurements of skull length (greatest length of skull,

TABLE 3.—*Geographic variation in mean external and cranial characters among selected samples of* Scalopus aquaticus, Scalopus montanus (*area 47*), *and* Scalopus inflatus (*area 48*). *Minimum and maximum values are given in parentheses.*

Area number	N	Mean	Mean	Mean
		Total length	*Tail length*	*Hind foot length*
2	4	160.2 (157-164)	28.0 (25-31)	22.5 (21-25)
5	5	154.2 (165-148)	24.2 (21-27)	19.8 (17-22)
8	6	158.5 (151-179)	27.7 (21-31)	19.2 (19-20)
14	6	156.8 (144-172)	31.7 (21-39)	19.8 (18-21)
17	8	159.2 (147-170)	28.6 (24-40)	21.9 (20-23)
26	6	165.2 (138-180)	25.0 (21-27)	21.0 (17-23)
27	1	151.0	22.0	19.0
28	11	144.4 (126-155)	22.4 (18-25)	18.2 (16-19)
29	14	146.9 (129-168)	23.6 (19-31)	18.4 (17-20)
36	4	154.0 (147-160)	25.2 (24-26)	20.0 (19-21)
38	6	164.0 (155-172)	26.7 (23-31)	20.0 (18-22)
43	8	140.0 (132-152)	24.2 (22-26)	17.6 (16-19)
46	6	137.0 (124-145)	24.2 (19-28)	17.9 (17-19)
47	1	150.0	27.0	20.0
		Greatest length of skull	*Basilar length*	*Mastoidal breadth*
4	5	37.4 (37.2-37.6)	32.3 (32.0-32.8)	19.2 (18.8-19.5)
5	5	34.3 (33.0-35.2)	29.0 (28.4-29.8)	18.1 (17.4-18.6)
7	10	34.6 (33.3-36.7)	29.0 (27.4-31.1)	18.1 (17.3-19.0)
8	6	34.5 (32.9-35.4)	29.1 (27.8-30.2)	17.8 (17.4-18.3)
14	6	34.8 (34.1-35.6)	29.3 (28.4-30.6)	18.1 (17.7-18.7)
17	10	35.8 (34.5-37.4)	30.5 (29.5-31.8)	18.3 (17.7-19.3)
26	6	35.7 (34.6-36.8)	30.4 (29.4-31.2)	18.4 (17.8-18.8)
27	3	32.1 (31.3-32.9)	27.2 (26.4-27.8)	17.0 (16.4-17.3)
28	11	32.3 (30.4-33.3)	26.7 (25.2-28.0)	17.1 (16.6-17.8)
29	14	33.1 (30.7-35.4)	27.7 (25.4-30.0)	17.2 (16.2-18.4)
32	21	32.8 (31.0-33.8)	27.3 (25.6-29.0)	17.3 (16.2-18.0)
36	4	33.7 (32.5-34.4)	28.1 (27.6-28.3)	17.9 (17.2-18.6)
38	6	34.8 (33.8-35.2)	28.8 (28.2-29.4)	18.2 (17.5-18.6)
39	10	37.2 (35.8-38.3)	31.3 (30.4-32.5)	19.0 (18.3-19.6)
43	10	30.9 (30.1-32.1)	25.8 (24.7-26.8)	16.6 (16.0-16.9)
44	2	33.0 (32.6-33.3)	27.6 (27.4-27.8)	17.2 (17.1-17.2)
	10	31.9 (31.2-32.6)	27.3 (26.5-27.8)	17.1 (16.3-17.6)
47	1	32.2	26.9	16.2
48	1			17.0

TABLE 3.—*Continued.*

		Interorbital breadth	*Length of maxillary toothrow*	*Length of palate*
4	5	7.6 (7.4-7.9	11.8 (11.6-11.9)	17.4 (17.2-17.6)
5	5	7.7 (6.8-8.2	11.1 (10.2-10.8)	15.7 (15.3-16.3)
7	10	7.5 (7.3-7.8)	10.9 (10.5-11.6)	15.6 (14.8-17.0)
8	6	7.5 (7.1-7.9)	10.9 (10.7-11.2)	15.7 (15.0-16.1)
14	6	7.7 (7.4-8.0)	11.3 (11.0-11.5)	16.0 (15.5-16.4)
17	10	7.6 (7.2-8.0)	11.1 (10.8-11.6)	16.4 (15.8-17.6)
26	6	7.5 (7.0-7.8)	11.3 (10.7-11.8)	16.2 (15.5-16.7)
27	3	6.9 (6.9-7.0)	10.0 (9.8-10.2)	14.7 (14.3-15.2)
28	11	6.8 (6.2-7.2)	10.2 (9.4-10.8)	14.2 (13.5-14.8)
29	14	6.9 (6.5-7.3)	10.4 (9.9-11.4)	14.6 (13.4-16.3)
32	21	7.1 (6.6-7.5)	10.1 (9.6-10.7)	14.3 (13.3-15.1)
36	4	7.3 (7.0-7.5)	10.3 (10.0-10.4)	15.0 (14.3-15.5)
38	6	7.3 (6.9-7.7)	10.6 (10.2-11.3)	15.0 (14.4-15.8)
39	10	7.5 (7.6-7.7)	11.5 (11.2-11.8)	16.9 (16.2-17.9)
43	10	6.8 (6.5-7.0)	10.2 (9.6-10.8)	14.0 (13.2-14.8)
44	2	6.4 (6.4-6.5)	10.4 (10.3-10.6)	15.2 (15.1-15.2)
46	10	6.8 (6.3-7.3)	10.4 (10.0-10.7)	14.6 (14.0-15.4)
47	1	7.0	10.1	14.4
48	1	6.9	11.0	15.1
49	1		10.6	

		Width across M2-M2	*Width across canines*	*Depth of skull*
4	5	10.9 (10.6-11.2)	5.1 (4.8-5.4)	10.6 (10.4-10.8)
5	5	10.0 (9.4-10.5)	4.3 (4.0-4.7)	10.3 (9.9-10.4)
7	10	9.6 (9.2-10.5)	4.2 (3.6-4.6)	10.2 (9.7-10.6)
8	6	9.7 (9.5- 9.9)	4.2 (4.0-4.5)	10.2 (9.8-10.5)
14	6	9.8 (9.2-10.2)	4.3 (3.7-5.0)	10.1 (9.8-10.4)
17	10	9.8 (9.4-10.4)	4.7 (4.5-5.0)	10.3 (9.8-10.8)
26	6	9.7 (9.4- 9.9)	4.4 (4.2-4.9)	10.4 (10.1-10.6)
27	3	9.7 (9.5-10.0)	4.2 (4.1-4.4)	9.4 (9.0- 9.8)
28	11	9.2 (8.9- 9.7)	3.8 (3.6-4.2)	9.6 (9.3- 9.8)
29	14	9.4 (8.6-10.3)	4.0 (3.6-4.5)	9.8 (8.8-10.4)
32	21	8.9 (8.3- 9.6)	3.7 (3.4-4.1)	9.8 (9.5-10.2)
36	4	9.0 (8.6- 9.2)	4.0 (3.8-4.1)	10.0 (9.6-10.3)
38	6	9.4 (9.0- 9.8)	4.0 (3.9-4.2)	10.2 (10.0-10.7)
39	10	10.1 (9.3-10.5)	4.6 (4.2-4.8)	10.6 (10.0-11.3)
43	10	9.0 (8.4- 9.6)	3.8 (3.4-4.1)	9.2 (8.8- 9.8)
44	2	10.0 (10.0-10.1)	4.5 (4.4-4.6)	9.6 (9.4- 9.6)
46	10	9.7 (9.4-10.1)	3.8 (3.4-4.5)	10.0 (9.5-10.9)
47	1	8.6	3.8	9.6
48	1	9.6	4.2	9.8
49	1	10.5	4.3	

basilar length, length of maxillary toothrow, length of palate); measurements dealing with skull breadth (mastoidal breadth, interorbital breadth, width across M2-M2, width across canines); and depth of skull.

In general, samples from Kansas, Missouri, Oklahoma, Arkansas, Louisiana, and extreme eastern Texas formed a group characterized by an average length of skull greater than that in samples from the rest of Texas and México. Moles from northeastern Kansas and Missouri (area 4) had the longest skulls (37.2-37.6); those from the Texas coast (areas 42, 43), the shortest (30-32). Samples from the Texas Panhandle, southern Kansas, Oklahoma, Arkansas, extreme eastern Texas and Louisiana (areas 1, 2, 5-17, 25, 26, 37, 39) formed a group characterized by a long skull. Those from Arkansas and Louisiana averaged slightly larger than other members of this group, but the change from one area to the other was more or less gradual. Samples from central and eastern Texas (areas 21-24, 27-34, 36) had, on the average, a skull shorter than that in samples to the north and east but longer than that in samples to the south (Table 3 and Fig. 2). Samples from extreme southern Texas and Tamaulipas, México (areas 44, 46, 48) had short skulls although they averaged slightly larger than those from Rockport to the north (area 43). Sample 47 from Coahuila, México, differed little from those in central Texas (areas 27, 28) in length of skull, but it was larger than those from south Texas. Basilar length, length of palate, and length of maxillary toothrow showed patterns of geographic variation similar to that described for greatest length of skull (Table 3).

Variation in mastoidal breadth followed closely the pattern of variation discussed above for those measurements involving length. Samples from northeastern Kansas and Missouri (area 4) averaged broader in mastoidal breadth than did other samples in the study area. Samples from southwestern Kansas, the Texas Panhandle, Oklahoma, Arkansas, extreme eastern Texas, and Louisiana (areas 1, 2, 5-17, 25, 26, 37, 38, 39) averaged slightly smaller in mastoidal breadth than did those from area 4 but larger than those from the rest of Texas and México. Moles from central and eastern Texas (areas 21-24, 27-34, 36), though averaging less in mastoidal breadth than those in samples to the east and north, differed only slightly from samples in southern Texas and Tamaulipas, México (areas 40-46, 48). Of the South Texas samples, individuals from area 43 had the least mean mastoidal breadth; specimens from area 47 in Coahuila also had a relatively narrow mastoidal breadth.

Interorbital breadth exhibited the least amount of variation of those measurements involving breadth. Little difference in mean interorbital breadth was apparent between specimens from area 4 and adjacent samples (areas 1, 2, 5-17, 25, 26, 37, 38, 39); samples from México, central, southern, and eastern Texas (areas 21-24, 27-36, 40-48) averaged smaller than the former group.

Width across M2-M2, width across the canines, and depth of skull showed, in general, the same pattern of geographic variation as that of greatest length of skull (Table 3). Of special importance, though, is width across M2-M2 for the single specimen examined of *Scalopus inflatus* (area 48). This measurement was essentially the same as that for samples from extreme southern Texas (area 46). However, width across M2-M2 for the single specimen of *S. a. texanus* from area 49 was noticeably larger than that for any adjacent sample.

Clinal patterns of geographic variation in greatest length of skull and width across M2-M2 are shown in Figs. 3 and 4, respectively. In general, there was a clinal decrease in size from north to south in all cranial characters. Greatest length of skull best exemplified the type of variation present in all cranial characters examined. Individuals from northeastern Kansas and Missouri (area 4) had the longest skulls with a decrease in mean skull length occurring in the Texas Panhandle, Oklahoma, Arkansas, extreme eastern Texas, and Louisiana (areas 5, 7, 8, 17, 25, 26, 39). Skull length continued to decrease through Texas to the gulf coast at Rockport (Fig. 3A).

A distinctive step occured in the cline between area 43 and areas 44 and 46. Instead of being shorter, skull length of moles from areas 44 and 46 was longer than in those individuals from area 43, which is located farther north. Similar patterns existed for other cranial measurements. Another step in the cline existed between area 4 in northeastern Kansas and Missouri and those areas to the south in Oklahoma and Arkansas.

Although more erratic, a gradual increase in greatest length of skull was evident also from west to east (Fig. 3B). The single specimen of *Scalopus montanus* from area 47 in Coahuila, México, individuals from area 27 at Mason (Texas), and those from area 28 all exhibited similar measurements for this variate. Skull length averaged slightly smaller in samples from Oklahoma than in those from Arkansas and Louisiana, indicating clinal variation along the west-east gradient as well.

All cranial features involving width showed much the same pattern of a north to south and east to west decrease in size as did greatest length of skull, with one noteworthy exception in respect to width across M2-M2. Mean width across the molars was considerably less in individuals from area 47 than it was in those from areas 27 or 28 (Table 3 and Fig. 4); otherwise the character remained essentially

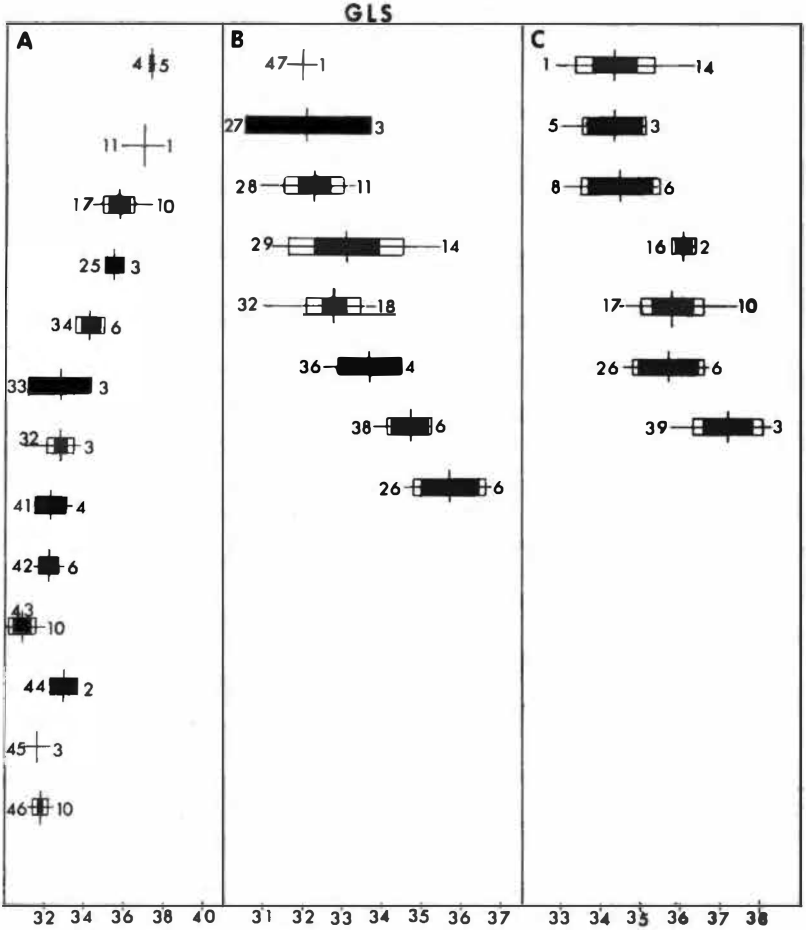

FIG. 3.—Clinal variation, expresssed by Dice-Leraas Diagrams, in greatest length of skull in selected samples of *Scalopus aquaticus*. The horizontal line represents the range; vertical line, mean; open rectangle, one standard deviation; closed rectangle, two standard errors of the mean. The number to the left of the grams is the area number, the one to the right is the sample size. See Fig. 2 and text for key to samples. "A" represents variation from north to south, "B" and "C" from west to east.

stable across Texas from west to east, with but a slight increase in extreme eastern Texas (area 38) and Louisiana (area 26). Little variation was noted from the Texas Panhandle eastward through Oklahoma, Arkansas, and Louisiana. Along the north-south gradient, there was a distinctive clinal break between area 43 and areas 44 and 46 (Fig. 4A). Width across M2-M2 averaged larger in samples from areas 44 and 46 than in those from area 43. The single known speci-

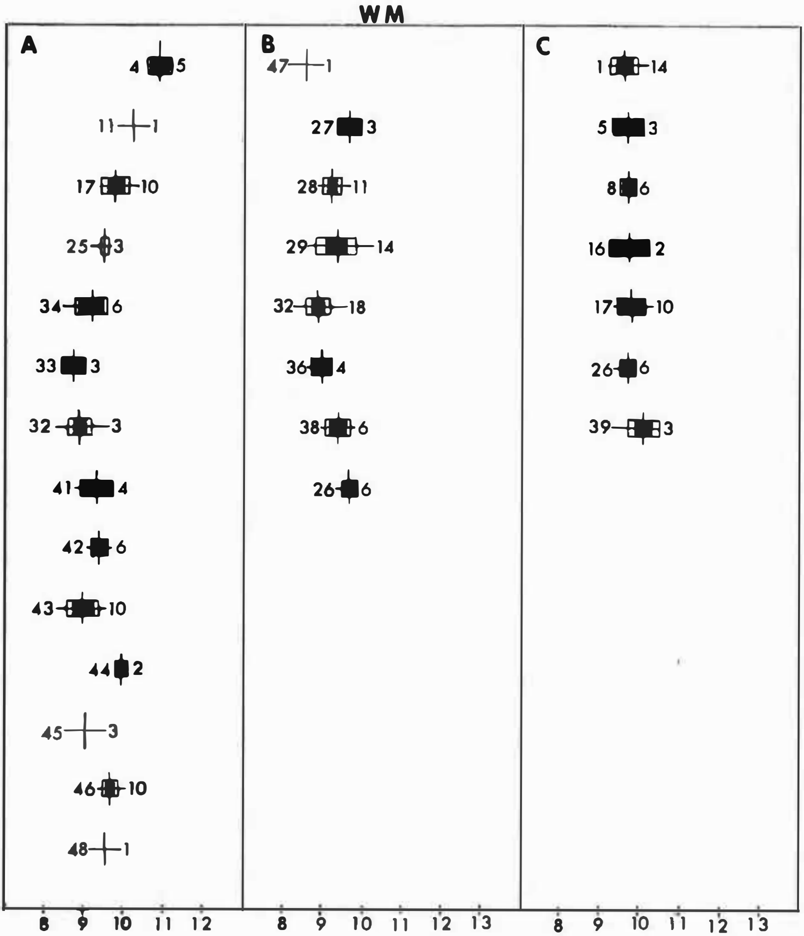

FIG. 4.—Clinal variation, expressed by Dice-Leraas Diagrams, in width across M2-M2 in selected samples of *Scalopus aquaticus*. For explanation of symbols, see Fig. 3.

men of *Scalopus inflatus* (area 48) exhibited essentially the same width across M2-M2 as did samples from area 46. These data indicate that individuals in area 44 have a closer affinity to those in areas 46 and 48 than to their closest geographic neighbors in area 43. Depth of skull showed essentially this same pattern.

Multivariate analysis.—To determine the amount of variation among samples considering all characters simultaneously, a multivariate analysis of variance (MANOVA) and a canonical analysis were used. Due to a large amount of missing data and a higher degree of variability, external measurements were not used in the multivariate portion of the study. Individuals from areas 3, 13, 19, 30, 48, and 49 were not included because of missing data.

Four different criteria (Hotelling-Lawley's Trace, Pilla's Trace, Wilk's Criterion, and Roy's Maximum Root Criterion) were used to test the hypothesis of no overall locality effect, that is, no significant morphological differences among samples. All four tests produced *F*-values that were significant at $P \leq 0.001$; thus, significant morphological differences among samples are assumed due to the effect of locality.

The variance-covariance matrix gave nine canonical variates among the nine characters for all 43 areas. The first canonical variate expressed 57.66 per cent of the phenetic variation; the second, 13.98; the third, 9.18; and the fourth, 7.22. Two dimensional plots of the first two canonical variates (including the mean and one standard deviation on each side of the mean for each area) are shown in Fig. 5. Examination of that figure reveals four major groupings of samples within the character space, labeled A-D: two groups of large moles, A and B, at the top; two groups of relatively small moles at the bottom, C and D. Group A consists of samples of *S. a. machrinoides* from northeastern Kansas and Missouri (area 4). Group B contains samples of the nominal subspecies *S. a. intermedius* (areas 1, 2, 5, 6, 7, 8, 10, 14, 15) and *S. a. aereus* (areas 11, 12, 16, 17, 25, 26, 35, 37, 39). Massive overlap occurs between many of these samples, which makes it impossible to detect any distinct separation between samples of *intermedius* and *aereus*.

Group C shows only slight overlap with samples in group B and there is no overlap of means. The former group actually appears to be composed of two subgroups, one on the extreme left and center consisting of samples formerly referred to *S. a. nanus* (areas 31, 32, 33), *S. a. aereus* (area 38), *S. a. cryptus* (areas 18, 20, 21, 22, 23, 24, 27, 29, 32, 34, 36), and *S. montanus* (area 47), and one subgroup on the right containing specimens formerly referred to *S. a. cryptus* (areas 28, 41) and *S. a. alleni* (areas 40, 42, 43, 45). Group D consists of samples referred to *S. a. alleni* (areas 44, 46). Little overlap exists between samples in group D and C.

The relative contributions of each character to the first two canonical variates are given in Table 4. Vector I primarily separates the two groups of large moles, A and B, from the two groups of small moles, C and D (Fig. 5), whereas Vector II separates the two groups of large moles from each other and the two groups of small moles from one another. Vector II also tends to distinguish two subgroups within group C of the small moles. Individuals in group A have skulls that

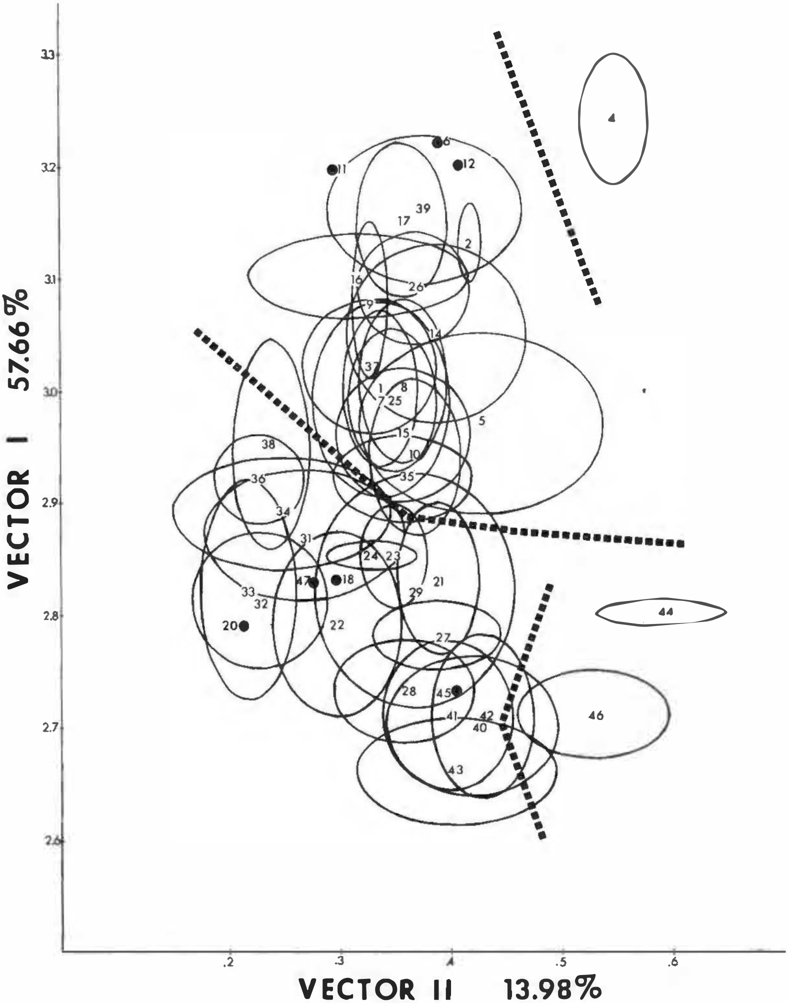

FIG. 5.—Projection of sample means plus or minus one standard deviation for the first two canonical variates in 43 samples of *Scalopus aquaticus*. Numbers represent grouped samples (areas) utilized in the study of geographic variation. Ellipses represent one standard deviation around the mean. Single dots are samples with only one specimen. Dotted lines indicate areas of little or no overlap between standard deviations of one group and the means of another.

are longer and wider than members of B, C, and D. Likewise, individuals in group B differ from those in C and D in having longer and wider skulls. Greatest length of skull and width across M2-M2 averaged larger for individuals in group D than for those in group C. This is to be expected because greatest length of skull, interorbital breadth, width across canines, width across M2-M2, and mastoidal breadth all exert a heavy influence on Vector I, whereas greatest length of skull and width across molars exert the heaviest influence on Vector II.

In order to compensate for some of the disadvantages of ordination techniques, cluster analysis was used to analyze the data. Means of each of the first four canonical variates from the MANOVA for each of the 43 areas were used in a NT-SYS clustering analysis. Standardization procedures were not performed on the canonical variates in order to perserve the discriminating power of each vector. A phenogram diagramming the phenetic relationships of all samples was computed by cluster analysis from distance matrices (Fig. 6). With the exception of area 44 (C), which branches off by itself, the samples in this phenogram divide into essentially two major clusters, one cluster of relatively large moles (A) and one of small moles (B), identical to the two major groups obtained with ordination techniques. The samples in cluster A also divide into two subclusters, samples from northeastern Kansas and Missouri (area 4) and samples from northern and extreme eastern Texas, Oklahoma, Arkansas, and Louisiana (areas 1, 8, 7, 10, 15, 5, 14, 37, 2, 6, 17, 9, 26, 25, 11, 39, 16). Samples in cluster B divide into two smaller subclusters, one comprised of samples from eastern Texas, central Texas, and Coahuila, México (areas 18, 20, 21, 22, 23, 24, 29, 31, 32, 33, 34, 35, 36, 38, 47); and a second consisting of samples from central and southern Texas (areas 27, 28, 40, 41, 42, 43, 45, 46). Although area 46 is in the same general cluster as other samples from southern and central Texas, it does not cluster very close to other members of that group. The cophenetic correlation coefficient for the phenogram is 0.685.

Taxonomic Conclusions

The previously recognized species *Scalopus inflatus* from Tamaulipas, México, and *S. montanus* from Coahuila, México, apparently represent relict populations of *S. aquaticus*, which was widely distributed across Texas and northern México during the late Pleistocene (Lundelius and Slaughter, 1971; Dalquest *et al.*, 1969). Remains of *S. aquaticus* have been found in cave faunas over much of the Edwards Plateau (Fig. 7) from Hill County as far west as Edwards County (Dalquest *et al.*, 1969; Frank, 1964). Baker (1951) gave specific rank to *S. montanus* because of the great degree of morphological difference between it and the geographically nearest subspecies of *S. aquaticus* (*S. a. texanus* and *S. a. intermedius*) and because of

TABLE 4.—*Eigenvalues of selected canonical variates showing the percentage influence of each cranial character in 43 samples of* Scalopus aquaticus. *Eigenvalues shown represent the normalized vector coefficient of each character. The median is a value in millimeters that reflects an approximate midpoint between the largest and smallest actual measurement of each character.*

Character	Median	Vector I		Vector II	
		Eigenvalue	Per cent influence	Eigenvalue	Per cent influence
Greatest length of skull	33.857	0.05264112	36.005	−0.08857566	34.700
Basilar length	28.334	0.00044726	0.256	0.00407943	1.336
Mastoidal breadth	17.750	−0.02817876	10.105	−0.01134076	2.330
Interorbital breadth	7.214	0.13195074	19.230	−0.13047621	10.890
Length of maxillary toothrow	10.677	0.00216509	0.427	0.9560970	11.815
Length of palate	15.190	0.02495295	7.657	0.06194991	10.890
Width across M2-M2	9.511	−0.05485359	10.540	0.13730225	15.110
Width across canines	4.048	0.13620095	11.137	0.07784402	3.647
Depth of skull	10.005	0.02278643	4.606	0.07997655	9.260

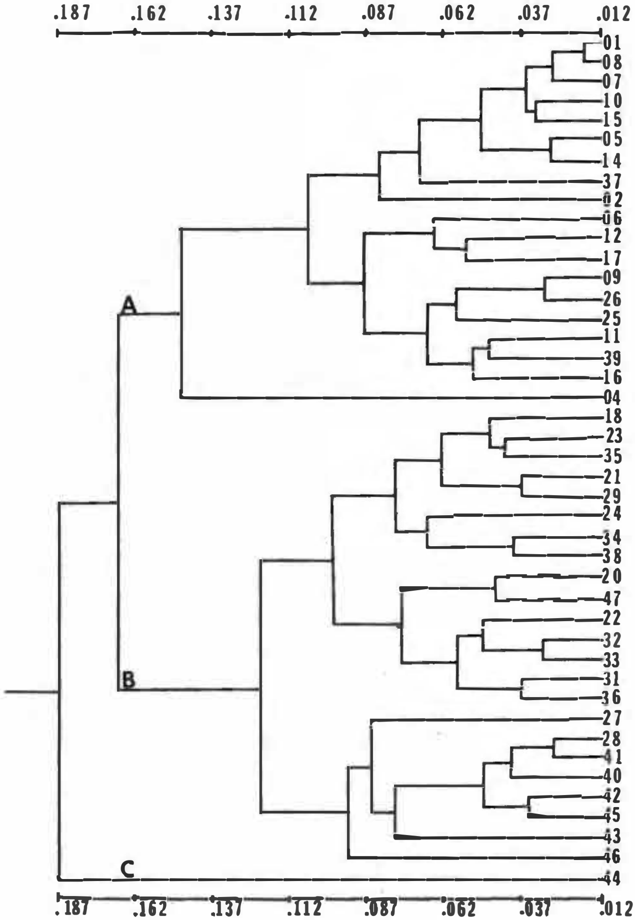

FIG. 6.—Distance phenogram of 43 samples (operational taxonomic units) based on four canonical variates. The cophenetic correlation coefficient is 0.685. A, B, and C represent major clusters.

its geographically isolated position. Our analysis indicates few morphological differences between *S. montanus* and samples of *S. aquaticus* from central Texas, especially those from Mason County. Based on the fossil record, the direction of dispersal of *S. aquaticus* during the late Pleistocene appears to have been from the east across the Edwards Plateau and not from the north across the Texas Panhandle and Trans-Pecos, Texas, as assumed by Baker (1951). Thus, the most appropriate comparisons to make are those between *S. montanus* and subspecies of *S. aquaticus* from central and southern Texas instead of with *S. a. intermedius* from the Texas Panhandle. The

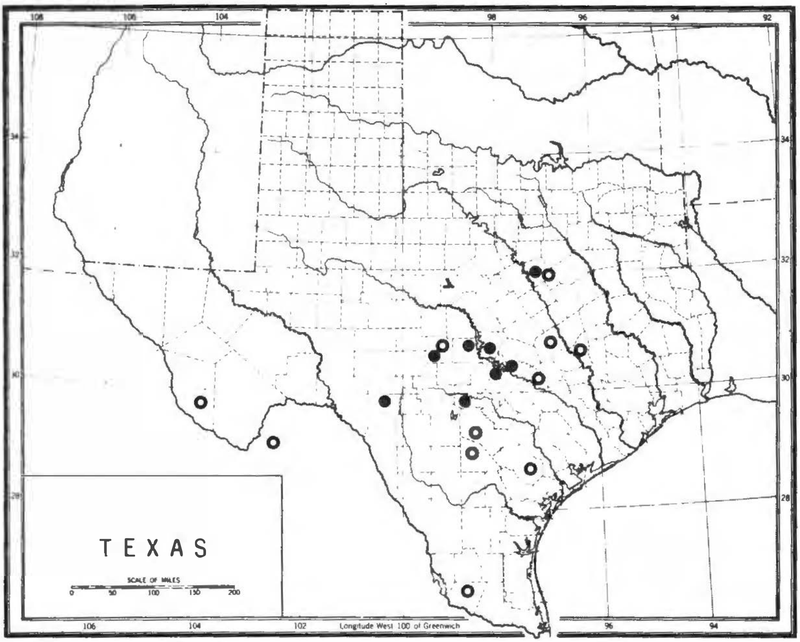

FIG. 7.—Location of caves on the Edwards Plateau, Texas, where fossil remains of *Scalopus aquaticus* have been found. Closed circles represent fossils; open circles, adjacent Recent populations.

differences between *S. montanus*, *S. texanus* in Presidio County, and populations of *S. aquaticus* in central and southern Texas are those expected between populations of one species. Thus, we are of the opinion that *S. montanus* and *S. aquaticus* are conspecific.

We also find little justification for recognizing *S. inflatus* as a distinct species. Although *inflatus* differs significantly in several characters from specimens from Rockport, Texas (see Jackson, 1914, for a detailed account), the degree of difference is no greater than that between other subspecies of *Scalopus aquaticus*. Furthermore, when *inflatus* is compared with samples of *aquaticus* from southern Texas, which are geographically closer to *inflatus* than the sample from Rockport, little morphological difference is evident. *S. inflatus* and *S. aquaticus* are best considered as conspecific.

In recognizing subspecies, we have followed Mayr's (1969:41) definition that "a subspecies is an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of a species, and differing taxonomically from other populations of the species." Based on an assessment of geographic variation in *S. aquaticus*, seven distinct units may be identified, which in our

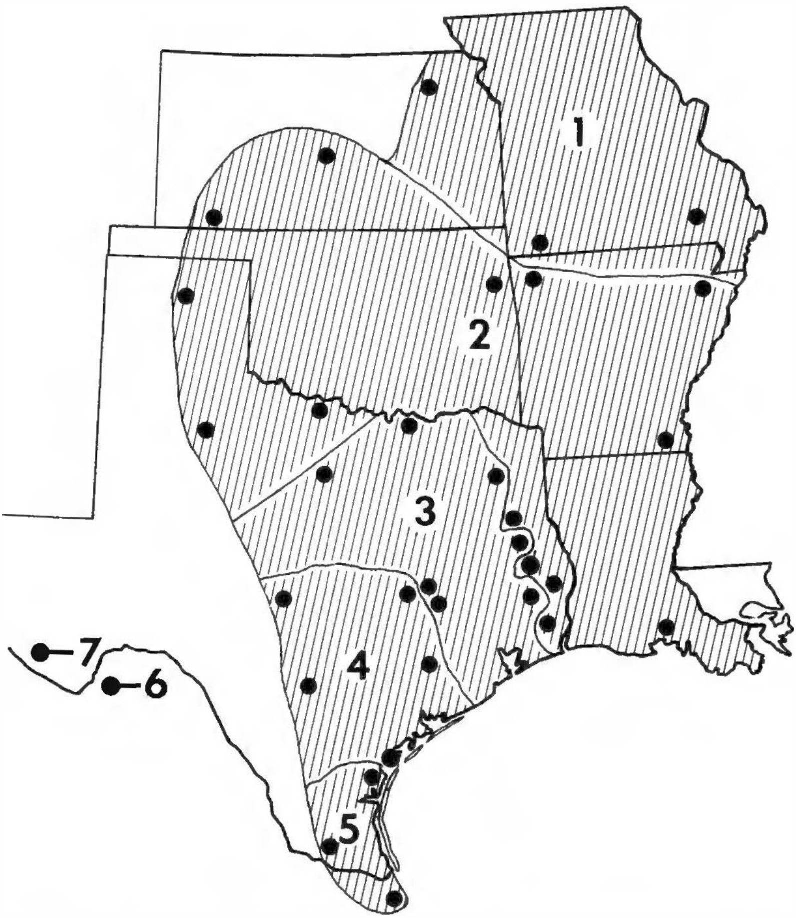

FIG. 8.—Geographic distribution of subspecies of *Scalopus aquaticus*: 1, *S. a. machrinoides*; 2, *S a. aereus*; 3, *S. a. cryptus*; 4, *S. a. alleni*; 5, *S. a. inflatus*; 6, *S. a. montanus*; 7, *S. a. texanus*.

opinion fit the above criteria; these seven units are the subspecies of *S. aquaticus* herein recognized (see Fig. 8). Two of them are characterized by large size. The largest individuals of the species occur in northeastern Kansas and Missouri and to this group the trinomial *Scalopus aquaticus machrinoides* Jackson applies. Another subspecies of large individuals is *Scalopus aquaticus aereus* (Bangs), which occurs from northern Texas and the Texas Panhandle, eastward through Oklahoma, portions of southern Kansas, Arkansas, Louisiana, and extreme eastern Texas. This subspecies encompasses samples formerly referred to *S. a. intermedius* and to *S. a. aereus*. Our analysis shows that the degree of morphological distinction between samples of *S. a. intermedius* and *S. a. aereus* is too small and erratic to warrant their separation. *S. a. aereus* (Bangs) has priority over *S. a. intermedius* (Elliot).

The five remaining subspecies are characterized by individuals of medium to small size. *S. a. cryptus* Davis (1942) occupies a range in central and eastern Texas that encompasses that of moles formerly referred to *S. a. nanus.* Davis (1942) based the original description of *S. a. nanus* on three female specimens, but a comparison of these with samples of females of *S. a. cryptus* reveals few differences. Also, a comparison of adult males from the range formerly ascribed to *S. a. nanus* with additional samples of *S. a. cryptus* reveals no significant differences. We feel the name *cryptus* most appropriate because this subspecies is not comprised of the smallest moles in Texas, as is implied by *nanus. S. a. alleni,* a subspecies of somewhat smaller sized individuals, occurs west of the Brazos River from Mason County south to Padre Island. Another subspecies of relatively small sized individuals, *S. a. inflatus,* occupies a range from Corpus Christi, Texas, southward to 45 miles south of Brownsville in northeastern México. The final two subspecies, *S. a. montanus* and *S. a. texanus,* are both known only from single specimens from their type localities in northern Coahuila, México, and Presidio County, Texas, respectively.

ACCOUNTS OF SUBSPECIES

Scalopus aquaticus aereus (Bangs)

1896. *Scalops texanus aereus* Bangs, Proc. Biol. Soc. Washington, 10:138, 28 December.

1912. *Scalopus aquaticus aereus*, Miller, Bull. U.S. Nat. Mus., 79:8, 31 December.

1899. *Scalops machrinus intermedius* Elliot, Field Columb. Mus. Publ. 37, Zool. Ser., 1:280, 15 May. Type locality Alva, Woods Co., Oklahoma.

1914. *Scalopus aquaticus pulcher* Jackson, Proc. Biol. Soc. Washington, 27: 20, 2 February. Type locality Delight, Pike Co., Arkansas.

1905. *Scalopus aquaticus intermedius*, Bailey, N. Amer. Fauna, 25:207, 24 October.

Holotype.—Adult female; skin and skull, MCZ 5475; Stilwell, Adair Co., Oklahoma.

Distribution.—Southwestern Kansas, Oklahoma, the Texas Panhandle, northern Texas along the Red River, Arkansas, Louisiana, and extreme eastern Texas.

Comparisons.—Compared with *Scalopus aquaticus machrinoides* in Missouri and northeastern Kansas, *S. a. aereus* has a shorter, narrower, shallower skull, and all cranial measurements, with the exception of interorbital breadth, average less (compare data for area 4 with those for areas 5, 7, 8, 14, 17, 26, 39 in Table 3). From *S. a. cryptus* in central and eastern Texas, *S. a. aereus* differs as follows: size generally larger; skull longer, greatest length of skull seldom less than 34.3; skull wider and deeper (compare data for areas 17, 26, 39 with those for areas 29, 32, 36 in Table 3).

Remarks.—This race of large individuals exhibits a relatively high degree of geographic variation throughout its range. In general, individuals from the northwestern portion of the range average slightly smaller in some cranial characters and are lighter in color than those from the more southern parts. The change is gradual, however. Individuals in area 39 (Lafayette and Avery Island, Louisiana) average unusually large for the subspecies. *S. a. aereus* apparently intergrades with *S. a. cryptus* in eastern Texas. Individuals in area 35 (vicinity of Lufkin) are probably intergrades, but are referred to *S. a. aereus* because in length of maxillary toothrow, length of palate, and width across molars, they are more like *aereus* than *cryptus.* Specimens from area 38 (vicinity of Jasper) are also intermediate between *S. a. aereus* and *S. a. cryptus,* but are referred to *S. a. aereus* because more characters are in agreement with that subspecies than with *S. a. cryptus.*

Specimens examined (184).—ARKANSAS: Ashley Co.: Wilmot, 1 (USNM); Craighead Co.: Lake City, 1 (USNM); Hot Springs Co.: 3 mi. N Malvern, 1 (LSUMZ); Quachita Co.: Camden, 1 (USNM); Pike Co.: Delight, 15 (USNM); Washington Co.: Fayetteville, 1 (KU); 5 mi. S Winslow, 1 (KU). KANSAS: Barber Co.: Atena, 1 (KU); 2 mi. N, 1.5 mi. E Sharon, 1 (KU); Meade Co.: 14 mi. SW Meade, 7 (KU); 17 mi. SW Meade, 1 (KU); State Park, 8 (KU); Seward Co.: 12 mi. NE Liberal, 1 (KU); Stafford Co.: Little Salt Marsh, 2 (KU); 12 mi. N, 6 mi. E Stafford, 1 (KU). LOUISIANA: Bienville Parish: Bienville, 1 (MVZ); Bossier Parish: Bossier City, 1 (LSUMZ); Caldwell Parish: Columbia, 1 (FMNH); Iberia Parish: Avery Island, 1 (TCWC); Lafayette Parish: Lafayette, 14 (LSUMZ); Natchitoches Parish: Provencal, 4 (LSUMZ). OKLAHOMA: Adair Co.: Stilwell, 1 (UIMNH), 1 (OSU); Blaine Co.: Canton Reservoir, 1 (OSU); Bryan Co.: 1 mi. S Blue, 2 (OSU); Cherokee Co.: 1 mi. SE Lowery, 1 (TNHC); Cleveland Co.: 3 mi. N Norman, 1 (OSU); Comanche Co.: Mount Scott, 4 (USNM); Wichita Mountains Wildlife Refuge, 3 (USNM); Cotton Co.: 2 mi. NE Burkburnett, 2 (MWU); 2 mi. NW Burkburnett, 1 (MWU); 3 mi. NE Burkburnett, 1 (MWU); 3 mi. E Burkburnett, 1 (MWU); 100 yards E U.S. Hwy. 281 on N bank of Red River, 1 (MWU); Dewey Co.: 5 mi. W Canton, 1 (KU); Jefferson Co.: 8 mi. N Byers, 1 (MWU); Lincoln Co.: Chandler, 1 (OSU); Logan Co.: 4 mi. N, ½ mi. E Guthrie, 1 (OSU); McCurtain Co.: ¼ mi. W Glover, 2 (TNHC); Noble Co.: 7 mi. W, ½ mi. S Red Rock, 1 (OSU); Oklahoma Co.: Edmond, 1 (OSU); Midwest City, 1 (MSUMC); Oklahoma City, 2 (KU); Osage Co.: 10 mi. NE Pawhuska, 1 (TNHC); Pawnee Co.: 7½ mi. N, 2¾ mi. W Pawnee, 1 (KU); Payne Co.: Boomer Lake Park, 2 mi. N Stillwater, 3 (OSU); Stillwater, 1 (UMDZ), 2 (OSU); 5 mi. W, ¾ mi. S Stillwater, 2 (OSU); 2 mi. W Stillwater, 1 (OSU); 2 mi. E, 2 mi. N Stillwater, 1 (OSU); 2 mi. SE Stillwater, 1 (OSU); 3 mi. N, ½ mi. W Stillwater, 1 (OSU); 8 mi. E, ¼ mi. S Stillwater, 2 (OSU); 5 mi. W Payne-Creek Co. boundary, 7 mi. S Payne-Pawnee Co. boundary, 1 (OSU); Pushmataha Co.: 1 mi. S Nashoba, 1 (TNHC); Rogers Co.: Alva, 1 (USNM), 2 (FMNH); Woodward Co.: Fort Supply, 1 (OSU), 1 (MSUMC). TEXAS: Angelina Co.: 1 mi. N Dibol, 1 (TCWC); Huntington City, 1 (SFA); 3 mi. W Lufkin, 1 (SFA); Baylor Co.: 8 mi. NW Bomarton, 1 (MWU); Seymour, 1 (MWU); 1.5 mi. NW Seymour, 1 (MWU); Bowie Co.: Texarkana, 1 (TCWC); Clay Co.: 12 mi. E Burkburnett, 1 (MWU); 2 mi. SW Charlie, 1 (MWU); 6 mi. NW Petrolia, 2 (MWU); 4 mi. NE Thornberry, 2 (MWU); Cottle Co.: 13 mi. N Paducah, 3 (TNHC); Dickens Co.: Dickens, 1 (MSUMC); Floyd Co.: 6 mi. S, 1 mi. W Quitaque, 1 (OSU); Hardin Co.: Sour Lake, 14 (USNM); Harrison Co.: 3 mi. SE Hallsville Post Office, 2 (SFA); Hemphill Co.: 6 mi. E Canadian, 1 (TTU); Hutchison Co.: 9 mi. E Stinnett, 3 (TNHC); Jasper Co.: 8.6 mi. W Jasper, 1 (TCWC); 8 mi. W Jasper, 2 (TCWC); 8 mi. W, 1.4 mi. N Jasper, 1 (TCWC); Lipscomb Co.: Lipscomb, 2 (USNM); Rusk Co.: 12 mi. S Henderson, 2 (TCWC); 1 mi. N Henderson, 1 (SFA); Newton Co.: 6.8 mi. N Burkeville, 1 (TCWC); 7.4 mi. N Burkeville, 2 (TCWC); 30 mi. N Orange, 1 (TCWC); Shelby Co.: Joaquin, 1 (USNM); Wheeler Co.: Mobeetie, 2 (USNM); Wichita Co.: Burkburnett, 1 (DMNHT); 8 mi. SE Burkburnett, 1 (MWU); 3 mi. SE Burkburnett, 1 (MWU); 7 mi. SE Burkburnett, 1 (MWU); 2 mi. N Red River Bridge, 2 (MWU); Perkins Reservation, 1 (SRSU), 4 (MWU).

Scalopus aquaticus alleni Baker

1951. *Scalopus aquaticus alleni* Baker, Univ. Kansas Publ., Mus. Nat. Hist., 5:22, 28 February.

1893. *Scalops texanus*, Allen, Bull. Amer. Mus. Nat. Hist., 5:200, 18 August.

1896. *Scalops aquaticus texanus*, True, Proc. U.S. Nat. Mus., 19:21, 21 December.

1915. *Scalopus aquaticus texanus*, Jackson, N. Amer. Fauna, 38:50, 30 September.

Holotype.—Adult male; skin and skull, AMNH 7189/5788; Rockport, Aransas Co., Texas; 29 January 1893; obtained by H. P. Attwater.

Distribution.—Southern Texas, west of the Brazos River, from Mason County south to Padre Island near Corpus Christi.

Comparisons.—From *S. a. cryptus* in central and eastern Texas, *S. a. alleni* differs as follows: size smaller; greatest length of skull seldom exceeding 32.5; skull less arched, depth of skull seldom exceeding 6.9 (compare data for areas 27, 28, 43 with those for areas 29, 32 in Table 3). From *S. a. inflatus* in extreme southern Texas and Tamaulipas, México, *S. a. alleni* differs as follows: size smaller; prelachrymal region not enlarged; skull shorter and less broad. *S. a. alleni* is distinguished most easily from *S. a. inflatus* by the following characters: basilar length seldom greater than 27.2; palate seldom greater than 14.8; prelachrymal region narrow; width across M2-M2 seldom greater than 9.7 (compare data for areas 27, 28, 32 with those for areas 44, 46, 48).

Remarks.—Moles referred to *S. a. alleni* in most respects are the smallest in Texas. The sample from Mason (area 27) probably represents a relict population, specimens of which appear to be intermediate in many characters between *S. a. cryptus* and *S. a. alleni* but are more like the latter and, thus, are referred to that subspecies. *S. a. alleni* intergrades with *S. a. cryptus* in a narrow zone along the Brazos River in Milam County and possibly elsewhere. The smallest individuals of this subspecies occur at Rockport on the Texas coast. Little variation occurs within this sample, possibly due to its isolated position. It is surrounded by water on three sides and by a heavy belt of clay on the fourth, which effectively reduces gene flow between it and neighboring populations.

Specimens examined (70).—TEXAS: Aransas Co.: Aransas Wildlife Refuge, 1 (TCWC); Fulton Beach, 1 (TCWC); Rockport, 12 (AMNH), 1 (FMNH), 4 (USNM), 3 (TCWC); 1½ mi. N Rockport, 1 (UIMNH); Atascosa Co.: 7 mi. E. Lytle, 7 (TNHC); Bastrop Co.: 2 mi. W Bastrop, 1 (TCWC); Bee Co.: Beeville, 1 (TNHC); Bexar Co.: San Antonio, 2 (AMNH), 2 (USNM); 3 mi. SW Somerset, 1 (KU); 7 mi. SW Somerset, 3 (KU); Colorado Co.: Eagle Lake, 1 (TCWC); Goliad Co.: 3.5 mi. N Goliad, 2 (TCWC); Lavaca Co.: 4 mi. S Hallettsville, 1 (TCWC); 33 mi. N Victoria, 1 (TCWC); Mason Co.: Mason, 2 (UIMNH), 2 (USNM); Milam Co.: 1.8 mi. NE Gause, 2 (TCWC); 6.2 mi. W Gause, 1 (TCWC); 7.4 mi. W Gause, 1 (TCWC); 3 mi. NE Gause, 1 (TCWC); 7.2 mi. S Gause, 1 (TCWC); 1 mi. E Gause, 1 (TCWC); 4 mi. E Milano, 1 (TCWC); 5 mi. E Milano, 1 (TCWC); 3 mi. E Milano, 1 (TCWC); 1 mi. S Rockdale, FM. 487, 1 (TCWC); 7.5 mi. S Rockdale, 1 (TCWC); Neuces Co.: Padre Island, 2 (USNM); Refugio Co.: Austwell, 1 (UIMNH); 3 mi. N Woodsboro, 5 (TCWC); Wilson Co.: 6.5 mi. NW Nixon, 1 (TCWC).

Scalopus aquaticus inflatus Jackson

1914. *Scalopus inflatus* Jackson, Proc. Biol. Soc. Washington, 27:21, 2 February.

Holotype.—Young adult, sex unknown; skin and skull, USNM 52709; Tamaulipas, México (45 mi. S Brownsville, Texas); 1892; obtained by Frank B. Armstrong.

Distribution.—Extreme southern Texas and northern Tamaulipas, México, from Corpus Christi to 45 mi. south of Brownsville, Texas.

Comparisons.—For a comparison of *S. a. inflatus* with *S. a. alleni* see acccount of the latter. From *S. a. montanus* in Coahuila, México, *S. a. inflatus* differs as follows: prelachrymal region much more inflated; maxillary toothrow longer; mastoidal breadth greater (compare data for areas 44, 46, 48 with those for area 47 in Table 3).

Remarks.—The original description of this subspecies was based on a specimen taken in Tamaulipas, México, 45 miles south of Brownsville, Texas. It lacks complete data and the posterior portion of the skull is broken; however, several cranial comparisons can be made. Of special interest is the unusually broad prelachrymal region. Width across M2-M2 is considerably greater in the holotype of *S. a. inflatus* than in specimens of *S. a. alleni* and *S. a. montanus*. Specimens formerly referred to *S. a. alleni* from Corpus Christi south to Brownsville also exhibit this inflated prelachrymal region and are thus referred to *S. a. inflatus*.

Specimens examined (14).—TEXAS: Brooks Co.: S of Falfurrias, 1 (SRSU); Cameron Co.: Brownsville, 2 (USNM); Hidalgo Co.: 1 mi. S Linn, 1 (TCWC); Kenedy Co.: 12 mi. S Sarita, 1 (TCWC); Kleberg Co.: 4 mi. E Riviera, 1 (TAIU); 8 mi. W, 1 mi. S Riviera, 2 (TCWC); Nueces Co.: Corpus Christi, 2 (USNM); 1 mi. N Flour Bluff, 1 (TCWC); Willacy Co.: 4.5 mi. N Raymondville, 1 (TAIU); 10 mi. NW Raymondville, 1 (TCWC). TAMAULIPAS: 45 mi. S Brownsville, Texas, 1 (USNM).

Scalopus aquaticus machrinoides Jackson

1914. *Scalopus aquaticus machrinoides* Jackson, Proc. Biol. Soc. Washington, 27:19, 2 February.

Holotype.—Adult male, skin and skull, USNM 169717; Biological Survey Collection; Manhattan, Kansas; 1 June 1910; obtained by W. E. Berg.

Distribution.—Northeastern Kansas, north to central Minnesota, south through northwestern Iowa and all of Missouri.

Comparisons.—From all other subspecies of *S. aquaticus* in Texas and adjacent areas, *S. a. machrinoides* differs in much larger size. Greatest length of skull seldom less than 37.2; length of maxillary toothrow seldom less than 11.6; length of palate seldom less than 17.2; width across the molars seldom less than 10.6; depth of skull seldom less than 10.4 (compare data for area 4 with those for all other areas in Table 3).

Remarks.—*S. a. machrinoides* represents one of the largest subspecies (in terms of size of individuals) of *S. aquaticus*. Although it does not occur in Texas, selected samples were included in this study to obtain more information on the degree of difference among the most divergent subspecies of *S. aquaticus*.

Specimens examined (12).—KANSAS: Riley Co.: Manhattan, 4 (USNM). MISSOURI: Barry Co.: Washburn, 1 (USNM); Boone Co.: Columbia, 6 (USNM); Wayne Co.: Camp Crowder, 1 (USNM).

Scalopus aquaticus montanus Baker

1951. *Scalopus montanus* Baker, Univ. Kansas Publ., Mus. Nat. Hist., 5:19, 28 February.

Holotype.—Adult male; skin and partial skeleton, KU 35668; Club Sierra del Carmen, 2 mi. N, 6 mi. W Piedra Blanca, Coahuila, México; 7 April 1950; obtained by J. R. Alcorn.

Distribution.—Known only from the type locality.

Comparisons.—For a comparison of *S. a. montanus* with *S. a. inflatus*, see account of the latter. From *S. a. alleni*, *S. a. montanus* differs as follows: skull slightly narrower; mastoidal breadth and width across M2-M2 average less (compare data for area 47 with those for areas 27, 28 in Table 3). From *S. a. texanus*, *S. a. montanus* differs as follows: maxillary toothrow shorter and width across M2-M2 and width across canines narrower (compare data for area 47 with those for area 49 in Table 3).

Remarks.—*S. a. montanus* is apparently a relict population of the once widely distribued *S. aquaticus*. It shows close affinities with specimens from Mason County (area 27) and other samples of *S. a. alleni*, but because it is geographically isolated and has a narrower skull, it is accorded subspecific status.

Specimens examined (1).—From the type locality.

Scalopus aquaticus cryptus Davis

1942. *Scalopus aquaticus nanus* Davis, Amer. Midland Nat., 27:383, March.
1942. *Scalopus aquaticus cryptus* Davis, Amer. Midland Nat., 27:384, March.

Holotype.—Adult male; skin and skull, TCWC 1454; College Station, Brazos Co., Texas; 23 November 1939; obtained by W. C. Parker.

Distribution.—Central and estern Texas, from Grayson County southward to Montgomery County; from the Brazos River eastward to Tyler County.

Comparisons.—For a comparison of *S. a. cryptus* with *S. a. aereus* and *S. a. alleni* see accounts of *aereus* and *alleni.*

Remarks.—*S. a. cryptus* is a medium-sized mole that occurs in central and eastern Texas. It contacts *S. a. aereus* in numerous areas of extreme eastern Texas and intergradation with that taxon occurs in these areas. Individuals in areas 23 and 24 are intermediate in many characters between these two subspecies; however, they have more characters in common with *S. a. cryptus* and are here referred to that taxon.

Specimens examined (107).—TEXAS: Anderson Co.: 10 mi. S. Athens, 1 (SFA); 20 mi. S Athens, 1 (SFA); 20 mi. NW Palestine, 1 (TNHC); 5 mi. SE Slocum, 1 (SFA); Bosque Co.: 7 mi. E Laguna Park, 1 (TCWC); Brazos Co.: Bryan, 3 (TCWC); College Station, 10 (TCWC); ¼ mi. N College Station, 1 (TCWC); 1 mi. W College Station, 1 (TCWC); 1 ½ mi. SW College Station, 1 (TCWC); 3 mi. SW College Station, 1 (TCWC); Cherokee Co.: ½ mi. N Maydelle, 2 (SFA); 1 mi. N Rusk, 1 (SFA); Denton Co.: 6.5 mi. W Lewisville, 1 (DMNHT); Grayson Co.: 3 mi. N Sherman, 1 (LSUMZ); Grimes Co.: Carlos, 1 (TCWC); Henderson Co.: Cedar Creek Lake, 1 (DMNHT); Hill Co.: 5 mi. NW junction FM. 933 and 2114 at Spivey Crossing, 4 (TCWC); 21 mi. N Waco, 1 (TCWC); Houston Co.: 3 mi. W Ratcliff, 1 (SFA); Leon Co.: 13 mi. E Centerville, 1 (TCWC); McClennan Co.: Waco, 1 (ANSP); Montgomery Co.: 1 mi. S Conroe, 30 (TCWC); 2 mi. N Conroe, 3 (TCWC); 10 mi. W Conroe, 1 (MSUMC); 1.6 mi. E Deckers Prairie, 1 (TCWC); Nacogdoches Co.: Nacogdoches, 2 (SFA); 2.5 mi. NW Nacogdoches, 1 (SFA); 4 mi. NW Nacogdoches, 1 (TTU); 5 mi. NE Nacogdoches, 2 (SFA); 10 mi. NE Nacogdoches, 1 (SFA); 10 mi. S Nacogdoches, 1 (SFA); Palo Pinto Co.: Possum Kingdom Lake, 1 (MWU); Polk Co.: 11 mi. W Woodville, 2 (TCWC); Robertson Co.: 1 mi. S Hearne, 2 (TCWC); Smith Co.: 18 mi. E Tyler, 2 (SFA); Trinity Co.: 1 mi. E Sebastopol, 4 (TCWC); Tyler Co.: 3 mi. E Chester, 1 (TCWC); 6.8 mi. N Spurger, 1 (TCWC); 9.5 mi. N Spurger, 1 (TCWC); 9.7 mi. N Spurger, 1 (TCWC); 5 mi. W Woodville, 1 (TCWC); Walker Co.: 10 mi. NW Huntsville, 1 (TCWC); 15 mi. S Huntsville, 1 (SFA); Wood Co.: 2 mi. S Hawkins, 1 (TCWC); 1 mi. W Mineola, 1 (TTU); 4 mi. S Winnsboro, 3 (TCWC); Upshur Co.: Gilmer, 1 (TCWC); Van Zandt Co.: 3½ mi. N Canton, 1 (TCWC); ½ mi. N Grand Saline, 2 (TTU).

Scalopus aquaticus texanus (J. A. Allen)

1891. *Scalops argentatus texanus* J. A. Allen, Bull. Amer. Mus. Nat. Hist., 3:221, 29 April.

1951. *Scalopus aquaticus texanus*, Baker, Univ. Kansas Publ., Mus. Nat. Hist., 5:21, 28 February.

Holotype.—Adult, sex unknown; skin and skull, AMNH 3448/2740; Presidio Co., Texas; September 1887; obtained by William Lloyd.

Distribution.—Known only from the type locality.

Comparisons.—From *S. a. aereus* to the north, *S. a. texanus* differs in shorter maxillary toothrow and greater width across M2-M2 (compare data for area 49 with areas 5, 7, 8, 14 in Table 3). From *S. a. alleni* to the east, *S. a. texanus* differs in longer maxillary toothrow and greater width across M2-M2 (compare data for area 49 with those for areas 27, 28, in Table 3). From *S. a. inflatus* to the southeast, *S. a. texanus* differs in greater width across the molars (see Table 3).

Remarks.—True (1896) believed that the holotype of *S. a. texanus* was collected in Aransas County rather than in Presidio County. The authenticity of the original locality record was discussed by Baker (1951), and, at present, there is no evidence that the type locality, Presidio County, as originally recorded is incorrect. Unfortunately, the holotype is an imperfect specimen and data are missing from the tag; only three of the cranial measurements used in this study (length of maxillary toothrow, width across M2-M2, and width across canines)

TABLE 5.—*Home range estimates (in square meters) of* Scalopus aquaticus *and five species of rodents.*

Species	Male	Female
Scalopus aquaticus (Harvey, 1976)	10640.0	2748.5
Dipodomys ordii (Garner, 1973)	1951.7	2230.5
Dipodomys elator (Roberts and Packard, 1968)	791.1	791.1
Reithrodontomys fulvescens (Packard, 1968)	1859.0	2333.7
Geomys bursarius (Wilks, 1963)	468.4	144.9
Thomomys bottae (Howard and Childs, 1959)	250.9	120.8

could be taken. More information is needed before the proper status of this subspecies can be determined.

Specimens examined (1).—From the type locality.

ECOLOGY AND REPRODUCTION

Based on the high degree of chromosomal and morphological variation found in fossorial rodents, one might expect a similar degree of variation in *Scalopus aquaticus*. However, Yates and Schmidly (1975) found moles to be karyotypically uniform. Reasons for this uniformity are difficult to explain. It could result from some genetic factor that affects the symmetry of the karyotype, or it might result from the ecological strategy of moles. Due to a need for large quantities of food, moles range over larger areas than do most other fossorial mammals, thereby increasing gene flow and reducing the likelihood of excessive inbreeding. Thus, the island model type of distribution common in pocket gophers is rare in moles. The average home range of the eastern mole in many cases exceeds that of many rodents. The home range of a male *S. aquaticus* averages almost 23 times as large as that of a male *Geomys bursarius*, 42 times as large as a male *Thomomys bottae*, and five times as large as a male *Dipodomys ordii* (Table 5). Males of *S. aquaticus* have considerably larger home ranges than do females, so that a trap placed on a given mole runway is more likely to take a male than a female. This may account for the fact that 66 per cent of the approximately 800 moles we examined in collections were males.

A number of parameters associated with the fossorial niche tend to limit dispersal, however, and reduce gene flow between populations. Soil type, condition, and moisture are among the most important (Arlton, 1936; Silver and Moore, 1941; Glass, 1943; Davis, 1966). *Scalopus aquaticus* prefers moist, loamy, or sandy soils and is scarce or absent in heavy clay, stony, or gravelly soils (Jackson, 1915; Arlton, 1936; Davis, 1942). Likewise, soil types that may be suitable for habitation but are exceedingly moist or exceedingly dry are often avoided by these animals (Davis, 1942; Glass, 1943). Moles seem to be absent altogether from arid lands (Silver and Moore, 1941).

It is doubtful that rivers present barriers to dispersal because the eastern mole supposedly is a good swimmer (Arlton, 1936). Most likely, the heavy clay soils associated with certain river systems form the real barrier to *Scalopus aquaticus* rather than the rivers themselves.

The eastern mole has a voracious appetite and consumes from 25 to 100 per cent of its weight in food daily (Hisaw, 1923; Christian, 1950; Davis, 1966). Its diet consists primarily of earthworms and insects, although vegetable matter is eaten occasionally, and, in captivity, it eats almost anything from ground beef (Hisaw, 1923) to mice and small birds (Christian, 1950). Factors such as soil acidity, which limit the availability of food items, therefore, present barriers to dispersal. We found that in captivity *Scalopus aquaticus* did well on Alpo dog food.

One of the few times when the eastern mole is known to disperse over the surface of the ground is during the breeding season. Only one litter, of two to five young, is born each year (Scheffer, 1949; Conaway, 1959); the exact gestation period is not known although most authors consider it to be four to five weeks. Davis (1966) and Lowery (1974) stated that the breeding season began in early February in Texas and Louisiana. However, we found that most males in Texas were in breeding condition by December and many as early as November. A female taken on 25 February 1975, near Jasper, Texas, contained three well-developed embryos, and a juvenile male was caught on 10 February 1941 Louisiana. These data indicate that the breeding season in East Texas and Louisiana probably begins as early as January.

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