A MORPHOLOGIC AND MORPHOMETRIC ANALYSIS OF THE "SOREX VAGRANS SPECIES COMPLEX" IN THE PACIFIC COAST REGION

Leslie N. Carraway

CONTENTS

In the first synopsis of shrews of the Pacific Northwest, the "*Sorex vagrans* species complex" included *Sorex bairdii, S. vagrans, S. obscurus*, and *S. pacificus* (Merriam, 1895). Later additions were *S. setosus* (Elliot, 1899), *S. yaquinae*, and *S. o. permiliensis* (Jackson, 1918). *Sorex bairdii, S. setosus, S. o. permiliensis*, and *S. obscurus* were synomized later as *S. monticolus* (Hennings and Hoffmann, 1977; Jackson, 1928).

In 1928, Jackson referred to a *Sorex vagrans-obscurus* (= *monticolus*) complex that included *Sorex vagrans, S. yaquinae, S. monticolus*, and *S. pacificus* (Fig. 1a). He noted that, whereas *S. vagrans* and *S. monticolus* could be distinguished readily in the Pacific Coast region, they were almost indistinguishable in the Rocky Mountain region. He stated also that there was considerable confusion in the systematics of *S. m. bairdii, S. pacificus*, and *S. yaquinae*. The only criteria Jackson (1928) used for separating *S. yaquinae* and *S. pacificus* at the species level was the smaller size of *S. yaquinae* and the apparent appropriateness of its known geographic distribution. Bailey (1936), without comment, reduced *yaquinae* to subspecific status within *S. pacificus* (Fig. 1b).

Sorex monticolus setosus and *S. m. obscurus* were considered to intergrade at many localities in western British Columbia and Washington; a single specimen from Conrad Meadows, Yakima County, Washington, was considered an intergrade between *S. m. setosus* and *S. m. permiliensis* of the northern Cascade Mountains of Oregon; another specimen from Detroit, Marion County, Oregon, was considered an intergrade between *S. m. permiliensis* and *S. m. bairdii*; and a series of specimens from Portland, Multnomah County, Oregon, was considered to consist of intergrades between *S. m. bairdii* and *S. m. permiliensis* (Jackson, 1928).

On the basis of general size and color alone, Findley (1955) stated that the *S. monticolus-vagrans* species complex actually was a Rassenkreis of subspecies of *S. vagrans* (Fig. 1c); he believed that *S. vagrans* and *S. monticolus* in the Rocky Mountain region were not reproductively isolated and that the taxonomic groups occurring in the Pacific Coast region were the noninterbreeding ends of the Rassenkreis. Consequently, he designated *pacificus, yaquinae*, and *monticolus* as subspecies of *S. vagrans*. Johnson and Ostenson (1959) disagreed completely with Findley's (1955) sweeping taxonomic revision of the *Sorex pacificus-monticolus-vagrans* species complex. They emphasized that Findley's (1955) revision required subspecies to be distributed sympatrically with no indication of ecological separation.

As early as 1858, the presence or absence of medial tines, and their position in relation to the red pigmentation, on the first upper incisors (I1) were considered characters of taxonomic importance (Baird, 1858); however, these characters were not applied again to North American soricids until the 1970s. By use of these characters and morphometric
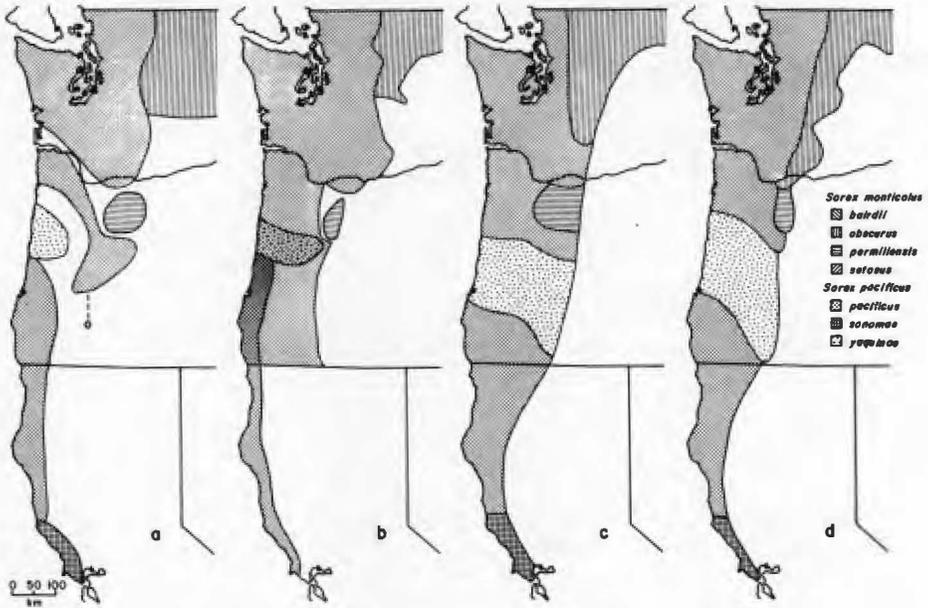
Fig. 1.—Maps of Washington, Oregon, and California overlaid with distributions of subspecies of *S. monticolus* and *S. pacificus* (*sensu* Hennings and Hoffmann, 1977) as described by: a, Jackson (1928); b, Dalquest (1948) for Washington, Bailey (1936) for Oregon, and Ingles (1947) for California; c, Findley (1955); and d, Hennings and Hoffmann (1977). Jackson (1928) considered *yaquinae* a distinct species, Ingles (1947) did not differentiate between subspecies of *S. pacificus*, and Findley (1955) subsumed all taxa into *S. vagrans*.

analyses, Hoffmann (1971) and Hennings and Hoffmann (1977) were able to show that *S. vagrans* and *S. monticolus* were morphologically and ecologically separated species in the Rocky Mountain region (Fig. 1d). They believed that the striking similarity between *S. vagrans* and *S. monticolus* was attributable to character convergence within local populations of *S. vagrans*, not intergradation of the two taxa as Findley (1955) suggested.

Some specimens from Taft, Lincoln County, and Philomath, Benton County, Oregon, areas within the Rassenkreis Findley (1955) described, have characteristics intermediate between *S. pacificus* and *S. m. bairdii* that caused Hennings and Hoffmann (1977) to suggest that they might be hybrids. In a ". . . zone of potential contact" extending "from Lincoln and Taft, Lincoln County, through Corvallis and Philomath, Linn [*sic*] County, and Vida, Lane County, to the crest . . ." of the Cascade Mountains, Oregon, some specimens have pelage characteristics of *S. pacificus* and dental characteristics of *S. m. bairdii* (Junge and Hoffmann, 1981:30). These authors (pp. 30-31) suggested "some hybridization may be occurring" in this zone.

In the Cascade Mountains of Oregon, *S. m. bairdii* was thought to occur as far northward as the north slope of Three Sisters and McKenzie
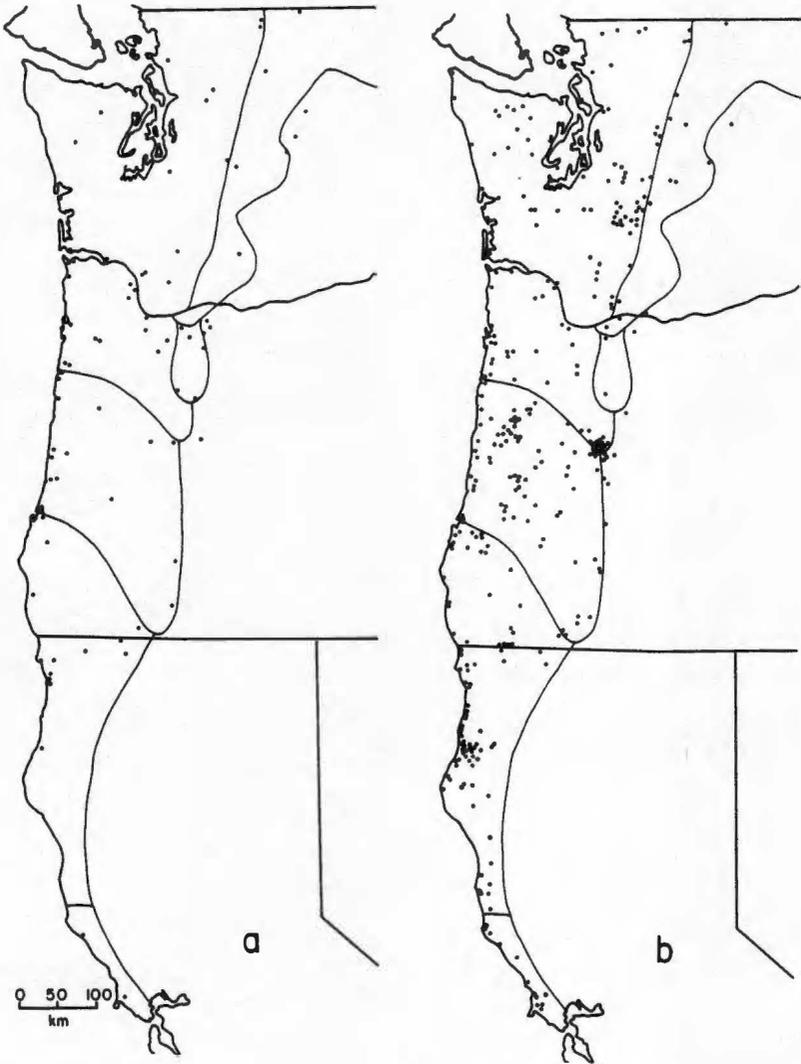
FIG. 2.—Maps of Washington, Oregon, and California overlaid with distributions of subspecies of *S. monticolus* and *S. pacificus* as described by Hennings and Hoffmann (1977) and illustrated in Figure 1d. Unique localities (based on lists of specimens examined) from which specimens were available for study by (a) Hennings and Hoffmann (1977) and (b) for my research are indicated by closed circles.

Bridge, Lane County, where it intergraded with *S. m. permiliensis* that was believed to be distributed as far northward as timberline, Mt. Hood, Hood River County (Hall, 1981; Hennings and Hoffmann, 1977). *S. m. permiliensis* was believed to intergrade to the north with either *S. m. setosus* (Bailey, 1936; Findley, 1955; Hall, 1981; Jackson, 1928) or *S. m.*

obscurus (Hennings and Hoffmann, 1977) at 2 mi. W Parkdale, Hood River County, Oregon.

Investigators who proposed the foregoing taxonomic arrangements did not have sufficient specimens from key areas within of the geographic ranges of the taxa under consideration (Fig. 2) or did not use modern techniques for grouping or analyzing morphometric data on which to base taxonomic conclusions. Because the systematic positions and geographic distributions of these shrews in Washington and western Oregon and California have been the subject of much debate and confusion for the last 90 years, a reevaluation of their systematics is warranted.

The objectives of this research were to describe and evaluate the morphologic and geographic variation within the "*Sorex vagrans* species complex" in the Pacific Coast region of the United States. Particular emphasis was to determine if variation was of a nature to suggest which taxa under consideration were geographic variants and which had specific integrity.

Because of the diverse topographic, edaphic, and vegetative characteristics in the Pacific Coast region, and because of man-induced habitat changes, a much more detailed approach than used heretofore obviously is required to understand geographic variation within the "*Sorex vagrans* species complex." This research represents the first quantitative, detailed evaluation of geographic variation and speciation in that complex in the Pacific Northwest of the United States.

METHODS

Specimens referable to (*sensu* Hennings and Hoffmann, 1977) *Sorex pacificus* (*n* = 776), *S. monticolus* (*n* = 592), and *S. vagrans* (*n* = 931—Carraway, 1987) from Washington, western Oregon, and western California north of San Francisco Bay were included in this study. Of 2777 specimens examined, 2299 adult specimens (based on Jackson's, 1928:14, criteria of possession of slightly to moderately worn teeth), with undamaged skulls, were measured. Holotypes referable to these taxa and their geographic races, within the study area, were examined and measured. For use as an out-group in phenetic analyses, 146 adult *Sorex bendirii palmeri* from western Oregon also were measured (Ward, 1985; Watrous and Wheeler, 1981). Adults that had overwintered and juveniles were excluded because of variation associated with Dehnel's phenomenon and allometric growth (Hyvärinen, 1968; Pucek, 1963, 1970).

Because of the difficulty in assigning individual specimens to taxa based on the published taxonomy of the "*Sorex vagrans* species complex" a more objective approach to classifying specimens was deemed necessary. Therefore, specimens referable to *S. pacificus*, *S. monticolus*, and *S. vagrans* were placed in *a priori* groups (Fig. 3) on the basis of the morphology of the medial edge of the first upper incisors (Hennings and Hoffmann, 1977).

Seventeen cranial and mandibular characters (Fig. 4) were measured on each specimen by use of an ocular micrometer mounted in a Bausch and Lomb binocular microscope or a Fowler Max-Cal electronic caliper. Three standard external measurements were recorded from specimen labels. Width across I1-I1, breadth of the zygomatic plate, length of unicuspid toothrow, greatest condylar depth, and widths of the lower and upper condylar facets were measured with an ocular micrometer. Values were not converted from number of ocular lines to millimeters for multivariate analyses; however, all reported values are in millimeters. All remaining cranial characters were measured with calipers to 0.01 millimeter. Selection of morphometric characters was based on dimensions that other investigators had found useful for distinguishing various taxa of shrews (Choate, 1972; Diersing, 1980; Diersing and Hoffmeister, 1977, 1981; Findley, 1955; Genoways and Choate, 1972; Hennings and Hoffmann, 1977; Junge and Hoffmann, 1981; Moncrief *et al.*, 1982; Pucek, 1963; van Zyll de Jong, 1980) and those characters that did not exhibit linear dependence (Dillon and Goldstein, 1984:63; Pimental and Smith, 1986*b* :19).

Specimens were classified also on the basis of position of the anastomosed infraorbital and lacrimal foramina on the zygomatic plate (Fig. 5) relative to the M1-M2 interface (van Zyll de Jong, 1980). The position of the foramen was coded as 1 for most posterior to 4 for most anterior of the M1-M2 interface.
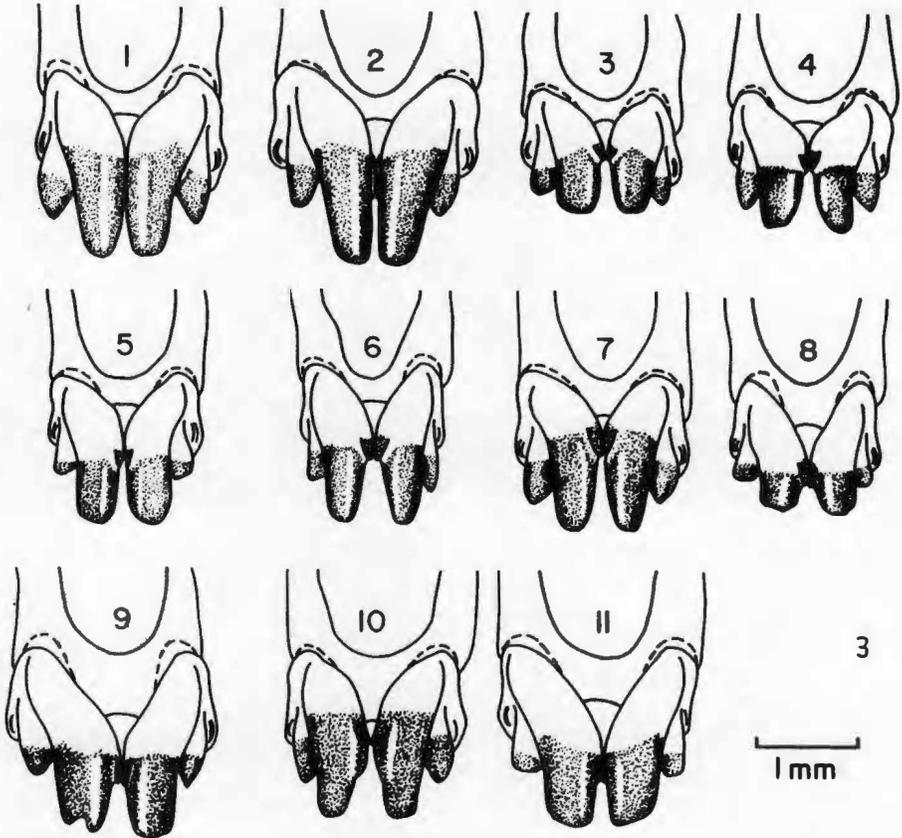
Fig. 3.—Camera-lucida tracings of anterior views of first upper incisors used to illustrate the 11 morphotypes present among individuals within the "*Sorex vagrans* species complex": 1, no projections present on medial edge, pigmented region extends high on teeth, OSUFW 7286; 2, a small ridge present at the posteriomedial edge, pigmented region extends to upper edge of ridge (in some specimens color value of red pigment distinctly different between left and right I1), OSUFW 8306; 3, a small, pointed tine, usually pigmented, present high on medial edge separated from the pigment of tooth that occurs completely vental to tine by a narrow gap of white enamel, OSUFW 1312. Morphotypes 4-9 have in common a large, blunt tine, always pigmented, present high on the medial edge of I1: 4, tine flat, pigmented region of tooth almost completely ventral to tine, flange present along medial edge from tine to tip of tooth, OSUFW 4777; 5, tine flat with pigmented region of tooth extending dorsally halfway alongside tine, OSUFW 4223; 6, tine robust, pigmented region of tooth extends dorsally three-fourths the way alongside tine, SDNHM 16971; 7, tine robust, pigmented region of tooth extends just to dorsal level of tine, OSUFW 4774; 8, tine robust, pigmented region of tooth continuous to tine and extends above tine only along medial edge, OSUFW 4830; 9, tine robust, pigmented region of tooth extends above tine, OSUFW 1038. Morphotype 10 has a large, robust, pointed tine, a large flange present from tine ventrally to twice the length of the tine, and the pigmented region of the tooth extends well above the tine, OSUFW 2979. Morphotype 11 has a large, flat tine, and the pigmented region of tooth extends well above the tine, PSM 14453.
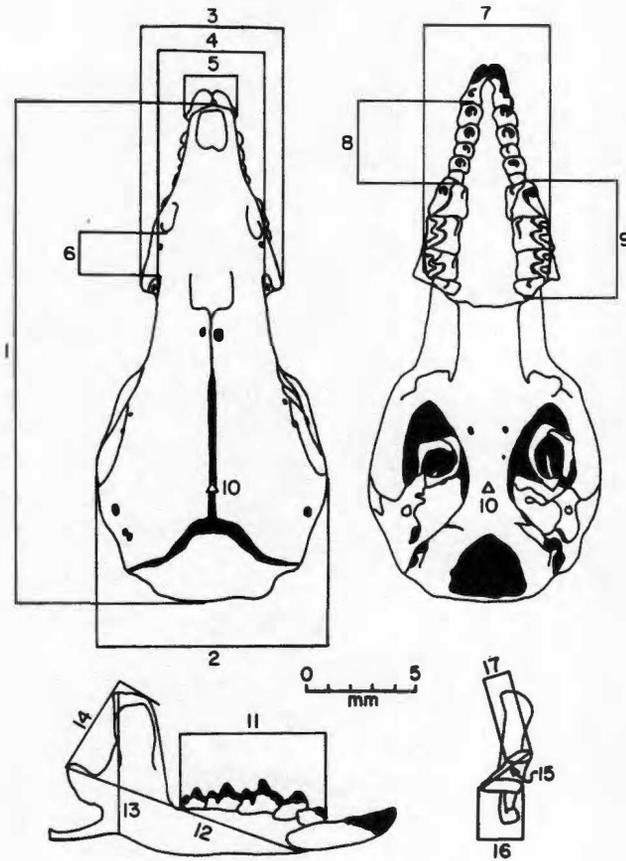
FIG. 4.—Camera-lucida tracing of skull of a *Sorex* (PSM 14425) illustrating skull dimensions measured (after van Zyll de Jong, 1980:67, fig. 1): 1, greatest length of skull; 2, cranial breadth; 3, maxillary breadth; 4, least interorbital breadth; 5, width across I1-I1; 6, breadth of zygomatic plate; 7, breadth at M2-M2; 8, length of unicuspid toothrow; 9, length of complex toothrow; 10, depth of cranium; 11, length of mandibular toothrow; 12, length of mandible; 13, height of coronoid process; 14, coronoid process-condyle length; 15, greatest condylar depth; 16, width of lower condylar facet; 17, width of upper condylar facet.

Sexes of each morphotype were not tested for significant sexual dimorphism initially because of the potential for more than one taxon being included in each morphotype, or conversely, more than one morphotype being referable to the same taxon. I assumed that even if females and
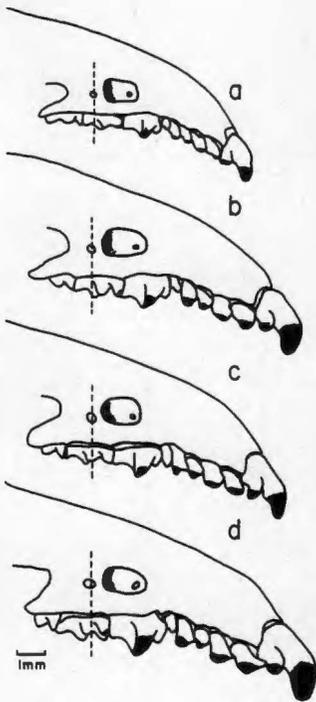
FIG. 5.—Camera-lucida tracings of the lateral view of the maxillary and adjacent regions of various taxa of *Sorex* with the position of the lacrimal foramen on the zygomatic plate relative to M1 illustrated (dashed line; after van Zyll de Jong, 1980:71, fig. 5): a, position 1, foramen more posterior to metacone of M1 than in position 2, but not overlapping the M1-M2 interface, PSM 2166; b, position 2, foramen immediately posterior to metacone of M1, OSUFW 4604; c, position 3, foramen directly in line with metacone of M1, OSUFW 4602; d, position 4, foramen anterior to metacone of M1, PSM 14424. Position of foramen determined by a line drawn through the center of the foramen to M1 perpendicular to the ventral plane of the maxillary.

males within a taxon were morphometrically different that they still would be more like each other than another taxon (Derrickson and Ricklefs, 1988). Therefore, after taxa were established, sexes within each taxon were tested to determine if significant sexual dimorphism was present. All skull drawings were made with the aid of either a Wield or Ziess camera lucida and all illustrated taxa are to the same scale.

Multivariate analyses were performed on data for the 11 morphotypes and subunits derived therefrom by use of the programs multigroup discriminant function analysis in BIOTAT II (Pimental and Smith, 1986*b*); covariance analysis in STATGRAPHICS (Statistical Graphics Corporation, 1987); and similarity for interval data by use of the Euclidean distance coefficient, minimum-spanning tree, unweighted pair-group method by use of arithmetic average cluster analysis, and Burnaby's methods for size adjustment in NTSYS-pc (Rohlf, 1988). Univariate analyses were performed by use of programs for frequency distributions, basic descriptive statistics, and one-way analysis of variance in BIOTAT I (Pimental and Smith, 1986*a*). Descriptive methods, regression analysis, nonparametric methods, mathematical functions, and procedures for plotting functions were performed in STATGRAPHICS (Statistical Graphics Corporation, 1987). In all analyses, a probability level of $P < 0.05$ was accepted as statistically significant.

Variable vectors, the standardized canonical vectors for within groups, were plotted on perpendicular axes by use of the same X, Y scales as the associated canonical axes. The plot of variable vectors, placed at the origin of the canonical-variates plot, provided an overview of the size relationships of characters that contributed to the separation of the forms (Jolicoeur, 1959).

I constructed 95 percent confidence ellipses around group centroids calculated from

canonical-variate scores. The ellipses were constructed for each form from eigenvalues and eigenvectors (Statistical Graphics Corporation, 1987) derived from the variance-covariance matrix (Statistical Graphics Corporation, 1987) based on the canonical-variate scores. The arc cosine of the first eigenvector was used as the angle of inclination from the canonical-variate axes for the major axis of the ellipse. The eigenvalues and n for each form then were used to calculate the half-lengths for the major and minor axes; the focal length was determined by the square root of the difference of the two squared half-lengths. The focal length and half-length of the minor axis then were used as the major and minor radii, respectively, of the ellipse (Owen and Chmielewski, 1985).

In species accounts, synonymies contain the original taxonomic designation, new name combinations, and junior synonyms. Brown (1970, 1974) described karyotypes of several taxa considered herein; however, species identifications, catalog numbers, and collection localities for specimens listed in his reports do not correspond with specimens in the mammal collection at the University of California at Davis. Therefore, karyotypic differences reported by Brown (1970, 1974) are not used in diagnoses or descriptions of taxa described in species accounts. In lists of specimens examined, specimens measured are ordered alphanumerically by state, county, and major geographic point in specific locality of collection site, and museum acronym and catalog number. Specimens misclassified in discriminant analyses are indicated with an asterisk. A small percentage of specimens were not cataloged at the time they were measured; therefore, they are referred to by museum acronym followed by the original collector's number including one or more letters as a prefix. On distribution maps, symbols for localities include all specimens for which the collection locality is within the diameter of the symbol. Such localities are indicated by italics in the specimens examined lists. A key to species is presented after the species accounts.

<center>RESULTS</center>

Summary statistics ($\bar{x} \pm SE$, range, and CV) were calculated for all 20 variables for the 2299 individuals classified into morphotypes 1 to 11 (Table 1). To evaluate the cohesiveness of these 11 morphotypes, I used them as *a priori* groups in a multiple discriminant analysis (Fig. 6). Only 50 percent of the 2299 individuals included were classified correctly into their *a priori* groups. The first two significant canonical-variate axes (V_1 = 6365.73, *d.f.* = 209; V_2 = 1772.33, *d.f.* = 180; V test—Dillon and Goldstein, 1984:405) accounted for 87.1 and 9.6 percent of the variation,
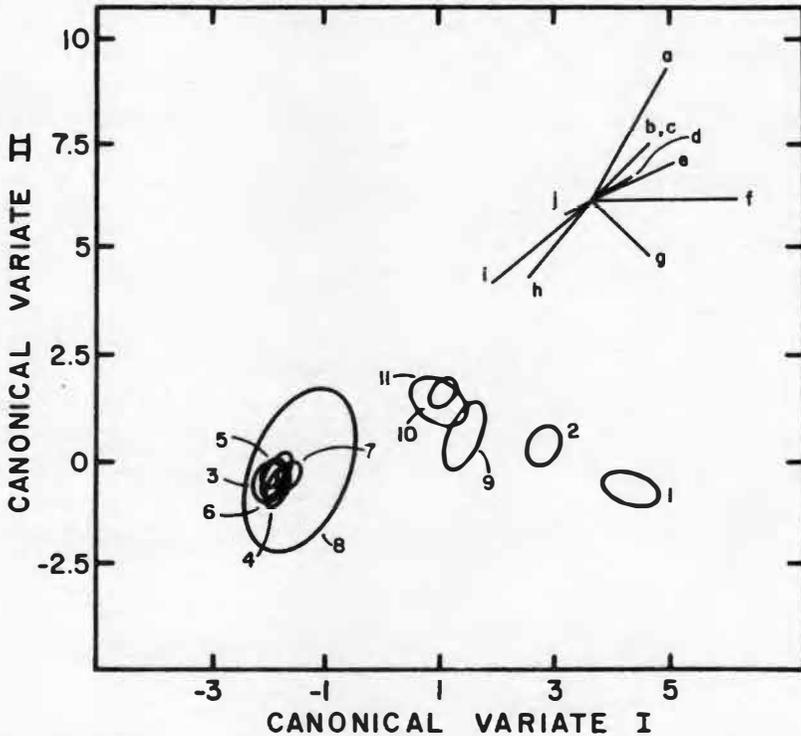
Fig. 6.—Canonical-variates plot of morphotypes 1 to 11 based on 20 variables with 95 percent confidence ellipses for the bivariate group centroids. Canonical-variate axis I accounted for 87.1 percent and canonical-variate axis II 9.6 percent of the variation present among the morphotypes. The confidence ellipse for morphotype 8 is distorted relative to the others because of small sample size. The 11 morphotypes sorted into four distinct morphologic units. Differences in cranial morphology among the four units are characterized by the variable vectors projected onto the upper right corner of the canonical-variates plot. The relationship of characters among the units are indicated by the length and orientation of the vector relative to the canonical-variate axes. From left to right, individuals in the four units have a deeper coronoid process, longer unicuspid toothrow, complex toothrow, mandibular toothrow, and tail, and wider least interorbital breadth, cranial breadth, and width across I1-I1. Variables are lettered as follows: a, length of tail; b, length of complex toothrow; c, least interorbital breadth; d, cranial breadth; e, width across I1-I1; f, height of coronoid process; g, length of unicuspid toothrow; h, length of mandible; i, maxillary breadth; and j, length of hind foot.

respectively, among morphotypes 1-11. The percentage of the variance of each of 13 of the 20 variables in the first canonical-variate axis ranged from 70.7 to 98.4 percent. Because there was such poor classification and so many variables were involved in the first canonical-variate axis, the 11 morphotypes were considered to have limited taxonomic meaning; however, they formed four morphologic units (Fig. 6): those with a smooth medial edge on I1 (morphotype 1), those with a ridge at the posteriomedial edge of I1 (morphotype 2), those with a small medial tine on I1 with pigment not extending above the level of the tine (morphotypes 3-8), and those with a large medial tine on I1 with pigment extending well above the tine (morphotypes 9-11; Fig. 3).

Because of the great size variation present among morphotypes 1-11, Burnaby's method for size adjustment (Burnaby, 1966; Rohlf, 1988; Rohlf and Bookstein, 1987) was applied to the data. The resultant principal-component analysis, with size variation removed, showed no relationship to the geographic distributions of the specimens involved. The remaining variation that related to shape, appeared to be biologically random and nonadaptive. Consequently, no attempt was made to remove size variation from the data in further analyses.

Among morphotypes 1-11 the most conspicuous nonconformity was that the coefficients of variation for all 20 variables were as much as 2.8 times greater for morphotype 1 than for any other morphotype category (Table 1). I believed that this was indicative of a polymorphic group; also, a plot of canonical-variate scores for individuals in morphotype 1 showed two distinct clouds of points (Fig. 7). Particularly apparent was the considerable variation in the length of the unicuspid toothrow exhibited by individuals in morphotype 1 relative to the other morphotypes (Table 1).

Morphotype 1

To analyze further the relationships among individuals in morphotype 1, I made three lists of specimens: those that fell within the upper 15 percent of the range, within the lower 15 percent of the range, and within 7.5 percent of the mean of length of the unicuspid toothrow. From each list I selected, by use of a table of random numbers, 30 individuals.

The groups of small, intermediate, and large individuals were analyzed by multiple discriminant analysis based on 19 variables; because length of the unicuspid toothrow was used to form the groups, it was excluded from this particular analysis. A diagnosis file also was produced from this discriminant analysis. In discriminant space, the group of small individuals was separated completely from the other two groups and the group of intermediate individuals overlapped with the group of large individuals by 13 percent. The remaining 541 specimens in morphotype 1 then were classified into the groups of small, intermediate,

TABLE 1.—*Means (±SE), ranges (in parentheses), and CVs of measurements (in mm.) of skull (exclusive of mandible) characters of specimens placed into 11 a priori groups based on morphology of 11. Groups contained individuals of the "Sorex vagrans species complex" (Findley, 1955) from Washington, western Oregon, and northern California.*

Type	n	Greatest length of skull	Cranial breadth	Maxillary breadth	Least interorbital breadth	Cranial depth	Breadth at M2-M2	Length of unicuspid toothrow	Length of complex toothrow	Width across 11-11	Breadth of zygomatic plate
1	631	20.79±0.05 (16.50-23.22) 6.19	10.09±0.02 (8.50-11.94) 5.55	6.24±0.02 (4.99-7.21) 7.95	4.13±0.01 (3.14-4.99) 6.78	5.53±0.01 (4.27-6.64) 6.15	5.56±0.02 (4.31-6.46) 7.55	3.35±0.01 (2.60-4.07) 10.45	5.11±0.01 (4.11-6.21) 6.26	2.08±0.01 (1.50-2.47) 9.47	1.51±0.01 (1.00-2.80) 11.92
2	144	19.27±0.06 (17.55-22.09) 3.92	9.40±0.03 (8.49-10.47) 3.37	5.62±0.02 (4.83-6.64) 4.98	3.82±0.02 (3.18-4.38) 5.50	5.47±0.02 (4.72-6.50) 4.94	5.07±0.02 (4.38-5.96) 5.33	2.99±0.01 (2.63-3.63) 5.73	4.75±0.02 (3.98-5.47) 5.05	1.84±0.01 (1.63-2.46) 6.52	1.37±0.01 (1.00-1.77) 10.07
3	188	16.32±0.03 (14.93-17.65) 2.51	8.10±0.02 (7.37-8.81) 2.75	4.65±0.02 (4.01-5.15) 4.45	3.13±0.01 (2.80-3.81) 4.94	4.71±0.02 (4.05-5.94) 6.45	4.18±0.01 (3.69-4.74) 4.42	2.26±0.01 (2.00-2.55) 3.86	4.00±0.01 (3.63-4.41) 3.81	1.39±0.01 (1.10-1.57) 5.22	1.07±0.01 (0.77-1.47) 11.50
4	238	16.47±0.03 (14.93-18.13) 2.76	8.18±0.02 (7.45-9.43) 3.25	4.71±0.01 (4.15-5.56) 4.85	3.16±0.01 (2.73-3.91) 4.61	4.78±0.02 (3.91-5.53) 5.91	4.24±0.01 (3.77-4.83) 4.65	2.28±0.01 (2.07-2.77) 3.96	4.02±0.01 (3.53-4.64) 3.94	1.39±0.01 (0.97-1.63) 5.75	1.08±0.01 (0.70-1.40) 10.87
5	335	16.38±0.02 (15.25-17.57) 2.42	8.10±0.01 (7.96-8.83) 2.90	4.63±0.01 (3.97-5.23) 4.35	3.11±0.01 (2.67-3.55) 4.46	4.82±0.01 (4.07-5.53) 5.43	4.18±0.01 (3.57-4.68) 4.14	2.28±0.00 (2.03-2.57) 3.67	4.02±0.01 (3.55-4.38) 3.58	1.37±0.00 (1.17-1.53) 4.81	1.05±0.01 (0.77-1.37) 10.49
6	78	16.54±0.05 (15.18-18.21) 2.74	8.15±0.03 (7.41-8.92) 3.21	4.72±0.02 (4.10-5.28) 4.13	3.16±0.02 (2.84-3.45) 4.39	4.85±0.04 (4.25-5.53) 6.61	4.26±0.02 (3.82-4.72) 4.56	2.30±0.01 (2.03-2.57) 3.84	4.06±0.02 (3.61-4.41) 4.05	1.38±0.01 (1.03-1.53) 5.95	1.08±0.01 (0.87-1.40) 9.37
7	73	16.57±0.08 (13.69-19.30) 4.17	8.21±0.04 (7.70-9.41) 3.81	4.75±0.03 (4.17-5.81) 5.33	3.18±0.03 (2.84-4.08) 6.79	4.86±0.03 (4.25-5.52) 5.99	4.27±0.03 (3.86-5.28) 5.30	2.32±0.02 (2.10-2.83) 5.89	4.07±0.02 (3.79-4.73) 4.63	1.39±0.01 (1.23-1.90) 6.75	1.06±0.02 (0.80-1.53) 12.40
8	19	16.77±0.23 (15.58-19.50) 6.02	8.37±0.11 (7.53-9.69) 5.60	4.86±0.09 (4.34-5.99) 8.54	3.26±0.06 (2.94-4.12) 8.37	4.78±0.07 (4.36-5.33) 6.19	4.38±0.08 (4.00-5.29) 7.97	2.34±0.05 (2.17-3.00) 9.40	4.13±0.06 (3.81-4.91) 6.95	1.44±0.03 (1.27-1.93) 11.67	1.11±0.02 (0.97-1.33) 8.02
9	39	18.43±0.11 (16.29-19.39) 3.74	9.06±0.05 (8.01-9.66) 3.75	5.40±0.04 (4.74-5.91) 5.00	3.70±0.04 (3.17-4.16) 5.95	5.05±0.04 (4.29-5.66) 5.49	4.84±0.04 (4.25-5.30) 5.56	2.73±0.03 (2.27-3.17) 6.92	4.52±0.03 (4.01-4.87) 4.58	1.71±0.02 (1.49-1.97) 7.54	1.34±0.03 (1.00-1.73) 12.76
10	428	17.99±0.04 (15.83-20.16) 4.51	8.81±0.02 (7.87-9.98) 4.51	5.15±0.01 (4.26-5.95) 5.71	3.54±0.01 (2.87-4.11) 5.54	5.24±0.01 (4.47-6.09) 5.80	4.67±0.01 (3.91-5.46) 5.33	2.61±0.01 (2.07-3.07) 7.82	4.45±0.01 (3.83-5.00) 4.70	1.61±0.01 (1.30-2.00) 9.07	1.23±0.01 (0.80-1.87) 12.76
11	125	17.97±0.07 (16.76-19.73) 4.17	8.81±0.03 (8.05-9.56) 4.20	5.17±0.02 (4.57-5.98) 5.15	3.57±0.02 (3.13-4.14) 5.92	4.99±0.03 (4.31-5.77) 5.61	4.69±0.02 (4.21-5.43) 4.58	2.61±0.02 (1.43-3.07) 8.05	4.44±0.02 (3.88-4.88) 4.66	1.62±0.01 (1.37-1.97) 8.46	1.23±0.01 (0.85-1.67) 13.37

TABLE 1.—*Continued.*

Type	n	Length of mandibular toothrow	Length of mandible	Height of coronoid process	Coronoid process-condylar length	Greatest condylar depth	Width of lower condylar facet	Width of upper condylar facet	Total length	Tail length	Length of hind foot
1	631	6.02±0.02 (4.72-6.78) 7.31	9.15±0.03 (7.59-10.41) 7.21	5.68±0.02 (4.27-6.68) 9.51	3.87±0.02 (2.62-6.07) 11.63	2.66±0.01 (1.80-3.13) 7.89	1.64±0.01 (1.00-2.10) 9.15	1.17±0.01 (0.83-1.93) 11.11	133.75±0.47 (105-180) 8.82	58.41±0.24 (36-85) 10.44	15.990±.06 (11-22) 9.32
2	144	5.48±0.02 (4.60-6.48) 5.26	8.34±0.03 (7.40-9.91) 4.77	5.00±0.02 (4.31-6.27) 5.96	3.38±0.02 (2.81-4.39) 7.40	2.39±0.01 (2.17-2.93) 5.65	1.45±0.01 (1.27-1.77) 6.48	1.04±0.01 (0.87-1.63) 9.62	121.92±0.74 (103-149) 7.34	53.94±0.44 (44-89) 9.91	14.69±0.08 (12-18) 6.44
3	188	4.56±0.01 (3.63-5.00) 3.82	7.03±0.02 (6.29-7.83) 3.54	3.65±0.01 (3.03-4.34) 4.66	2.66±0.01 (2.07-3.11) 6.65	2.03±0.01 (1.63-2.40) 5.00	1.17±0.01 (0.97-1.33) 5.94	0.83±0.01 (0.63-1.00) 8.90	99.95±0.57 (80-130) 7.89	39.62±0.28 (25-53) 9.82	12.04±0.06 (10-14) 6.84
4	238	4.59±0.01 (3.88-5.33) 3.97	7.09±0.02 (6.29-7.88) 3.42	3.68±0.01 (3.28-4.39) 4.74	2.69±0.01 (2.27-3.28) 6.70	2.06±0.01 (1.77-2.47) 5.36	1.19±0.01 (1.00-2.10) 7.91	0.84±0.00 (0.67-1.07) 8.48	99.89±0.47 (79-120) 7.27	40.56±0.29 (27-53) 9.69	12.37±0.06 (10-18) 7.23
5	335	4.59±0.01 (4.15-5.00) 3.18	7.02±0.01 (6.42-7.81) 3.34	3.64±0.01 (3.20-4.26) 4.56	2.65±0.01 (2.26-3.11) 6.00	2.02±0.01 (1.80-2.70) 5.30	1.17±0.00 (1.00-1.83) 6.37	0.83±0.00 (0.67-1.03) 8.11	97.98±0.37 (80-119) 7.01	40.13±0.20 (23-55) 9.16	12.28±0.05 (10-18) 7.50
6	78	4.64±0.02 (3.53-5.00) 4.26	7.11±0.03 (6.51-7.97) 3.39	3.71±0.02 (3.34-4.19) 4.49	2.68±0.02 (2.23-2.97) 6.49	2.06±0.01 (1.73-2.27) 4.64	1.18±0.01 (1.00-1.30) 5.62	0.85±0.01 (0.70-1.07) 7.98	98.23±0.71 (86-116) 6.38	40.59±0.39 (32-49) 8.64	12.19±0.12 (10-17) 8.47
7	73	4.65±0.03 (4.27-5.66) 5.11	7.11±0.04 (6.48-8.43) 4.71	3.72±0.03 (3.41-5.10) 6.03	2.71±0.02 (2.34-3.39) 6.75	2.07±0.01 (1.87-2.40) 5.36	1.19±0.01 (1.07-1.43) 6.30	0.85±0.01 (0.70-1.10) 9.31	99.02±0.92 (83-128) 7.95	41.68±0.61 (30-58) 12.49	12.29±0.12 (10-16) 8.19
8	19	4.66±0.11 (3.49-5.79) 10.09	7.29±0.11 (6.90-8.81) 6.76	3.83±0.10 (3.46-5.13) 11.85	2.73±0.07 (2.42-3.45) 10.62	2.04±0.04 (1.70-2.50) 8.33	1.18±0.03 (1.06-1.53) 10.93	0.83±0.02 (0.73-1.07) 10.48	100.95±2.56 (87-128) 11.05	40.58±1.12 (32-58) 14.17	12.21±0.33 (10-16) 11.77
9	39	5.26±0.04 (4.64-5.74) 4.87	8.00±0.05 (7.31-8.61) 4.13	4.45±0.06 (3.64-5.08) 7.87	3.09±0.04 (2.65-3.65) 8.09	2.27±0.02 (2.03-2.43) 5.07	1.35±0.02 (1.20-1.57) 7.19	1.01±0.01 (0.83-1.17) 8.61	122.77±1.32 (100-138) 6.79	53.63±0.83 (35-63) 9.77	14.55±0.17 (12-16) 7.62
10	428	5.12±0.01 (4.15-5.77) 4.82	7.68±0.02 (6.60-8.76) 5.51	4.26±0.02 (3.45-5.34) 10.26	2.97±0.01 (2.40-3.75) 8.28	2.13±0.01 (1.77-2.57) 7.65	1.25±0.01 (0.80-1.57) 9.92	0.90±0.01 (0.70-1.30) 10.89	117.79±0.36 (82-143) 6.32	52.45±0.22 (32-64) 8.64	13.82±0.05 (10-18) 8.14
11	125	5.11±0.02 (4.72-5.65) 4.11	7.67±0.03 (6.84-8.62) 5.06	4.28±0.03 (3.61-5.09) 9.37	2.95±0.02 (2.47-3.50) 8.78	2.14±0.02 (1.50-2.90) 8.36	1.27±0.01 (1.07-1.50) 9.29	0.89±0.01 (0.67-1.20) 12.70	119.94±0.68 (103-142) 6.38	52.83±0.37 (41-70) 7.91	13.95±0.08 (12-19) 6.80
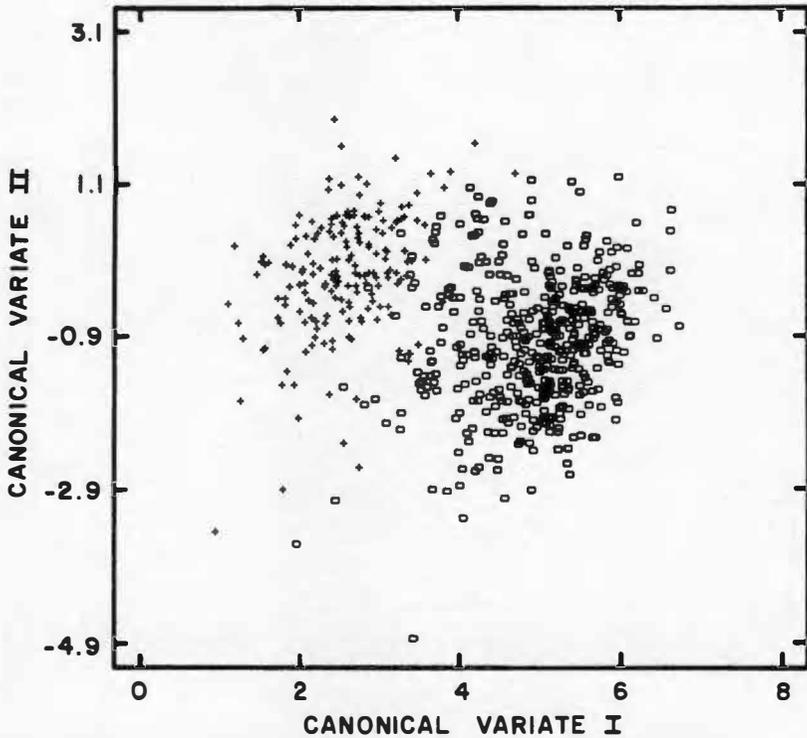
Fig. 7.—Enlargement of canonical-variates plot of morphotype 1 in Figure 6 used to illustrate presence of two distinct clouds of points in canonical space. The cloud of points at the upper left represents small individuals and at the lower right large individuals.

or large individuals based on the diagnosis file previously produced. Of these, 139 were classified as small individuals, 239 as intermediate individuals, and 163 as large individuals. These specimens then were added to their respective parent-groups and a multiple discriminant analysis, based on all 20 variables, was performed on all 631 specimens placed into the three *a priori* groups. This resulted in 92 percent correct classification. Of the 50 misclassified specimens, 13 were from the group of intermediate individuals that had high probabilities (59-96 percent) of belonging with the group of small individuals. These 13 specimens were collected within the geographic distribution of the small individuals; consequently, they were placed with the group of small individuals in subsequent analyses. Two canonical-variate axes were significant (V_1 = 1295.71, *d.f.* = 57; V_2 = 81.04, *d.f.* = 36); however, the percentage of variance of 17 of the 20 variables in canonical-variate axis I ranged from 72.5 to 100.0 percent. All Mahalanobis' D^2 values (D^2 [small/ intermediate] = 18.67, D^2 [small/large] = 42.72, D^2 [intermediate/large] = 5.79) were significant (Z = 94.48, *d.f.* = 20, 430; Z = 175.98, *d.f.* = 0, 328; Z = 30.51, *d.f.* = 20, 441, respectively; Z test—Dillon and Goldstein,
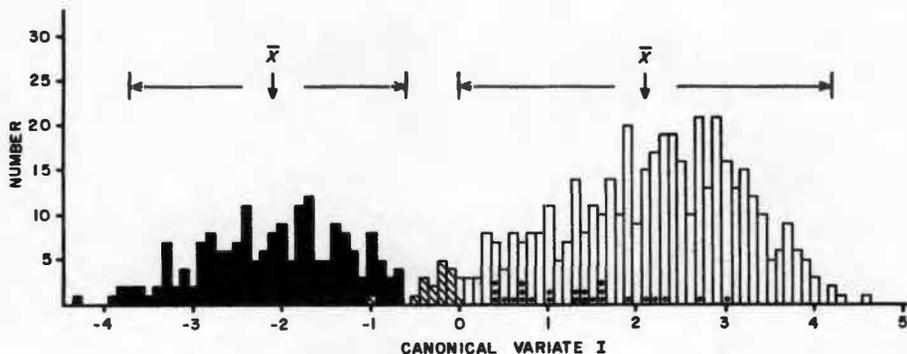
FIG. 8.—Canonical-variate plot of small (n = 182; left) and large (n = 450, right) individuals in morphotype 1 with group centroids ($\bar{x}$) and 95 percent confidence intervals (arrows) indicated. Individuals misclassified (n = 17) are indicated by cross-hatching. *Sorex pacificus sonomae* is represented by closed circles.

1984:369). The confidence limit for the group of small in- dividuals did not overlap either of the other groups; however, the con- fidence limits for the groups of intermediate and large individuals overlapped by 45 percent. The centroids for the groups of intermediate and large individuals were not significantly different (t = 1.65, $d.f.$ = 460). Analysis, by minimum-spanning tree, of the groups of small, intermediate, and large individuals indicated that the latter two groups were much closer to one another in taxonomic space (distance value = 4.87) than either was to the former (distance value = 14.69). Furthermore, collection localities for the intermediate individuals completely overlapped those of large individuals, whereas the distribution of the group of small individuals was parapatric with that of the groups of intermediate and large individuals.

The group of small individuals and the combined group of inter- mediate and large (hereafter referred to as large) individuals then were submitted to a multiple discriminant analysis that resulted in 98 percent correct classification of individual specimens (Fig. 8). The canonical- variate axis was significant (V = 948.92, $d.f.$ = 38) as was the Ma- halanobis' D^2 = 17.64 (Z = 110.77, $d.f.$ = 20, 610). Fourteen of the vari- ables had high positive coefficients of correlation with the canonical- variate axis: greatest length of skull (0.820); cranial breadth (0.672); maxillary breadth (0.781); least interorbital breadth (0.600); breadth at M2-M2 (0.759); length of unicuspid toothrow (0.777); length of complex toothrow (0.718); length of mandibular toothrow (0.879); length of man- dible (0.790); height of coronoid process (0.774); coronoid process- condylar length (0.551); greatest condylar depth (0.655); width of lower condylar facet (0.553); and width across I1-I1 (0.729). Thus, the vari- ables involved with the canonical-variate axis indicated that individuals
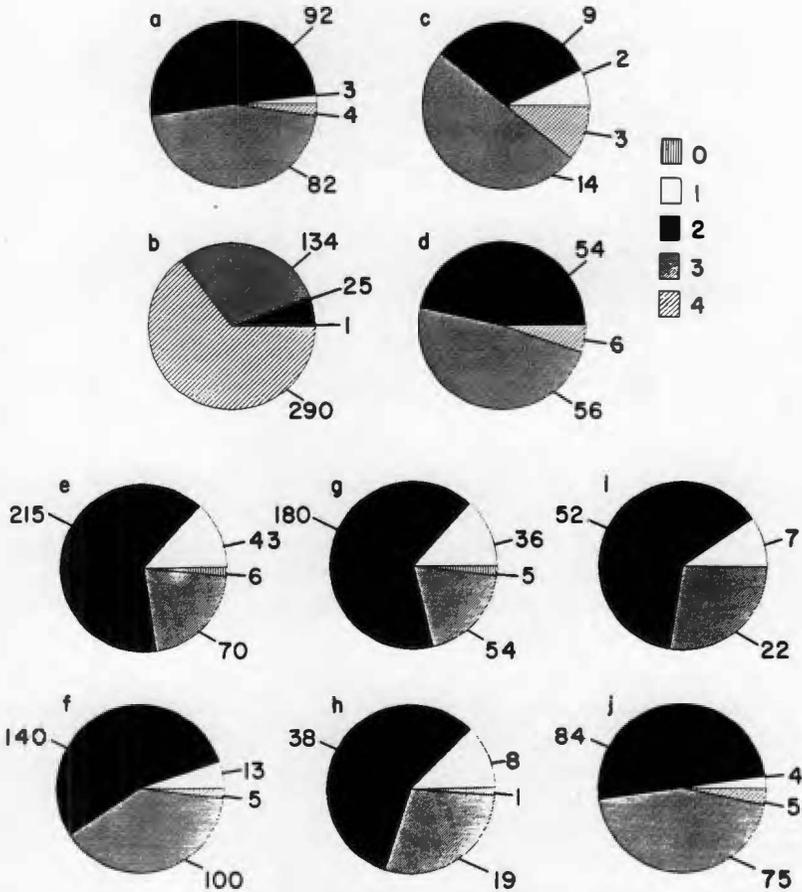
FIG. 9.—Pie diagrams illustrating the proportions of individual shrews without a foramen on the zygomatic plate (0) and with the foramen in positions 1, 2, 3, and 4 for subunits of morphotype 1–a) group of small individuals, b) group of large individuals; morphotype 2–c) group of individuals from the Coast Range, d) group of individuals from the Cascade Mountains; morphotypes 9-11–e) group of individuals north of the Columbia River, f) group of individuals south of the Columbia River, g) group of individuals from western Washington (includes seven specimens from northern Hood River County and eastern Multnomah and Clackamas counties, Oregon), h) group of individuals from eastern Washington, i) group of individuals from Coast Range in Oregon, and j) group of individuals from Cascade Mountains in Oregon. Positions of the foramen on the zygomatic plate for all 10 pie diagrams are as indicated in key; numerals surrounding pie diagrams are samples sizes. Proportions for a-b, e-f, and i-j are significantly different ($P < 0.05$).

increased in size from left to right in the canonical-variate plot (Fig. 8). These groups of small and large individuals correspond to the upper left and lower right clouds of points, respectively, in Figure 7. The proportions of the positions of the foramen in the zygomatic plate for the groups of small and large individuals (Fig. 9) were significantly different (G = 302.16, $d.f.$ = 3). The groups of small and large individuals, with
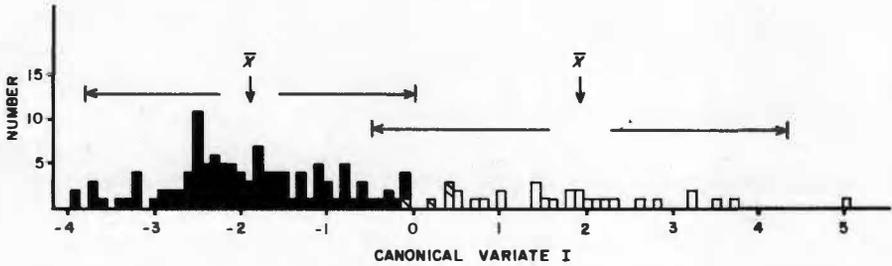
Fig. 10.—Canonical-variate plot of individuals in the Cascade Mountains (n = 113, left) and Coast Range (n = 27, right), Oregon, in morphotype 2 with group centroids ($\bar{x}$) and 95 percent confidence intervals (arrows) indicated. Individuals misclassified (n = 4) are indicated by cross-hatching.

a taxonomic distance of 16.98, will be considered separate groups in subsequent analyses. Of the 20 variables, only the means for length of unicuspid toothrow, width across I1-I1, and width of upper condylar facet were significantly different (t = 2.98, 2.34, 2.56, respectively, $d.f.$ = 174) between sexes for the group of small individuals; only the means for cranial depth, width across I1-I1, and height of coronoid process were significantly different (t = 2.54, 2.55, 2.27, respectively, $d.f.$ = 426) between sexes for the group of large individuals.

Morphotype 2

There is a 69-kilometer gap within the geographic distribution of individuals in morphotype 2; no specimens were available from T5W through T2E between the Coast Range and the Cascade Mountains, Oregon. Consequently, I assigned individuals in morphotype 2 into either a Coast Range (n = 28) group or Cascade Mountains (n = 116) group. Proportions of positions of foramen on the zygomatic plate for groups from the Coast Range and Cascade Mountains (Fig. 9) were not significantly different (G = 79.03, $d.f.$ = 3). However, multiple discriminant analysis of these two groups resulted in 97 percent correct classification (Fig. 10); the canonical-variate axis was significant (V = 154.65, $d.f.$ = 38). Morphometrically, the individuals in the Coast Range group are larger than those in the Cascade Mountains group and the high positive coefficients of correlation that greatest length of skull (0.515), maxillary breadth (0.516), breadth at M2-M2 (0.577), length of unicuspid toothrow (0.604), length of mandibular toothrow (0.537), length of mandible (0.534), total length (0.618), tail length (0.523), and length of hind foot (0.568) have with the canonical-variate axis supports this assessment. The groups from the Coast Range and Cascade Mountains have significantly different means (t values range from 2.35 to 10.73, $d.f.$ = 142) for all variables except depth of cranium. The Mahalanobis' D^2 = 14.02 was significant (Z = 13.69, $d.f.$ = 20, 123)

and the group centroids (Coast Range group, 1.872; Cascade Mountains group, -1.872) also were significantly different (t = 2.47, $d.f.$ = 142). Consequently, the groups from the Coast Range and Cascade Mountains in morphotype 2 were considered separate groups in subsequent analyses. Of the 20 variables, there were no significant differences between sexes for the Coast Range group and only the mean for length of unicuspid toothrow was significantly different (t = 3.22, $d.f.$ = 109) between sexes for the Cascade Mountains group.

Morphotypes 3-8

Morphotypes 3, 4, 5, 6, 7, and 8 were used as *a priori* groups in a multiple discriminant analysis that resulted in 31 percent correct classification. There were no discernable subunits in the discriminant space and the 95 percent confidence ellipses completely overlapped (Fig. 6). Geographically, the individuals in each of these six groups are distributed from Washington to California in no discernable pattern. The means for all 20 variables among morphotypes 3-8 were not significantly different (Table 1). For the 20 variables used in the discriminant analysis there was a mixture of low positive and negative coefficients of correlation to canonical-variate axes I and II. This indicated that no single variable or combination of variables distinguished among morphotypes 3-8. Six Mahalanobis' D^2 values among the 15 pair-wise combinations of groups (D^2 [3 and 4] = 0.36; D^2 [3 and 5] = 0.60, Z = 3.50, $d.f.$ = 502; D^2 [3 and 6] = 1.12, Z = 2.85, $d.f.$ = 245; D^2 [3 and 7] = 1.21, Z = 2.94, $d.f.$ = 240; D^2 [3 and 8] = 3.16; D^2 [4 and 5] = 0.52; D^2 (4 and 6] = 0.71, Z = 2.86, $d.f.$ = 294; D^2 [4 and 7] = 0.64; D^2 [4 and 8] = 2.98, Z = 2.43, $d.f.$ = 235; D^2 [5 and 6] = 0.52; D^2 [5 and 7] = 0.61; D^2 [5 and 8] = 3.54, Z = 3.01, $d.f.$ = 333; D^2 [6 and 7] = 0.41; D^2 [6 and 8] = 3.16; D^2 [7 and 8] = 3.25) were significant. Analysis of morphotypes 3-8 by minimum-spanning tree indicated that they formed a tight cluster (distance values ranged from 0.59 to 1.4) far removed from other morphotypes (a distance value of 20.25 separated morphotypes 3-8 from all others). Therefore, I combined morphotypes 3-8 in subsequent analyses. Of the 931 specimens, 0.8 percent had the foramen on the zygomatic plate in position one, 42.6 percent in position two, 53.4 percent in position three, and 2.9 percent in position four; four specimens (0.4 percent) had no foramen on the zygomatic plate. Of the 20 variables, only the means for greatest length of skull, cranial breadth, maxillary breadth, width across I1-I1, breadth of zygomatic plate, length of mandible, greatest condylar depth, and tail length were significantly different (t = 3.20, 4.27, 2.00, 3.00, 2.00, 2.61, 3.00, 2.90, respectively, $d.f.$ = 756) between sexes for the combined morphotypes 3-8.
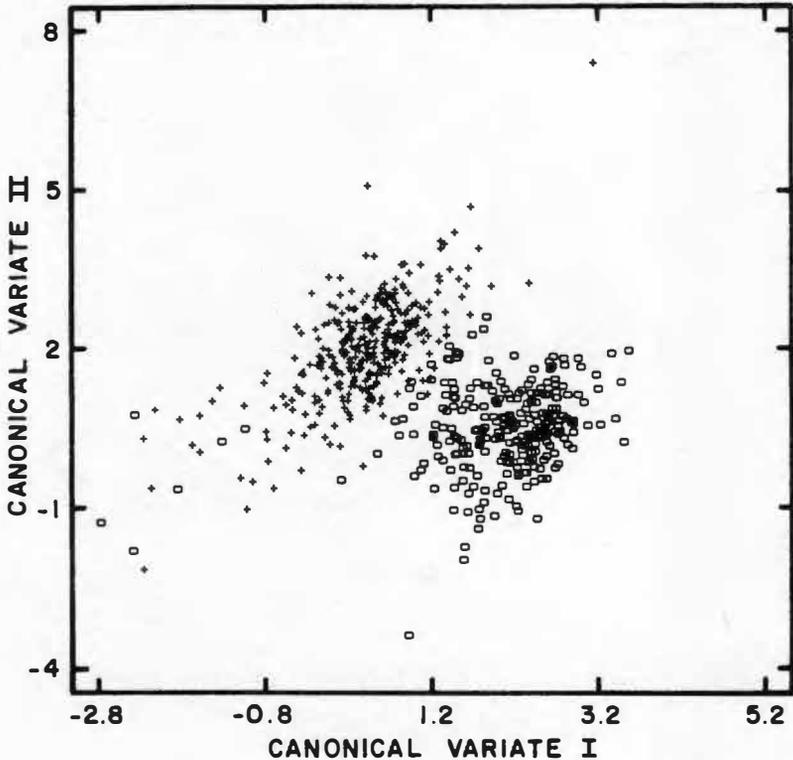
FIG. 11.—Enlargement of canonical-variates plot of morphotypes 9-11 in Figure 6 used to illustrate presence of two distinct clouds of points in canonical space. The cloud of points at the upper left represents individuals from Washington and at the lower right individuals from Oregon.

Morphotypes 9-11

Morphotypes 9, 10, and 11 were used as *a priori* groups in a multiple discriminant analysis that resulted in 63 percent correct classification. Although the first two canonical-variate axes were significant (V_1 = 217.76, *d.f.* = 57; V_2 = 76.46, *d.f.* = 36) and the three Mahalanobis' D^2 values (D^2 [9 and 10] = 3.42, D^2 [9 and 11] = 2.89, D^2 [10 and 11] = 1.35) were significant (Z [9 and 10] = 6.02, *d.f.* = 20, 450; Z [9 and 11]) = 3.86, *d.f.* = 20, 144; and Z [10 and 11] = 6.33, *d.f.* = 20, 535), 12 of the 20 variables accounted for 96.5 percent of the variation in the first axis. The combination of a low level of correct classification and the large number of variables involved in the first axis indicated that the *a priori* groups had limited taxonomic meaning. Also, the geographic
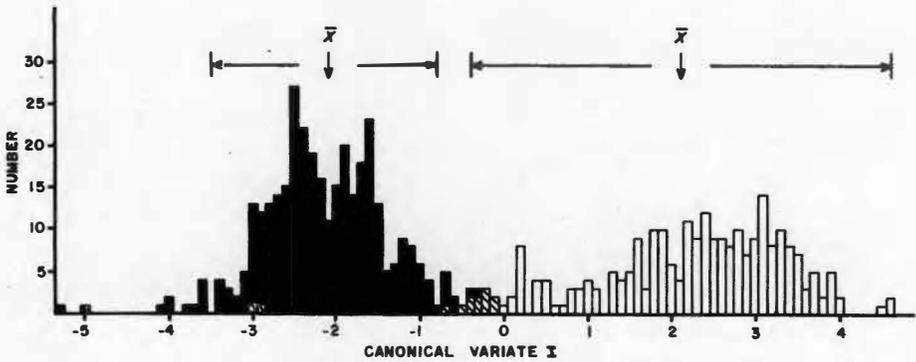
Fig. 12.—Canonical-variate plot of individuals from Oregon (n = 244, right) and Washington (n = 334, left) in morphotypes 9-11 with group centroids ($\bar{x}$) and 95 percent confidence intervals (arrows) indicated. Individuals misclassified (n = 14) are indicated by cross-hatching.

distribution of each of these three morphotypes showed no distinct pattern except that more individuals in morphotype 9 occurred in Oregon, individuals in morphotype 10 in Washington, and individuals in morphotype 11 occurred with equal frequency in both states. However, I noticed that in both canonical-variates plots of morphotypes 9-11 (Figs. 11 and 12) that two distinct clouds of points were discernable.

Because the foregoing analyses did not provide geographically meaningful results, I analyzed specimens classified into morphotypes 9-11 from a more traditional approach for this group of shrews (Findley, 1955; Hennings and Hoffmann, 1977; Jackson, 1928; Merriam, 1895) and divided the specimens into two groups: north (n = 334) and south (n = 258) of the Columbia River. Complete separation of confidence intervals for the two groups and 98 percent correct classification were obtained on the significant (V = 992.67, $d.f.$ = 38) canonical-variate axis (Fig. 12). The Mahalanobis' D^2 = 18.34 also was significant (Z = 129.34, $d.f.$ = 20, 572). High positive coefficients of correlation to the canonical- variate axis occurred for greatest length of skull (0.659), cranial breadth (0.581), length of unicuspid toothrow (0.687), length of mandible (0.584), height of coronoid process (0.816), greatest condylar depth (0.590), width of lower condylar facet (0.606), and width across I1-I1 (0.690), indicating that individuals from Oregon averaged larger than those from Washington. Kurtosis values on many of the 20 variables in the Washington and Oregon groups were high, which could indicate that more than one taxon was involved in each of the geographic regions (Pimental and Smith, 1986b; Zar, 1984). The proportions of the positions of the foramen on the zygomatic plate for Oregon and Washington (Fig. 9) were significantly different (G = 432.24, $d.f.$ = 3).
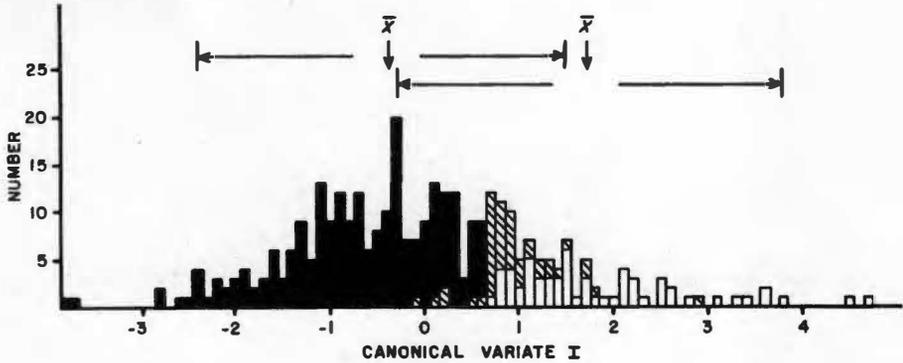
FIG. 13.—Canonical-variate plot of individuals from west (*n* = 268, left) and east (*n* = 66, right) of the Cascade Mountains, Washington, in morphotypes 9-11 with group centroids ($\bar{x}$) and 95 percent confidence intervals (arrows) indicated. Individuals misclassified (*n* = 45) are indicated by cross-hatching.

I divided specimens collected in Washington into three groups: those with collection localities west of 122.00°W longitude (*n* = 149), those collected east of 121.00°W longitude (*n* = 18), and those collected in between (*n* = 167). This method of categorizing the specimens was chosen because those collected between 122.00° and 121.00°W longitude are from an area that includes the Cascade Mountains, a possible barrier to gene flow for populations of *Sorex* located west and east of the mountains. Multiple discriminant analysis of groups of specimens located west of 122.00° and east of 121.00°W longitude resulted in 86 percent correct classification; from this analysis a diagnosis file was formed. The canonical-variate axis was significant (V = 63.45, *d.f.* = 38) as was the Mahalanobis' D^2 = 4.94 (Z = 3.69, *d.f.* = 20, 148). The 167 unknowns then were classified into one of the groups not located between 122.00° and 121.00°W longitude. This diagnostic analysis resulted in 126 specimens classified with the western Washington group and 41 specimens classified with the eastern Washington group. As a last step, these specimens were added to their respective parent-groups and a multiple discriminant analysis was performed on all 335 specimens now placed into two *a priori* groups (Fig. 13); a diagnosis file was formed from this analysis. This resulted in 87 percent correct classification and a significant canonical-variate axis (V = 176.09, *d.f.* = 38) and Mahalanobis' D^2 = 4.55 (Z = 5.33, *d.f.* = 20, 315). The two group centroids also were significantly different (t = 15.31, *d.f.* = 333). Of the 45 misclassified specimens, most were collected from Mt. Rainier National Park, Pierce County, directly southward to the Columbia River, Skamania County, or in North Cascades National Park, Whatcom and Skagit counties, Washington. Therefore, the populations west and east of the Cascade Mountains, Washington, were considered separate
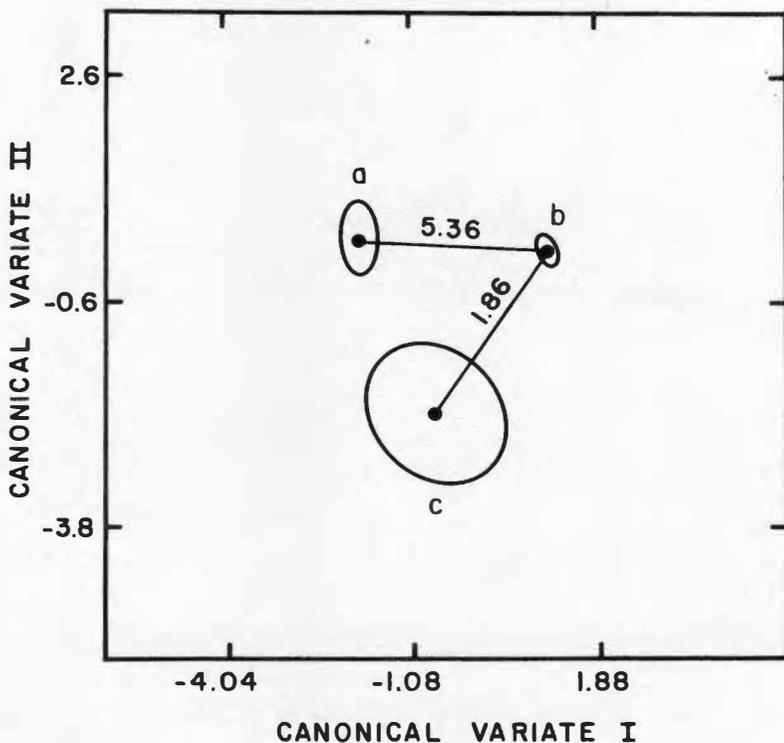
FIG. 14.–Canonical-variates plot of individuals in Oregon in morphotypes 9-11. Groups labeled are: a, Coast Range (n = 81); b, southern Cascade Mountains (n = 156); and c, Pamelia Lake (n = 14). Group centroids (closed circles), minimum-spanning tree with superimposed Mahalanobis' D^2 values, and 95 percent confidence ellipses for the bivariate group centroids are indicated. The differences in cranial morphology among these groupings are characterized, from left to right by greater cranial depth and height of the coronoid process, and wider lower condylar facet.

groups in subsequent analyses. The proportions of the positions of the foramen on the zygomatic plate for individuals west and east of the Cascade Mountains, Washington (Fig. 9), were not significantly different (G = 2.60; $d.f.$ = 2). Of the 20 variables, there were no significant differences between sexes for the eastern Washington populations and only the mean for cranial depth was significantly different (t = 2.07, $d.f.$ = 174) between sexes for the western Washington populations.

Also, I divided the Oregon specimens into four groups: specimens collected in Hood River and eastern Multnomah and Clackamas counties, Oregon, previously indicated to be more closely related to *Sorex* in Washington (n = 7—excluded from further analyses of Oregon specimens); specimens collected in the Cascade Mountains from south of Hood River County to Pamelia Lake at the southwest base of Mt. Jefferson, Lane County (n = 14); specimens collected south of Mt. Jefferson to southern
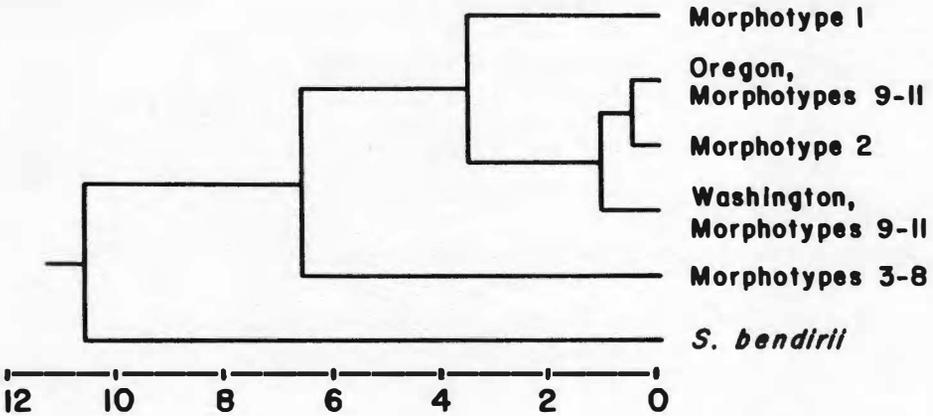
FIG. 15.—Phenetic relationships within the "*Sorex vagrans* species complex" with morphotypes 1, 2, and 3-8 considered separate species and morphotypes 9-11 two additional species. *Sorex bendirii* was used as an out-group. Morphotype 2, and Oregon and Washington morphotypes 9-11 are separated from morphotype 1 by a taxonomic distance of 2.92 and from morphotypes 3-8 by a taxonomic distance of 5.13.

H. J. Andrews Experimental Forest, Linn County, and east of 122.50°W longitude (n = 156); and specimens collected west of 122.50°W longitude in the Coast Range (n = 81). The separation at 122.50°W longitude was deemed appropriate because there is a wide break in the geographic distribution of specimens centering on this longitude. The three latter groups were used as *a priori* groups in a multiple discriminant analysis that resulted in 88 percent correct classification (Fig. 14) and two significant canonical-variate axes (V_1 = 316.71, $d.f.$ = 57; V_2 = 62.13, $d.f.$ = 36). Analysis of these three *a priori* groups by minimum-spanning tree indicated that only two relationships existed (Fig. 14): the groups from the southern Cascade Mountains and Coast Range are distantly related (taxonomic distance = 5.36, Z = 13.02, $d.f.$ = 20, 149) and the groups from the Pamelia Lake region and southern Cascade Mountains are closely related (taxonomic distance = 1.86, Z = 8.16, $d.f.$ = 20, 215). Based on cluster analysis, groups from the Pamelia Lake region and the southern Cascade Mountains formed a tight cluster separated from the Coast Range group by a taxonomic distance of 6.07. The proportions of positions of the foramen on the zygomatic plate for groups from the Coast Range and Cascade Mountains (Fig. 9) were significantly different (G = 14.71, $d.f.$ = 3). Therefore, groups from the Pamelia Lake region and southern Cascade Mountains were combined in subsequent analyses and were considered separate from the Coast Range group. Of the 20 variables, there were no significant differences between sexes in the group from the Cascade Mountains and only the means for cranial breadth, width across I1-I1, breadth of zygomatic plate, total length, and

tail length were significantly different (t = 2.17, 2.24, 2.27, 2.69, 2.37, respectively, $d.f.$ = 80) between sexes in the Coast Range group.

Based on the aforementioned analyses, shrews of the "*Sorex vagrans* species complex*," within the study area, herein are classified into nine taxa. Morphotypes 1, 2, and 3-8 are considered three separate species and morphotypes 9-11 are considered two additional species (one in Oregon and one primarily in Washington). The species composed of individuals classified as morphotypes 1, 2, morphotypes 9-11 in Oregon, and morphotypes 9-11 in Washington each are made up of two subspecies. Arguments in support of these decisions are presented in individual species accounts. Based on cluster analysis (Fig. 15), with *Sorex bendirii* as an out-group, the three taxa composed of individuals in morphotype 2 and morphotypes 9-11 are much more closely allied to each other than any are to the taxa composed of individuals in morphotype 1 (taxonomic distance = 2.92, Z = 16.70, $d.f.$ = 20, 754) or in morphotypes 3-8 (taxonomic distance = 5.13, Z = 63.02, $d.f.$ = 20, 1251).

Systematics and Taxonomy

Order Insectivora
Family Soricidae
Subfamily Soricinae
Tribe Soricini
Genus *Sorex*
Subgenus *Otisorex*

Sorex sonomae sonomae Jackson
Fog Shrew

1921. *Sorex pacificus sonomae* Jackson, J. Mamm., 2:162, August.
1955. *Sorex vagrans sonomae*, Findley, Univ. Kansas Publ., Mus. Nat. Hist., 9:32, December.

Holotype.—Adult male, skin and skull with moderately worn teeth; MVZ 19658; "Sonoma County side of Gualala River, Gualala, California"; obtained on 2 July 1913 by Alfred C. Shelton, original number 227. Holotype examined and measured.

Distribution.—*Sorex sonomae sonomae* occurs along the Pacific Coast from Newport, Lincoln County, east to Corvallis, Benton County, Oregon, thence southward to Crescent City, Del Norte County, and Inverness, Marin County, California (Fig. 16).

Description.—This taxon is composed of the group of large individuals classified as morphotype 1.

Sorex sonomae sonomae is the largest of the Pacific Coast brown shrews. In adults, the dorsal pelage, based on 20 specimens collected in August, is light dark-brown (< 7.5YR 3/2 of Munsell Color, 1975; Mummy Brown of Ridgeway, 1912); the ventral pelage is dark brown (7.5YR 3/2) to Saccardo's Umber (no comparable Munsell color). Bases of hairs are neutral black (7.5YR N2/0) on the dorsum and neutral very dark-gray (7.5YR N3/0) on the venter. Flank glands of 10 adult males in the same sample are covered with bristles colored Saccardo's Umber. In 20 subadults obtained in August, the dorsal pelage is medium light-brown (between 7.5YR 4/2 and 7.5YR 4/4 of Munsell Color, 1975; Sepia of Ridgeway, 1912) and the ventral pelage is Saccardo's Umber. The entire tail is colored the same as the dorsum in all age classes. There are four pairs of digital friction pads on the second to fourth toes of the hind feet.

The skull is large and robust (Fig. 17), comparable in size with that of *S. bendirii*. The bone of the cranium is dense, not translucent as in the other geographic race. There is a large ridge around most of the lateral edge of the cranium (Fig. 17). The foramen on the zygomatic plate (Fig. 5) in 64.6 percent of individuals examined is anterior to the metacone of M1 (Fig. 9b). The zygomatic processes of the maxillary (Dötsch, 1985) are rounded in all *S. sonomae* (Fig. 17), not finely pointed as in other taxa

considered herein. The coronoid process is broad, heavy, rugose, and deep (Fig. 17). The spiculum coronoideum is prominent and robust to aid in anchoring the temporalis muscle at its point of insertion.

Lacking medial projections, the first upper incisors abut for the entire length of the pigmented region (Fig. 17). The unicuspids are large, robust, straight-sided, and tightly appressed from near the alveolus to crown. U1 and U2 are almost square or square. U5 is usually rectangular and usually there is a gap between U5 and P4; however, P4 never overlays U5. When slightly or moderately worn, the lower molariform teeth are not as deep from alveolus to crown as is the mandible below the molariform toothrow.

Measurements.—Only three of 20 variables were significantly different between the sexes (Table 2).

Remarks.—Individuals classified in morphotype 1 form a distinct morphologic (Figs. 17 and 18) and morphometric (Fig. 6) unit characterized by a smooth medial edge on the first upper incisors. Because the holotype of *S. pacificus sonomae* has this unique characteristic, but the holotype for *S. p. pacificus* (USNM 3266) does not, it becomes necessary to elevate *S. p. sonomae* to specific status.

In canonical-variates space (Fig. 8) specimens of *S. s. sonomae*, formerly referred to as *S. pacificus sonomae* (Fig. 1), are spread throughout most of the canonical-variates plot of the large individuals in morphotype 1 with no evidence of clumping. Consequently, what formerly was referred to as *S. pacificus sonomae* is now considered to be at the small end of the size range for *S. s. sonomae* with no justification for considering it a distinct taxon from other populations of that subspecies.

The ratio of the coronoid process-condylar length to length of the mandible, 0.432, is significantly different ($q = 4.397$, $k = 9$, $v = 284$; Tukey test—Zar, 1984:188) from ratios of all other taxa considered. Because of the much greater mechanical advantage of the temporal muscle afforded *S. s. sonomae* (van Zyll de Jong, 1980), it is not surprising that it has deeper coronoid processes, stronger dentition, larger I1s, and more robust jaws than other taxa examined. This may be indicative of a diet consisting of a higher percentage of hard materials compared with the diets of other taxa in the "*Sorex vagrans* species complex" (van Zyll de Jong, 1980).

Specimens to which this specific name applies are much more widely distributed than previously considered; therefore, the vernacular name "Sonoma shrew," for Sonoma County, California, is no longer appropriate. As the distribution of *S. sonomae* is restricted primarily to the fog belt (usually 150 to 200 centimeters precipitation per year—Loy, 1976) of the California and Oregon coastlines (Fig. 16), the vernacular name "fog shrew" is herein applied to this taxon.

Specimens examined.—CALIFORNIA (228).—*Del Norte Co.*: Cresent City, 10 (KU 14713, USNM 17090, 68166, 68167, 97612, 97615, 97616, 97621, 140486, 140487); 6 mi. E Crescent City, 1 (CM 12346); 8 mi. E Cresent City, Mill Creek, 1 (CM 46432); Gasquet, 2 (USNM 91552, 91554); 6 mi. N Klamath, 2 (MVZ 102104, 102105); 8 mi. N Klamath, Wilson Creek, 2 (CM 18131, 18133); 1.5 mi. N mouth Klamath River, 1 (SOSC 1115); Smith River, 2 (USNM 140482, 140483); 5 mi. NE Smith River, 3 (WFB 1101, 1102, 1159); T14N, R1E, sec. 21/22, 2 (OSUFW X1282, X1300); *T14N, R1E, sec. 21/28*, 12 (OSUFW X1133-X1136, X1138, X1140-X1142, X1145, X1186, X1187, X1296); T19N, R6E, sec. 32, 1 (OSUFW X1301). *Humboldt Co.*: Arcata, 7 (HSU 994, MVZ 11780, OSUFW X1179-X1181, X1270, X1355); 3 mi. E Arcata, Fickel Hill Rd., 1 (HSU 583); *5 mi. E Arcata, Fickel Hill Rd.*, 1 (HSU 1128); *Arcata, Fickel Hill* [T5N, R2E, SW¼], 2 (HSU 1052, 1190); Arcata, Jolly Giant Creek, T6N, R1E, sec. 28, 2 (HSU 341, 581); *Arcata, Jolly Giant Dam*, 1 (HSU 983); Arcata, 0.25 mi. W Lazy L Ranch, Fickel Hill Rd. [T6N, R1E, sec. 34], 1 (HSU 1013); Arcata, Little River, 2 (HSU 820, 821); 2.3 mi. E Bayside, 1 (MVZ 112851); *2.8 mi. E Bayside*, 1 (MVZ 112853); 5.5 mi. E Bayside, 1 (MVZ 112854); 7 mi. E Bayside, 2 (MVZ 112855, 112856); Big Lagoon, 23 (HSU 303, 1605, 1606, MVZ 99516, 99517, 99519, 99520, 112961-112970, 112973-112977, UCD 2632); Cape Mendocino, 1 (USNM 98409); Carlotta, 1 (UCD 68); 1 mi. E Carlotta, 1 (MVZ 99524); 5 mi. E Carlotta, 1 (MVZ 81119); Coyote Peak, 3000 ft., T9N, R3E, N central sec. 32, 1 (MVZ 58859); Crannell, Little River [T7N, R1E, sec. 8], 1 (HSU 840); Cuddeback, T2N, R2E, S half, 1 (MVZ 11777); 5 mi. S Dyerville, 1 (USNM 98536); 2 mi. W Elk Grove, 4 (MVZ 105781, 105782, 105785, 105786); Eureka, 7 (MVZ 11753, 11754, 11756-11758, USNM 63520, 63521); 5 mi. S Eureka along Elk River, 2 (CM 12350, 12351); Fair Oaks [= Kneeland], T4N, R2E, SE¼sec. 15, 7 (MVZ 11761, 11763, 11765-11768, 11774); Ferndale, 1 (MVZ 19005); Gold Bluff Beach, 1 (HSU 340); Humboldt Bay, 1 (USNM 97248); Humboldt Bay, Carson's Camp, Mad River, 3 (USNM 97286, 97608, 97609); Jacoby Creek, Sunny Brae, T6N, R1E, sec. 33, 1 (HSU 1085); Korbel area, 3 (HSU 1874, 2051, 2323); 1 mi. SE Korbel, 2 (HSU 1875, 2406); Orick, 9 (USNM 140488-140490, 140723, 140725-140729); about 0.7 mi. N Orick, Prairie Creek, 1 (CM 16342); 4 mi. N Orick, 50 ft., 2 (MVZ 106420, 106421); Patrick's Point State Park, 1 (HSU 580); Trinidad, 4 (HSU 4056, MVZ 11786, 11791, 11793); 3 mi. N Trinidad, 300 ft., 4 (MVZ 97408-97411); 4 mi. N Trinidad, 1 (HSU 2402); Trinidad Head [T8N, R1W, sec. 23], 1 (USNM 97611); 3 mi. N Willow Creek, 700 ft., 4 (MVZ 112978-112981); 4.5 mi. N, 1.5 mi. E Willow Creek, 800 ft., 2 (MVZ 112982, 112983); T1S, R4E, sec. 2, 2 (OSUFW X1128, X1333); T6N, R3E, sec. 8/17, 2 (OSUFW X1267, X1281); T7N, R2E, sec. 25, 6 (OSUFW X1261, X1262, X1264, X1272, X1295, X1299); T7N, R2E, sec. 30, 2 (OSUFW X1130, X1131); T7N, R5E, sec. 30, 2 (OSUFW X1277, X1294). *Marin Co.*: Inverness, 1 (USNM 246741); 2 mi. WNW Inverness, 5 (MVZ 96217-96221); 1 mi. SE Inverness, 1 (MVZ 138733). *Mendocino Co.*: Brandon Gulch, 1.5 mi. NE jct. rds. 360 and 361, T18N, R16W, SE ¼sec. 17, 1 (UCD 4037); Brandon Gulch, Jackson St. Forest, 1 (UCD 4707); *Gualala*, 2 (MVZ 19654, 19669); Gualala, Sonoma Co. side Gualala River, 1 (MVZ 19658—holotype of *Sorex pacificus sonomae*); Mendocino City, 5 (MVZ 19677, USNM 91637-91639, 91641); 1.5 mi. E Mendocino, 1 (MVZ 135346); 7 mi. E Mendocino along Big River, 1 (CM 12358); 4 mi. W Navarro, 1 (MVZ 136092); Point Arena, 3 (MVZ 19671, 107734, 107735); about 6 mi. SE Point Arena along Garcia River, 2 (CM 12334, 12355); Russian Gulch St. Park, 16 (MVZ 95632-95640, 95642-95648); T21N, R16W, sec. 26, 5 (OSUFW X1265, X1266, X1306, X1307, X1356). *Siskiyou Co.*: 12 mi. NW Happy Camp, Poker Flat, 5 (MVZ 69064, 121847, 121848, 121850, 121851); 3 mi. W Klamath River, Clear Creek, 1400 ft. [T46N, R9W, sec. 3], 1 (MVZ 69067). *Sonoma Co.*: 7 mi. W Cazadero, 1 (MVZ 19646); 6 mi. N Ft. Ross, 1 (UCD 2596); south side Gualala River bridge near Gualala, 4 (MVZ 120410-120413); Sonoma Co. side Gualala River near Gualala, 2 (MVZ 19652, 19668); *mouth Gualala River, about 1 mi. S Gualala*, 1 (CM 16344); 1 mi. SE Gualala along Gualala River, 1 (CM 12328).

OREGON (222).—*Benton Co.*: 1 mi. S, 6 mi. W Alpine, 1 (OSUFW 3108); 2 mi. S, 1 mi. E Alsea, 1 (CM 65011); 3.75 mi. S, 5.5 mi. E Alsea, 1 (CM 65010); Mary's Peak, T12S, R7W, sec. 28, 1 (PSM 12035*); 8.5 mi. SW Philomath, 1 (OSUFW 8239*); Prairie Mt. rd., T14S, R6W, sec. 31, 1 (PSM 12037); T12S, R7W, sec. 11/14, 1 (USNM 561132*); T14S, R7W, sec. 9, 2 (USNM 561153,

561156); T14S, R7W, sec. 32, 1 (USNM 561157*). *Coos Co.*: 1.75 mi. E Bandon, 100 ft., T28S, R14W, SE¼sec. 29, 11 (PSM 13614, 13631, 13632, 13634, 14413, 14414, 14425-14427, 15141, 15143); 9 mi. NE Bandon, 250 ft., 1 (PSM 13615); 3 mi. SE Bandon, 1 (PSM 15139); 4 mi. SE Bandon, 250 ft., T29S, R14W, SW¼sec. 9, 3 (PSM 13604, 13605, 15140); *4 mi. SE Bandon*, 400 ft., T29S, R14W, NW¼sec. 16, 14 (PSM 14415-14421, 14424, 14429-14431, 15135, 15136, 15138); Marshfield [= Coos Bay], 2 (FMNH 9631, USNM 69443); Myrtle Point, 1 (USNM 69441); 3.2 km. N, 0.3 km. W Remote, 1 (USNM 563103); 7.3 km. N, 4 km. W Sitkum, T27S, R10W, sec. 17/20, 2 (USNM 561225, 563094); *7.4 km. N, 4.2 km. W Sitkum, T27S, R10W, sec. 17,* 7 (USNM 561226-561231, 561237); T27S, R10W, sec. 18, 1 (USNM 561236); T27S, R11W, sec. 21, 2 (USNM 561232, 561233); 250 ft., T27S, R13W, NW¼sec. 18, 1 (PSM 13616); T28S, R9W, sec. 19, 3 (USNM 561238-561240); T28S, R9W, sec. 23, 1 (USNM 561241); T28S, R9W, sec. 27, 2 (USNM 561244, 561245); 50 ft., T28S, R14W, SE¼sec. 29, 1 (PSM 13610); T29S, R10W, sec. 21, 3 (USNM 561247, 561249, 561250); 100 ft., T29S, R14W, NE¼sec. 6, 1 (PSM 13602). *Curry Co.*: 10 mi. E Brookings, 240 ft., T41S, R12W, NW¼sec. 3, 2 (PSM 14732, 14733); Gold Beach, 2 (PSM 5897, SDNHM 17049); 3 mi. N Gold Beach, 3 (MVZ 54902-54904); 0.5 mi. N Harris Beach St. Park, 1 (SOSC 1274); Port Orford, 1 (CMNH 14880). *Douglas Co.*: 10 km. N, 10.5 km. W Drain, T21S, R6W, sec. 7, 2 (USNM 560066, 561199); 11.3 km. N, 10.5 km. W Drain, T21S, R6W, sec. 5, 1 (USNM 560065); 15.5 km. S, 5.8 km. W Elkton, T24S, R8W, sec. 10, 1 (USNM 560073); 25.2 km. S, 5.4 km. W Elkton, T25S, R8W, sec. 10, 3 (USNM 560067, 560070, 561219); Francis Creek, T24S, R1W, SE¼SE¼ sec. 12, 1 (SOSC JB2); *Francis Creek, upstream Rd. 12.1, T24S, R1W, SE SE ¼ SE ¼ sec 12*, 3 (SOSC 1792, 1796,1798);*Francis Creek downstream Rd.* 12. 1, T24S, R1W, SE ¼ SE¼sec. 12, 1 (SOSC 1794); Gardiner, 6 (FMNH 9633, 9634, MVZ 81111-81113, USNM 69445); 1.3 mi. E Gardiner, 3 (MVZ 120405, 120407*, 120409); Louis Creek, T28S, R3W, NW1/4 SW1/4 sec. 29, 7 (SOSC 1838-1840, 1842, 1845*, 1846, 1847); *Louis Creek, T28S, R3W, SE ¼ SE ¼ sec. 30*, 1 (SOSC 1860); Middle Creek, T31S, R6W, SW¼sec. 30, 1 (SOSC TF23); Oxbow Burn, 300 ft., T20S, R7W, sec. 19, 12 (PSM 11886-11888, 11891, 711893, 11894, 11896-11898, 11953, 13337, 13338); Pass Creek, 0.4 mi. from Caton Creek, T24S, R1W, SE¼sec. 26, 1 (SOSC 1806); 4 km. N, 12.1 km. W Sutherlin, T25S, R7W, sec. 1, 5 (USNM 560079, 561214, 561215, 561222, 561223); 4.9 km. S, 4.5 km. W Yoncolla, T25S, R5W, sec. 19, 1 (USNM 563087); T21S, R12W, SE¼sec. 9, 1 (PSM 14548); T22S, R5W, sec. 7, 1 (USNM 561196); T23S, R8W, sec. 20, 4 (USNM 561200-561203); *T23S, R8W, sec. 28*, 3 (USNM 561205-561207); T24S, R8W, sec. 9, 5 (USNM 561204, 561208, 561209, 561218, 561220); T27S, R3W, SE¼ sec. 35, 13 (OSUFW 7195, 7196*, 7197, 7198, 7199*, 7200-7203, 7204*, 7205-7207). *Jackson Co.*: Upper Ashland Natural Research Area, T40S, R1E, SE¼SE¼sec. 4, 1 (SOSC CK6); *Ashland Research Natural Area, T40S, R1E, SE ¼ sec 4*, 1 (SOSC 1053); ½mi. SW of T40S, R1E, sec. 3/10 sign, 1 (SOSC 946). *Josephine Co.*: Bolan Lake, 5551 ft. [T41S, R6W, sec. 7], 2 (PSM 2556, 2557); Grants Pass, 1 (CM 3722); Page Mtn., T41S, R7W, sec. 8, 2 (OSUFW X1153, X1159); Sourgrass Creek, T35S, R9W, sec. 2, 1 (SOSC TF12); *Sourgrass Creek, T35S, R9W, sec. 3*, 2 (SOSC TF8, TF14); *Sourgrass Creek, T35S, R9W, SW ¼ NE ¼ sec. 3*, 1 (SOSC 1800); *Sourgrass Creek, T35S, R9W, SE¼NE¼ sec. 3*, 3 (SOSC BB3, BB4, TF13); T39S, R6W, sec. 8, 1 (OSUFW X1298); T39S, R6W, sec. 33, 2 (OSUFW X1169, X1278); T41S, R7W, sec. 7, 3 (OSUFW X1154, X1157, X1158); *T41S, R7W, sec. 8*, 3 (OSUFW X1160, X1176, X1334); *T41S, R7W, sec. 8/9/16/17*, 2 (OSUFW X1268, X1358). *Lane Co.*: 5 mi. N Alpha, 4 (OSUFW 4562, 4600, 4602, 4604); 5 mi. N, 6 mi. W Alpha, 2 (OSUFW 6886*, 6887); 4 mi. S, 8 mi. W Alpha, 1 (OSUFW 4563); Eugene, 3 mi. W Spencer Butte, 1 (SDNHM 17040*); Fall Creek Reservoir, 1 (OSUFW 8363); 0.4 km. N, 18.5 km. W Lorane, T20S, R7W, sec. 12, 7 (USNM 561166, 561167, 561168*, 561169, 561171-561173); 5 mi. E Lowell, 1 (OSUFW 8507); Mapleton, 1 (USNM 205273); Mercer [= Florence], 1 (MVZ 71221); Vida, 1 (USNM 204458); 11 mi. S Yachats, 6.5 mi. E Hwy. 101 on Big Creek, 1 (UCD 4705*); T15S, R12W, sec. 12, 1 (USNM 561159); 1800 ft., T16S, R4E, NE¼sec. 19, 1 (PSM 19730); T16S, R5E, sec. 26, 1 (USNM 556757); 3000 ft., T18S, R5E, sec. 23, 1 (PSM 13342); T19S, R06W, sec. 31, 1 (USNM 561191); T19/20S, R7W, sec. 32/5, 1 (USNM 561194); T20S, R5W, sec. 5, 4 (USNM 561176, 561177, 561179, 561180); T20S, R7W, sec. 1, 6 (USNM 561183-561185, 561187, 561188*, 561190); T20S, R7W, sec. 19, 1 (PSM 22621); T20S, R12W, NE¼sec. 4, 1 (PSM 14547). *Lincoln Co.*: Newport, 3 (MVZ 81109*, 81110, OSUFW 6048*); T12S, R10W, sec. 13/24, 1 (USNM 561130).

Sorex sonomae tenelliodus, new subspecies

Holotype.—Adult, female, skin and skull; USNM 565663; "4 mi. S, 10½ mi. E Blue River, East Fork Creek, T17S, R6E, sec. 7, Lane County, Oregon"; obtained on 13 May 1983 by R. G. Anthony, original number X-560; pregnant, embryos (3 left by 4 right), crown-rump length 13.5 mm.; originally cataloged as OSUFW 8251, transferred to National Museum of Natural History on 2 May 1989.

Distribution.—*Sorex sonomae tenelliodus* occurs in Oregon from Taft and Newport, Lincoln County, southeastward to Coberg Hills, Lane County, and eastern Linn County, thence southward on the west slope of the Cascade Mountains to Hilt, Siskiyou County, California (Fig. 16).

Diagnosis.—Overall, *S. s. tenelliodus* is smaller and paler in color than *S. s. sonomae* (Figs. 17 and 18; Table 2). The dorsal and ventral pelages of three specimens collected in May and September are medium brown (7.5YR 4/2—Munsell Color, 1975) to dark gray (5YR 4/1) and pinkish white (5YR 8/2), respectively. Bases of hairs on both dorsum and venter are neutral dark-gray (7.5YR N4/0). The tail is indistinctly bicolored, medium-brown above and pinkish-white (7.5YR 8/2) below, not unicolored as in *S. s. sonomae*. Flank glands on one adult male collected in May were covered with pinkish-white bristles. There are four pairs of digital friction pads on the second to fourth toes of the hind feet.

The skull of *tenelliodus* is fragile, smooth, and small (Fig. 18) compared with *S. s. sonomae* (Fig. 17). The bone of the cranium is translucent and sutures among the bones commonly are loose and easily separated. The foramen on the zygomatic plate (Fig. 5) in 97.0 percent of individuals examined is either immediately posterior to, or directly in line with, the metacone of M1 and in only 2.1 percent of individuals examined was the foramen anterior to the metacone of M1 (Fig. 9a); in *S. s. sonomae* the foramen usually is anterior to the metacone of M1 (Fig. 9b).

Lacking medial projections, the first upper incisors usually abut only in the dorsal half of the pigmented region. U1 to U5 are small, particularly as compared with *S. s. sonomae;* U5 is usually rectangular. The placement of U5 in relation to that of P4 is the same as for *S. s. sonomae.*

Description.—This taxon is composed of the group of small individuals classified as morphotype·1. *S. s. tenelliodus* is similar to *S. s. sonomae* except as noted in the diagnosis.

Measurements.—Only three of 20 variables were significantly different between the sexes (Table 2). Measurements for the holotype are: greatest length of skull, 18.64; cranial breadth, 9.62; maxillary breadth, 5.90; least interorbital breadth, 3.87; cranial depth, 4.48; breadth at M2-M2, 5.08; length of unicuspid toothrow, 2.90; length of complex toothrow, 4.66; width across I1-I1, 1.80; breadth of zygomatic plate, 1.33; length of mandibular toothrow, 5.27; length of mandible, 8.00;
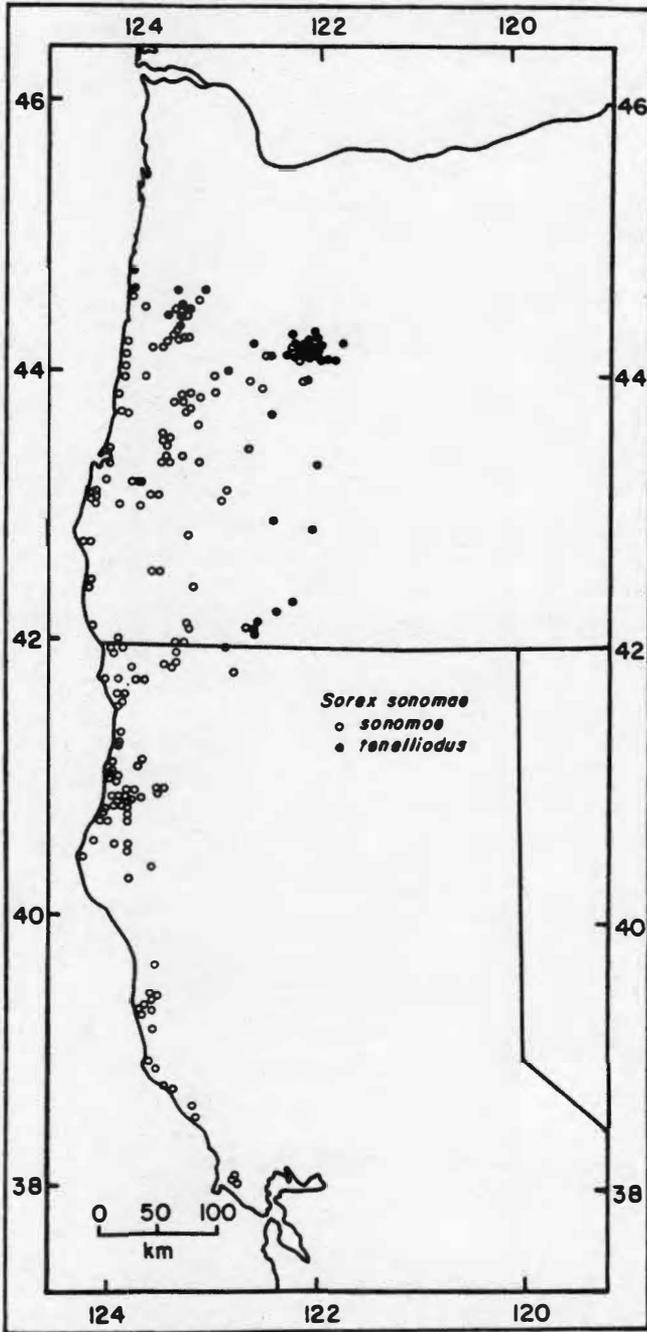
FIG. 16.—Localities in Oregon and California at which museum specimens of *Sorex sonomae sonomae* (open circles, 173 localities, 154 localities plotted; *n* = 449) and *S. s. tenelliodus* (closed circles, 70 localities, 45 localities plotted, *n* = 181) used in this research were collected.

TABLE 2.—*Mean (± SE), range, and CV of measurements (in mm.) of skull and skin characters for female and male* Sorex sonomae.

| Character | Sorex sonomae sonomae | | | | | | Sorex sonomae tenelliodus | | | | | |
| | Females (n = 212) | | | Males (n = 216) | | | Females (n = 67) | | | Males (n = 109) | | |
	x̄ ± SE	Range	CV	x̄ ± SE	Range	CV	x̄ ± SE	Range	CV	x̄ ± SE	Range	CV
Greatest length of skull	21.41±0.05	19.34-23.08	3.52	21.57±0.05	19.34-23.22	3.29	19.06±0.07	16.50-20.00	3.04	19.10±0.05	17.94-20.21	2.66
Cranial breadth	10.33±0.03*	9.22-11.34	3.77	10.4±20.02*	9.44-11.15	3.29	9.38±0.03	8.50-10.10	2.95	9.40±0.03	8.61-10.00	2.99
Maxillary breadth	6.48±0.02	5.68-7.11	4.62	6.52±0.02	5.66-7.21	4.30	5.60±0.03	5.00-6.09	4.02	5.58±0.02	4.99-6.14	4.39
Least interorbital breadth	4.25±0.01	3.73-4.99	4.23	4.28±0.01	3.56-4.90	4.31	3.80±0.02	3.27-4.26	4.95	3.77±0.02	3.14-4.16	5.21
Cranial depth	5.61±0.02	4.27-6.64	5.52	5.65±0.02	4.58-6.35	4.99	5.23±0.04	4.48-5.96	5.55	5.30±0.03	4.54-6.04	5.74
Breadth at M2-M2	5.77±0.02	5.02-6.31	4.29	5.79±0.02	5.18-6.46	4.01	5.03±0.03	4.43-5.53	4.50	5.00±0.02	4.31-5.47	4.84
Length of unicuspid toothrow	3.53±0.02	2.90-4.03	6.23	3.54±0.01	2.73-4.06	5.83	2.94±0.02*	2.70-3.33	4.27	2.88±0.01*	2.60-3.27	4.74
Length of complex toothrow	5.28±0.01	4.76-6.21	3.48	5.28±0.01	4.67-5.90	3.63	4.70±0.02	4.14-5.21	4.05	4.69±0.02	4.11-5.14	4.33
Width across I1-I1	2.17±0.01*	1.87-2.43	5.67	2.20±0.01*	1.87-2.43	5.46	1.87±0.01*	1.70-1.97	3.47	1.84±0.01*	1.50-2.37	5.71
Breadth of zygomatic plate	1.56±0.01	1.10-2.80	11.53	1.58±0.01	1.03-1.93	9.80	1.39±0.02	1.13-1.70	9.92	1.35±0.01	1.00-1.67	9.83
Length of mandibular toothrow	6.25±0.02	5.54-6.68	3.65	6.28±0.02	5.43-6.78	3.59	5.46±0.02	4.97-5.90	3.47	5.41±0.02	4.72-5.90	4.04
Length of mandible	9.48±0.03	8.30-10.26	4.05	9.51±0.03	8.33-10.33	4.01	8.30±0.04	7.62-9.24	3.54	8.27±0.03	7.59-8.96	3.65
Height of coronoid process	5.93±0.02*	5.05-6.52	5.48	6.00±0.02*	5.20-6.68	5.19	4.97±0.02	4.43-5.53	3.87	4.95±0.02	4.27-5.77	4.89
Coronoid process-condylar length	4.07±0.02	3.13-4.72	7.60	4.09±0.02	2.94-5.02	7.09	3.34±0.03	2.66-3.73	7.13	3.33±0.02	2.62-4.10	7.45
Greatest condylar depth	2.76±0.01	2.27-3.07	5.16	2.77±0.01	2.37-3.13	4.84	2.40±0.02	1.80-2.63	5.36	2.39±0.01	2.07-2.73	4.58
Width of lower condylar facet	1.70±0.01	1.00-2.10	6.95	1.72±0.01	1.43-2.03	6.07	1.47±0.01	1.33-1.80	5.83	1.46±0.01	1.07-1.67	6.13
Width of upper condylar facet	1.22±0.01	0.93-1.93	9.28	1.21±0.01	0.93-1.60	9.09	1.06±0.01*	0.90-1.23	7.08	1.03±0.01*	0.83-1.20	7.59
Total length	137.25±0.76	105-180	8.20	139.07±0.70	107-163	7.36	124.66±0.79	112-143	5.22	122.94±0.67	106-145	5.70
Tail length	60.75±0.39	36-85	9.31	60.52±0.33	45-71	8.13	53.57±0.53	37-66	8.09	52.99±0.43	41-64	8.45
Length of hind foot	16.54±0.08	12-22	7.19	16.68±0.08	11-19	6.93	14.43±0.13	12-19	7.46	14.53±0.10	12-19	7.04

*Means of the variable for the two sexes within a taxon are significantly different ($P < 0.005$).
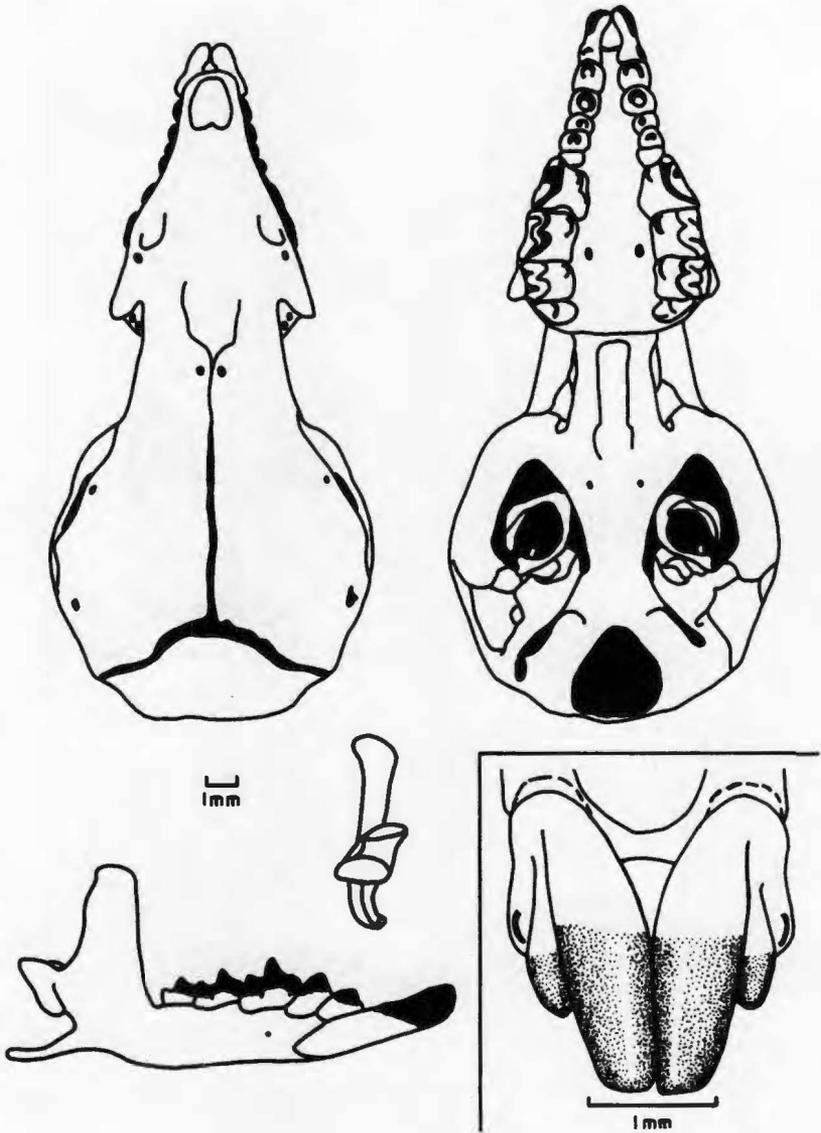
Fig. 17.—Camera-lucida tracings of dorsal and ventral views of skull, lateral and posterior views of mandible, and anterior view of I1 of an adult male *Sorex sonomae sonomae* (PSM 14424) from 4 mi. SE Bandon, T29S, R14W, NW ¼ sec. 16, Coos Co., Oregon.

height of coronoid process, 4.74; coronoid process-condylar length, 3.37; greatest condylar depth, 2.33; width of lower condylar facet, 1.50; width of upper condylar facet, 1.0; total length, 120.0; length of tail, 51.5; and length of hind foot, 13.0. Also recorded on the specimen label was length of ear from notch, 7.5.
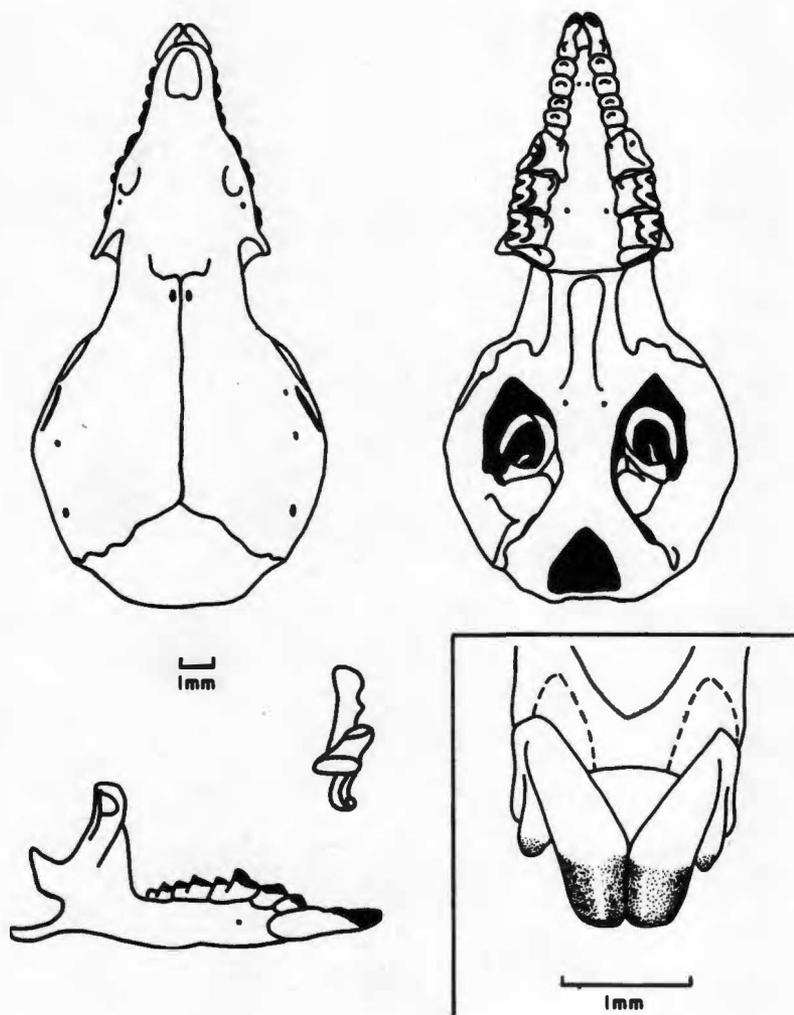
FIG. 18.—Camera-lucida tracings of dorsal and ventral views of skull, lateral and posterior views of mandible, and anterior view of I1 of an adult female *Sorex sonomae tenelliodus* (USNM 565663) from 4 mi. S, 10.5 mi. E Blue River, Lane Co., Oregon.

Etymology.—The subspecific name is derived from the Latin *tenellus* meaning "quite delicate" and the Greek *odous* meaning "tooth" (Jaeger, 1978).

Remarks.—The large coefficients of variation determined for specimens classified as morphotype 1 (Table 1) strongly indicated that more than one taxon was involved. Canonical analyses of individuals in morphotype 1 resulted in two groups (Figs. 7 and 8) corresponding to *S. s. sonomae* and *S. s. tenelliodus*. "A study of the population structure and of the attributes

of . . . species shows that the differences between . . . subspecies . . . within a single species are often very pronounced" (Mayr, 1963:284). All of the 17 misclassified specimens (Fig. 8) had high probabilities of being members of the group of small individuals and were considered referable to *S. s. tenelliodus*. The misclassified specimens were collected near the boundary between the geographic distributions of these two taxa, thus they may represent intergrades. After recalculation of the univariate statistics for individuals in morphotype 1 (Table 2), sorted into the groups indicated by canonical analysis, the coefficients of variation declined by more than 50 percent. This is the expected result when a polymorphic group is divided into its constituent parts. I consider the small individuals distributed along the west slope of the Cascade Mountains that possess no medial projection on the first upper incisor as a distinct geographic race.

Specimens examined.—CALIFORNIA (1).—*Siskiyou Co.*: 15 mi. W Hilt, Donomore Meadow, 1 (MVZ 69068).

OREGON (180).—*Benton Co.*: 5 mi. N, 5 mi. E Alsea, 1 (OSUFW 3264); 6 mi. N Corvallis, 1 (PSM 12038); 5 mi. SW Philomath, 1 (USNM 231657); *6 mi. SW Philomath, 550 ft.*, 1 (OSUFW 8590); *3 mi. S, 9 mi. W Philomath*, 1 (OSUFW 8238); *3 mi. S, 9 mi. W Philomath, Mary's Peak*, 1 (OSUFW 4831); 650 ft., T11S, R7W, SW¼ sec. 8, 2 (PSM 22618, 22619); T12S, R7W, sec. 11/14, 2 (USNM 561133, 561134); *T12S, R7W, sec. 13*, 1 (USNM 561135); *T12S, R7W, sec. 14*, 4 (USNM 561136-561138, 561140); T12S, R7W, sec. 24/25, 2 (USNM 561144, 561146); T13S, R8W, sec. 20, 2 (USNM 561149, 561151); T14S, R7W, sec. 9, 1 (USNM 561154). *Douglas Co.*: 4 mi. N, 17 mi. E Diamond Lake, 1 (SOSC 306); 1 mi. S, 33 mi. E Days Cr. at Abbott Cr., T30S, R2E, sec. 24/25, 2 (OSUFW 8587, 8589). *Jackson Co.*: 6 mi. S Ashland, 3 (SOSC 215, 219, 222); 3 mi. S, 10 mi. E Ashland, 1 (SOSC 223); Lower Ashland Natural Research Area, T39S, R1E, SW¼ sec. 28, 1 (SOSC CK35); *Upper Ashland Natural Research Area, T40S, R1E, SE ¼SE ¼ sec. 4*, 1 (SOSC CK11); T37S, R4E, sec. 23, 1 (SOSC MGS86). *Klamath Co.*: 1.8 mi. S park headquarters, Crater Lake National Park, 1 (SOSC RAM14). *Lane Co.*: 5.5 mi. NE Blue River, 1500 ft., 2 (PSM 15703, 15704); East Fork Creek, T16S, R6E, sec. 7, 5 (OSUFW 8251, 8534, 8559, 8600, 8612); Elk Creek, T16S, R4E, sec. 19, 4 (OSUFW 8246, 8307, 8530, 8533); Eugene, 5 mi. S Spencer Butte, 2 (SDNHM 17038, 17039); *Foley Ridge* [T16S, R6E, sec. 20/21], 1 (OSUFW 8616); *H. J. Andrews Experimental Forest, 1700 ft.*, 1 (OSUFW 4753); Hagan Creek, T16S, R3E, sec. 22, 6 (OSUFW 8361, 8509, 8540, 8560, 8570, 8577); King Creek, T16S, R5E, sec. 26, 3 (OSUFW 8573, USNM 556758, 556765); Lookout Creek, T15S, R6E, sec. 30, 3 (OSUFW 8535, 8561, 8608); *Mack Creek tributary, T15S, R5E, sec. 35*, 1 (OSUFW 8566); *2.6 km. S McKenzie Bridge*, 1 (USNM 556760); 1.6 km. S, 5.2 km. W McKenzie Bridge, 460 m., T16S, R5E, sec. 20, 5 (USNM 556746, 556747, 556750, 556753, 557786); McRae Lookout, T15S, R5E, SW¼ SW¼ sec. 26, 1 (OSUFW 8537); 1 mi. W Mohawk River, T15S, R1W, *SE ¼ NE ¼ sec. 13*, 1 (SOSC MGS88); 5 mi. W Oakridge, Shady Del campground [T21S, R2E, sec. 15], 2 (UCD 4664, 4665); Spring Creek, T16S, R6E, sec. 26, 1 (OSUFW 8536); Swamp Creek, T16S, R5E, sec. 20, 7 (OSUFW 7286, 8506, 8508, 8531, 8569, 8571, 8591); Upper Lookout Creek tributary, T15S, R5E, sec. 24, 4 (OSUFW 8247, 8388, 8394, 8539); Vida, 3 (SDNHM 17067, USNM 204441, 204478); *3500 ft., T15S, R5E, NW ¼ sec. 24*, 4 (PSM 19865, 19871, 19874, 19876); *T15S, R5E, sec. 25*, 14 (USNM 556603, 556611, 556698, 556700, 556702, 556703, 556706, 556712, 556714, 556716, 556718, 557762, 557763); *T15S, R5E, sec. 26*, 1 (USNM 556732); *2000 ft., T15S, R5E, NW ¼ sec. 28*, 1 (PSM 19700); *1600 ft., T15S, R5E, NE ¼ sec. 32*, 6 (PSM 19843, 19850, USNM 556719, 556721, 556726, 556728); *2000 ft., T15S, R5E, NE ¼ sec. 32*, 4 (PSM 19679, 19680, 19682, 19683); *2500 ft., T15S, R5E, SW ¼ sec. 33*, 6 (PSM 19766, 19771, 19781, 19783, 19788, 19790); *2700 ft., T15S, R5E, NW ¼ sec. 34*, 2 (PSM 19867, 19869); T15S, R6E, sec. 26, 1 (USNM 557776); T15S, R8W, sec. 11, 1 (USNM 561163); *1800 ft.*,

T16S, R4E, NE ¼sec. 19, 9 (PSM 16730, 19716, 19720, 19721, 19724, 19726, 19733, 19735, 19737); 1400 ft., T16S, R4E, NE¼sec. 24, 13 (PSM 16675, 16728, 16731, 19741, 19743, 19744, 19747, 19750, 19751, 19756, 19760, 19763, 19764); T16S, R5E, sec. 3, 3 (USNM 556735, 556738, 556739); *1600 ft., T16S, R5E, SW ¼ sec. 6*, 1 (PSM 19694); *T16S, R5E, sec. 7*, 1 (USNM 556745); *T16S, R5E, sec. 25*, 1 (USNM 556756); T16S, T7E, sec. 32, 4 (USNM 556772, 556775, 556776, 557809); *T16S, R7E, sec. 33*, 1 (USNM 556777); 3000 ft., T18S, R5E, sec. 23, 3 (PSM 11956, 12034, 13344). *Lincoln Co.*: Newport, 1 (MVZ 81107); 9 mi. N Newport, 1 (SDNHM 17048). *Linn Co.*: about 10 mi. SE Cascadia, 1 (SUVM 9852); 4400 ft., T14S, R6E, NE¼ sec. 20, 2 (PSM 19815, 19817); 4600 ft., T14S, R6E, NE¼sec. 28, 2 (PSM 19861, 19864); T15S, R5E, sec. 1, 2 (USNM 556680, 556681); *3200 ft., T15S, R5E, SE ¼ sec. 11*, 1 (PSM 19832); 3000 ft., T15S, R5E, SW¼ sec. 13, 5 (PSM 19796, 19803, 19806, 19809, 19814); *T15S, R5E, sec. 14*, 4 (USNM 556692, 556694, 556696, 557455); 4300 ft., T15S, R6E, NE¼ sec. 7, 2 (PSM 19712, 19821).

Sorex bairdii bairdii Merriam
Baird's Shrew

1895. *Sorex bairdii* Merriam, N. Amer. Fauna, 10:77, December.
1918. *Sorex obscurus bairdii* Jackson, Proc. Biol. Soc. Washington, 31:127, November.
1955. *Sorex vagrans bairdii*, Findley, Univ. Kansas Publ., Mus. Nat. Hist., 9:35, December.
1977. *Sorex monticolus bairdii*, Hennings and Hoffmann, Occas. Papers Mus. Nat. Hist., Univ. Kansas, 68:12, July.

Holotype.—Adult female, skin and skull; USNM 17414/24318; "Astoria, [Clatsop Co.], Oregon"; obtained on 2 August 1889 by T. S. Palmer, original number 270. Holotype examined and measured.

Distribution.—*Sorex bairdii bairdii* occurs in northwestern Oregon from the Pacific Coast and Columbia River eastward to Portland, Multnomah County, Wilhoit Springs, Clackamas County, and southward to Corvallis, Benton County, and Reed, Lane County (Fig. 19).

Description.—This taxon is composed of individuals distributed in the Oregon Coast Range classified as morphotypes 9-11. The dorsal and ventral pelages of three specimens collected in April and June are light medium-brown (7.5YR 5/2—Munsell Color, 1975) to dark medium-brown (7.5YR 4/2) and pinkish gray (5YR 7/3 to 7.5YR 7/2), respectively. Bases of hairs are neutral dark-gray (7.5 YR N4/0) on the dorsum and neutral very dark-gray (7.5YR N3/0) on the venter. The tail is indistinctly bicolored, dark brown (7.5YR 3/2) above and white (5YR 8/1) below. Flank glands of one adult male collected in June are covered with pinkish-gray bristles.

The foramen on the zygomatic plate (Fig. 5) in 63.8 percent of individuals is immediately posterior to the metacone of M1 (Fig. 9i). *Sorex bairdii* (Fig. 20, Table 3) can be distinguished from *S. sonomae* (Fig. 17 and 18, Table 2) by its smaller size and presence of a tine on the medial edge of the first upper incisors. Also, it can be distinguished from *S. s. tenelliodus* by its darker brown dorsal pelage and gray instead of white ventral pelage.

Measurements.—Only five of 20 variables were significantly different between the sexes (Table 3).

Remarks.—Individuals classified as morphotypes 9-11 form a distinct morphologic and morphometric (Fig. 6) unit characterized by the presence of a tine on the medial edge of the first upper incisors with pigment extending well above the dorsal level of the tine. Canonical analyses of this unit resulted in two well-defined groups (Figs. 11 and 12) corresponding to *Sorex bairdii* occurring in Oregon (mostly within areas receiving 150 to 200 centimeters precipitation per year—Loy, 1976) and *Sorex monticolus* occurring primarily in Washington. On the basis of its geological history (Baker *et al.*, 1987; Baldwin, 1966; Lawrence and Lawrence, 1958; McKee, 1972) the Columbia River has served as a barrier to gene flow, except for possible fortuitous dispersal, for several species of mammals (for example, *Phenacomys longicaudus, Sylvilagus bachmani*, and until historic times *Spermophilus beecheyi*), likely including shrews.

In 1918, Jackson subsumed *S. bairdii* into *S. obscurus* (= *S. monticolus*); however, he presented no explanation for this nomenclatural change. Because of the strong morphometric separation (Figs. 11 and 12) of these taxa and the lack of taxonomic basis for regarding *S. bairdii* as a synonym of *S. monticolus*, I consider the elevation of *S. monticolus bairdii* to specific level warranted.

Specimens examined.—OREGON (82).—*Benton Co.*: 2 mi. W Corvallis, 1 (PSM 12850); Mary's Peak, T12S, R6W, NW¼ sec. 30, 2 (OSUFW 4832, 4833); 650 ft., T11S, R7W, SW¼ sec. 8, 1 (PSM 22620). *Clackamas Co.*: Oregon City, 1 (USNM 56899); Wilhoit Springs [T6S, R2E, sec. 16], 1 (PSM 6243). *Clatsop Co.*: Astoria, 6 (USNM 17335, 17336, 17413, 17414—holotype of *Sorex bairdii*, 89020, 89129); Seaside, 1 (PSM 8631); T8N, R7W, NE¼sec. 18, 1 (PSM 26586); T8N, R10W, W½ sec. 6, 4.(PSM 26580-26583). *Columbia Co.*: 1 mi. W Rainier, 1 (PSM 11931); 7 mi. SE Rainier, 1 (MVZ 95881); 1 mi. N, 0.5 mi. W Vernonia, 1 (UWBM 20061); 7 mi. NE Vernonia, 1 (PSM 15502); T4N, R1W, N½ sec. 34, 1 (PSM 26657); T6N, R1W, SW¼ sec. 7, 1 (PSM 26575). *Coos Co.*: Delmar, 9 mi. S Marshfield [= Coos Bay], 1 (MVZ 63461). *Lincoln Co.*: Cascade Head, 240 ft., T6S, R10W, SW¼ sec. 21, 17 (PSM 4419, 13587-13591, 13594, 13595, 13597, 13726, 13741, 14451-14454, 14458, 14459); Newport, 3 (MVZ 81106, SDNHM 17045, 17047); Otis, 2 (USNM 264889, 264890); Taft, 3 (MVZ 64790, 64791, 71219). *Multnomah Co.*: Portland, 1 (USNM 142007). *Polk Co.*: 3.75 mi. S, 2 mi. W Gold Creek, T7S, R7W, sec. 5, 1 (OSUFW X1020). *Tillamook Co.*: 14 mi. E Beaver, 1 (UCD 4687); Blaine, 1 (OSUFW 6111); Cloverdale, 1 (OSUFW 6109); 5 mi. SW Cloverdale, 1 (CMNH 7344); 5 mi. E Hebo Lake, 1600 ft., 1 (UCD 4686); 2 mi. up Miami River, 2 (PSM 7003, 7004); Netarts, 10 (OSUFW 1042, PSM 3339, SDNHM 17053-17059, 17064); 1 mi. E Netarts, 2 (PSM 3341, 3342); *Netarts Bay*, 1 (SDNHM 17065); *Netarts summit*, 1 (PSM 6308); Tillamook, 8 (KU 52538, 52539, MMNH 1172, OSUFW 6110, PSM 8116, SDNHM 17050, 17051, USNM 262292); *Tillamook, Alderbrook golf course*, 1 (USNM 262287); 5 mi. S Tillamook, 2 (PSU 703, 715).

Sorex bairdii permiliensis Jackson

1918. *Sorex obscurus permiliensis* Jackson, Proc. Biol. Soc. Washington, 31:128, November.
1955. *Sorex vagrans permiliensis*, Findley, Univ. Kansas Publ., Mus. Nat. Hist., 9:36, December.
1977. *Sorex monticolus permiliensis*, Hennings and Hoffmann, Occas. Papers Mus. Nat. Hist., Univ. Kansas, 68:14, July.
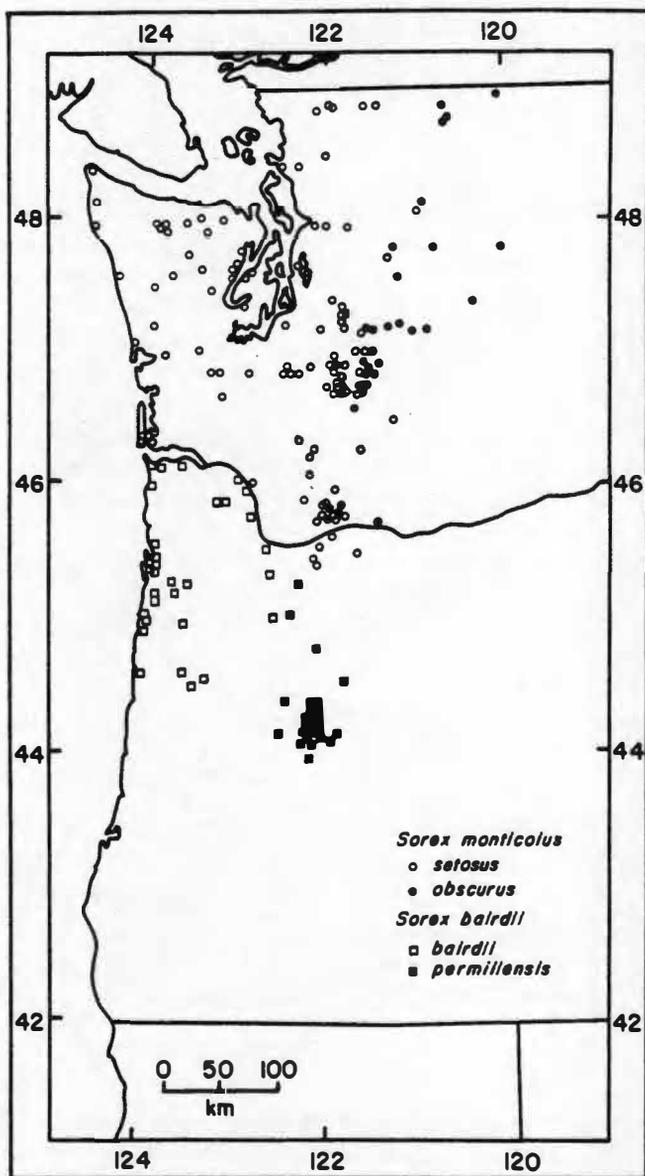
FIG. 19.—Localities in Oregon and Washington at which museum specimens of *Sorex bairdii bairdii* (open squares, 34 localities, 31 localities plotted, *n* = 82), *S. b. permiliensis* (closed squares, 41 localities, 26 localities plotted, *n* = 170), *Sorex monticolus setosus* (open circles, 102 localities, *n* = 273), and *S. m. obscurus* (closed circles, 35 localities, *n* = 66) used in this research were collected.

Holotype.—Adult male, skin and skull; USNM 91048; ''Permilia [= Pamelia] Lake, west base of Mount Jefferson, Cascade Range, [Linn
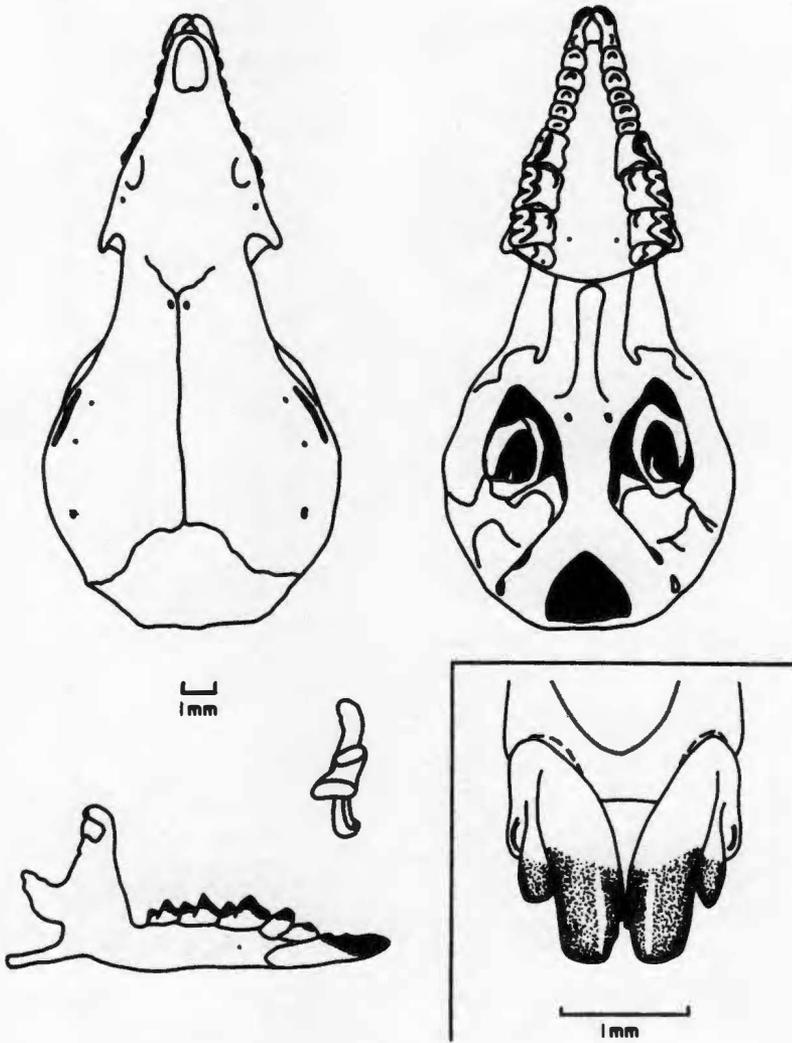
Fig. 20.—Camera-lucida tracings of dorsal and ventral views of skull, lateral and posterior views of mandible, and anterior view of I1 of an adult female *Sorex bairdii bairdii* (OSUFW X1020) from 3.75 mi. S, 2 mi. W Gold Creek, Polk Co., Oregon.

County], Oregon''; obtained on 2 October 1897 by J. A. Loring, original number 4756. Holotype examined and measured.

Distribution.—*Sorex bairdii permiliensis* occurs in the Cascade Mountains of Oregon from the Columbia River southward to southern Lane County (Fig. 19).

Description.—This taxon is composed of individuals distributed in the Oregon Cascade Mountains classified as morphotypes 9-11. The dorsal
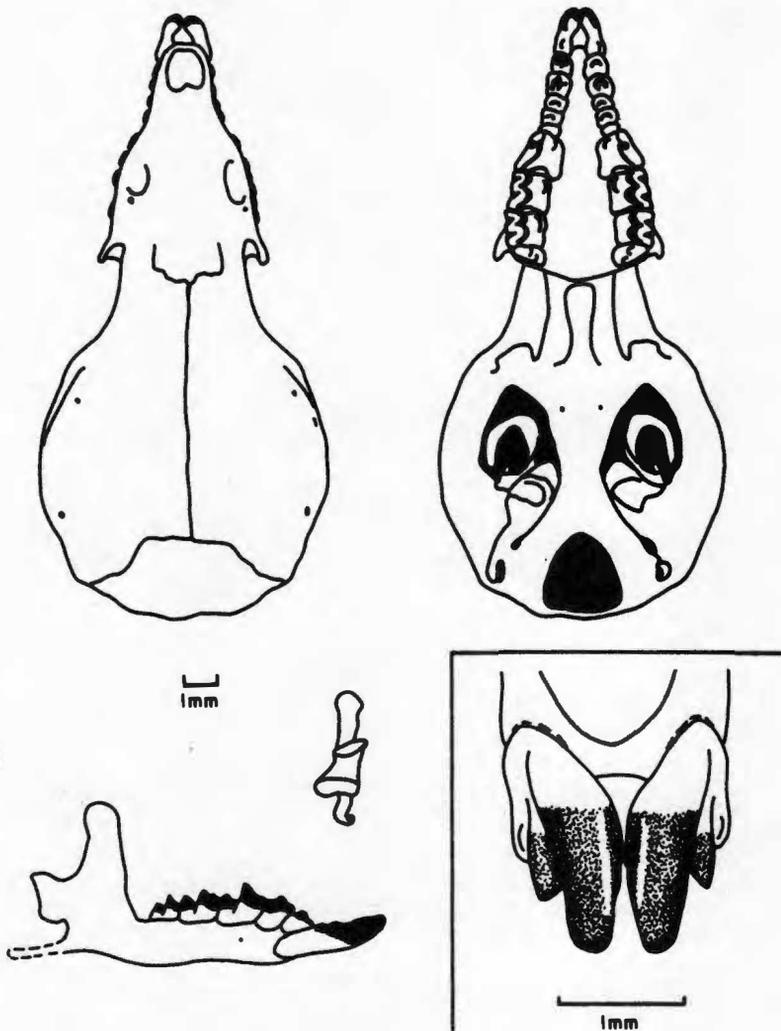
Fig. 21.—Camera-lucida tracings of dorsal and ventral views of skull, lateral and posterior views of mandible, and anterior view of I1 of an adult female *Sorex bairdii permiliensis* (OSUFW 8583) from about 10 mi. NE Blue River, Lane Co., Oregon. Angle of jaw from right dentary was missing; dashed area indicates shape and position of the angle of the jaw from the left dentary.

and ventral pelages of four specimens collected in June, July, and October are medium brown (7.5YR 4/2—Munsell Color, 1975) to dark brown (7.5YR 3/2) and pinkish light-brown (7.5YR 7/4), respectively. Bases of hairs are neutral very dark-gray (7.5YR N3/0) on the dorsum and neutral dark-gray (7.5YR N4/0) on the venter. The tail is indistinctly bicolored, medium to dark brown above and pinkish-white (7.5YR 8/2)

TABLE 3.—Mean (± SE), range, and CV of measurements (in mm.) of skull and skin characters for female and male *Sorex bairdii*.

| Character | *Sorex bairdii bairdii* | | | | | | *Sorex bairdii permiliensis* | | | | | |
| | Females (n = 40) | | | Males (n = 42) | | | Females (n = 84) | | | Males (n = 81) | | |
	x̄ ± SE	Range	CV	x̄ ± SE	Range	CV	x̄ ± SE	Range	CV	x̄ ± SE	Range	CV
Greatest length of skull	18.61 ± 0.13	15.83-20.07	4.49	18.87 ± 0.08	17.88-20.16	2.63	18.80 ± 0.05	17.66-19.58	2.28	18.78 ± 0.06	17.36-19.57	2.66
Cranial breadth	9.06 ± 0.05*	8.02-9.57	3.66	9.20 ± 0.04*	8.71-9.66	2.79	9.21 ± 0.03	8.63-9.85	2.55	9.19 ± 0.03.	8.61-9.98	2.84
Maxillary breadth	5.42 ± 0.05	4.62-5.98	5.80	5.49 ± 0.03	5.20-5.94	3.36	5.42 ± 0.02	4.85-5.89	4.03	5.39 ± 0.02	4.74-5.95	4.09
Least interorbital breadth	3.70 ± 0.04	3.03-4.16	6.49	3.77 ± 0.02	3.50-4.11	3.70	3.68 ± 0.02	3.31-4.06	4.94	3.67 ± 0.02	3.27-4.05	4.88
Cranial depth	5.19 ± 0.04	4.47-5.86	5.21	5.17 ± 0.05	4.67-5.94	5.74	5.35 ± 0.03	4.69-6.09	5.72	5.31 ± 0.04	4.63-5.98	6.00
Breadth at M2-M2	4.93 ± 0.05	4.10-5.43	5.83	4.94 ± 0.03	4.67-5.33	3.65	4.86 ± 0.02	4.39-5.32	3.99	4.84 ± 0.02	4.34-5.46	4.08
Length of unicuspid toothrow	2.77 ± 0.03	2.07-3.03	7.24	2.82 ± 0.02	2.57-3.07	4.41	2.83 ± 0.01	2.60-3.17	3.83	2.82 ± 0.01	2.43-3.00	3.52
Length of complex toothrow	4.60 ± 0.03	4.05-4.99	4.76	4.64 ± 0.02	4.38-4.94	3.08	4.57 ± 0.02	4.07-4.95	4.24	4.59 ± 0.02	4.08-5.00	4.45
Width across I1-I1	1.69 ± 0.02*	1.30-1.97	8.13	1.75 ± 0.02*	1.57-2.00	5.83	1.77 ± 0.01	1.53-1.97	4.38	1.78 ± 0.01	1.53-1.97	4.12
Breadth of zygomatic plate	1.28 ± 0.02*	0.93-1.60	11.21	1.35 ± 0.02*	1.06-1.67	10.00	1.36 ± 0.02	1.07-1.87	10.29	1.34 ± 0.01	1.03-1.67	9.73
Length of mandibular toothrow	5.34 ± 0.04	4.71-5.74	4.85	5.41 ± 0.03	5.02-5.77	3.26	5.30 ± 0.02	4.85-5.73	3.30	5.29 ± 0.03	4.15-5.65	4.30
Length of mandible	8.03 ± 0.07	6.75-8.76	5.45	8.14 ± 0.04	7.49-8.72	3.43	8.08 ± 0.03	7.39-8.73	3.46	8.08 ± 0.03	7.39-8.73	3.52
Height of coronoid process	4.54 ± 0.06	3.51-5.34	8.81	4.58 ± 0.04	3.97-5.08	5.39	4.78 ± 0.03	4.03-5.23	4.88	4.79 ± 0.02	4.16-5.32	4.61
Coronoid process-condylar length	3.11 ± 0.04	2.59-3.58	7.61	3.19 ± 0.03	2.85-3.60	5.79	3.17 ± 0.03	2.47-3.72	7.49	3.22 ± 0.03	2.64-3.75	7.14
Greatest condylar depth	2.26 ± 0.02	1.80-2.57	6.51	2.27 ± 0.02	2.10-2.53	4.46	2.32 ± 0.01	2.00-2.90	5.25	2.30 ± 0.01	2.03-2.53	4.65
Width of lower condylar facet	1.33 ± 0.01	1.10-1.50	6.72	1.35 ± 0.01	1.23-1.53	6.00	1.39 ± 0.01	1.17-1.57	5.27	1.40 ± 0.01	1.17-1.57	5.93
Width of upper condylar facet	1.00 ± 0.02	0.77-1.17	10.91	1.00 ± 0.01	0.83-1.13	7.25	1.00 ± 0.01	0.73-1.20	8.07	0.99 ± 0.01	0.83-1.30	8.61
Total length	121.53 ± 1.60*	100-141	8.33	126.67 ± 1.04*	110-143	5.30	119.71 ± 0.59	107-132	4.54	118.53 ± 0.54	102-127	4.09
Tail length	53.03 ± 1.00*	32-64	11.97	55.86 ± 0.64*	48-64	7.47	52.54 ± 0.41	41-62	7.17	52.26 ± 0.36	42-59	6.25
Length of hind foot	14.80 ± 0.20	12-18	8.55	15.33 ± 0.15	14-19	6.22	14.3 ± 0.07	13-15	4.45	14.46 ± 0.07	12-16	4.38

* Means of the variable for the two sexes within a taxon are significantly different ($P < 0.05$).

below. I was unable to examine skins of unquestionably male animals, thus the color of the bristles cannot be reported.

Sorex bairdii permiliensis can be distinguished from *S. b. bairdii* by its greater cranial depth and height of coronoid process and wider lower condylar facet (Table 3). Also, in *S. b. permiliensis* the first lower incisor is inserted in the dentary at an angle such that the tooth is pointed slightly upward (Fig. 21) instead of directly in line with the horizontal ramus of the dentary as in *S. b. bairdii* (Fig. 20). The foramen on the zygomatic plate (Fig. 5) in 97.7 percent of individuals examined is either immediately posterior to, or directly in line with, the metacone of M1 (Fig. 9j). The skull of *S. b. permiliensis* is smaller than that of *S. s. tenelliodus* (Fig. 17, Table 2); however, external body measurements are similar.

Measurements.—No variables were significantly different between the sexes (Table 3).

Remarks.—*Sorex bairdii permiliensis* and *S. b. bairdii* are separated geographically (Fig. 19). Also, discriminant (Fig. 14) and cluster analyses indicated that *permiliensis* and *bairdii* are morphometrically distinct (a taxonomic distance of 6.07 separates these two taxa).

As most of the specimens of *S. b. permiliensis* are known from either Pamelia Lake, Linn County, or H. J. Andrews Experimental Forest, Linn and Lane counties, I believe that if samples of specimens were available from intervening areas, a morphological cline of small to large individuals likely could be demonstrated.

The name for *S. b. permiliensis* was derived from its type locality, which was misspelled in the original description (Jackson, 1918).

Specimens examined.—OREGON (170).—*Clackamas Co.*: Estacada, 1 (KU 10141); 8 mi. SE Molalla, 1 (PSM 6244). *Lane Co.*: 6.8 km. N, 7.6 km. E Blue River, T15S, R5E, sec. 32, 14 (USNM 556620, 556621, 556624-556629, 556722, 556724, 557367, 557770, 557771, 557873); about 10 mi. NE Blue River, 1 (OSUFW 8583); McKenzie Bridge, 1 (PSM 8115); 3.8 km. S, 14.8 km. E McKenzie Bridge, 1070 m. T16S, R7E, sec. 33, 2 (USNM 556678, 556679); *4.4 km. S, 14.3 km. E McKenzie Bridge, T16S, R7E, sec. 32*, 3 (USNM 556666, 556670, 556672); 1 mi. N Mohawk River, T15S, R1W, SE¼NE¼sec. 13, 1 (SOSC 1865); upper tributary Lookout Creek, T15S, R5E, sec. 25, 19 (USNM 556597-556602, 556604, 556606, 556612-556615, 556617, 556619, 557758-557761, 557764, 557766); Vida, 1 (USNM 204457); *2700 ft., T15S, R5E, NW ¼ sec. 24*, 1 (PSM 19870); *3500 ft., T15S, R5E, NW ¼ sec. 24*, 6 (PSM 19872, 19873, 19875, 19877-19879); *T15S, R5E, sec. 26*, 1 (USNM 556618); 2000 ft., T15S, R5E, NW¼sec. 28, 2 (PSM 19701, 19704); *1650 ft., T15S, R5E, NE ¼ sec. 32*, 8 (PSM 19840, 19848, 19849, 19851, 19852, 19854, 19856, 19858); *2000 ft., T15S, R5E, NE ¼ sec. 32*, 6 (PSM 19681, 19684-19687, 19689); *2500 ft., T15S, R5E, SW ¼ sec. 33*, 3 (PSM 19767, 19768, 19774); T15S, R6E, sec. 26, 2 (USNM 556631, 556632); 1400 ft., T16S, R4E, NE¼sec. 24, 4 (PSM 16729, 19738, 19746, 19759); T16S, R5E, sec. 3, 10 (USNM 556633, 556634, 556636, 556638, 556639, 556641, 556643, 556645, 556733, 557045); *T16S, R5E, NW ¼ sec. 6*, 1 (PSM 19881); *1600 ft., T16S, R5E, SW ¼ sec. 6*, 5 (PSM 19689-19691, 19693, 19695); *T16S, R5E, sec. 7*, 3 (USNM 557783, 557785, 560394); T16S, R5E, sec. 20, 6 (USNM 556650, 556652, 557789-557792); T16S, R5E, sec. 26, 4 (USNM 556656, 556660, 556764, 557798); T16S, R6E, sec. 35, 3 (USNM 556664, 557773, 557932); *T16S, R7E, sec. 32*, 5 (USNM 556665, 556667, 556668, 556673, 557808); *T16S, R7E, sec. 33*, 3 (USNM 557812-557814); 3000 ft., T18S, R5E, sec. 23, 1 (PSM 11955). *Linn Co.*: 9.2 km. N, 1.2 km. W McKenzie Bridge, 810 m., T15S, R5E, sec. 14, 1 (USNM 557751); Permilia [= Pamelia] Lake, W base Mt. Jefferson, 13 (USNM 91045, 91047,

91048—holotype of *Sorex monticolus permiliensis*, 91050, 91052 91057-91059, 91061, 91062); Trout Creek F., 1200 ft., T13S, R3E, NE¼NW¼sec. 32, 2 (PSM 11974, 11975); 4400 ft., T14S, R6E, NE¼sec. 20, 3 (PSM 19816, 19818, 19820); 4600 ft., T14S, R6E, NE¼sec. 28, 1 (PSM 19860); T15S, R5E, sec. 1, 2 (USNM 556586, 557746); 3200 ft., T15S, R5E, SE¼sec. 11, 4 (PSM 19835-19838); *3000 ft., T15S, R5E, SW ¼ sec. 13*, 5 (PSM 19795, 19800-19802, 19807); *T15S, R5E, sec. 14*, 12 (USNM 556587-556591, 556593-556596, 556689, 557747, 557753); 4300 ft., T15S, R6E, NE¼ sec. 7, 4 (PSM 19706-19708, 19711); *5000 ft., T15S, R6E, NW ¼ sec. 7*, 4 (PSM 19824, 19829-19831). *Marion Co.*: 14 mi. N Detroit at Elk Lake, 1 (UCD 6001).

Sorex monticolus setosus Elliot
Dusky Shrew

1899. *Sorex setosus* Elliot, Field Columb. Mus., Zool. Ser., 1:274, May.
1955. *Sorex vagrans setosus*, Findley, Univ. Kansas Publ., Mus. Nat. Hist., 9:36, December.
1977. *Sorex monticolus setosus*, Hennings and Hoffmann, Occas. Papers Mus. Nat. Hist., Univ. Kansas, 68:14, July.

Holotype.—Adult male, skin and skull; FMNH 6213/238; "Happy Lake, Olympic Mountains, Clallam County, Washington"; obtained on 18 August 1898 by D. G. Elliot. Holotype not examined.

Distribution.—*Sorex monticolus setosus* occurs west of the crest of the Cascade Mountains in Washington, in Hood River County and far eastern Clackamas and Multnomah counties, in Oregon (Fig. 19), and beyond the limits of the study area to the north.

Description.—This taxon is composed of individuals distributed west of the crest of the Cascade Mountains, Washington, and of seven individuals from northern Hood River County and eastern Multnomah and Clackamas counties, Oregon, classified as morphotypes 9-11.

The dorsal and ventral pelages of one specimen collected in June are brown black (5YR 2.5/1—Munsell Color, 1975) and light brown (7.5YR 6/2), respectively. Bases of the hairs on the dorsum and venter are neutral very dark-gray (7.5YR N3/0). In *S. m. obscurus*, the dorsal pelage has yellow overtones and the venter is white (5YR 8/1). The tail is distinctly bicolored, brown-black above and pinkish-gray (7.5YR 7/2) below. Flank glands of one adult male are covered with pale brown bristles.

The skull of *S. m. setosus* (Fig. 22, Table 4) is smaller than that of *Sorex bairdii* (Fig. 20, Table 3). *Sorex m. setosus* can be distinguished from *S. b. permiliensis* (Fig. 21) by the anteriorly directed angle of the coronoid ramus and the first lower incisor inserted in the dentary directly in line with the horizontal ramus of the dentary. The foramen on the zygomatic plate (Fig. 5) in 65.7 percent of individuals examined is immediately posterior to the metacone of M1 (Fig. 9g).

Measurements.—Only one of 20 variables was significantly different between the sexes (Table 4).

Remarks.—Canonical analyses of a distinct morphologic and morphometric (Fig. 6) unit composed of individuals classified as morphotypes 9-11
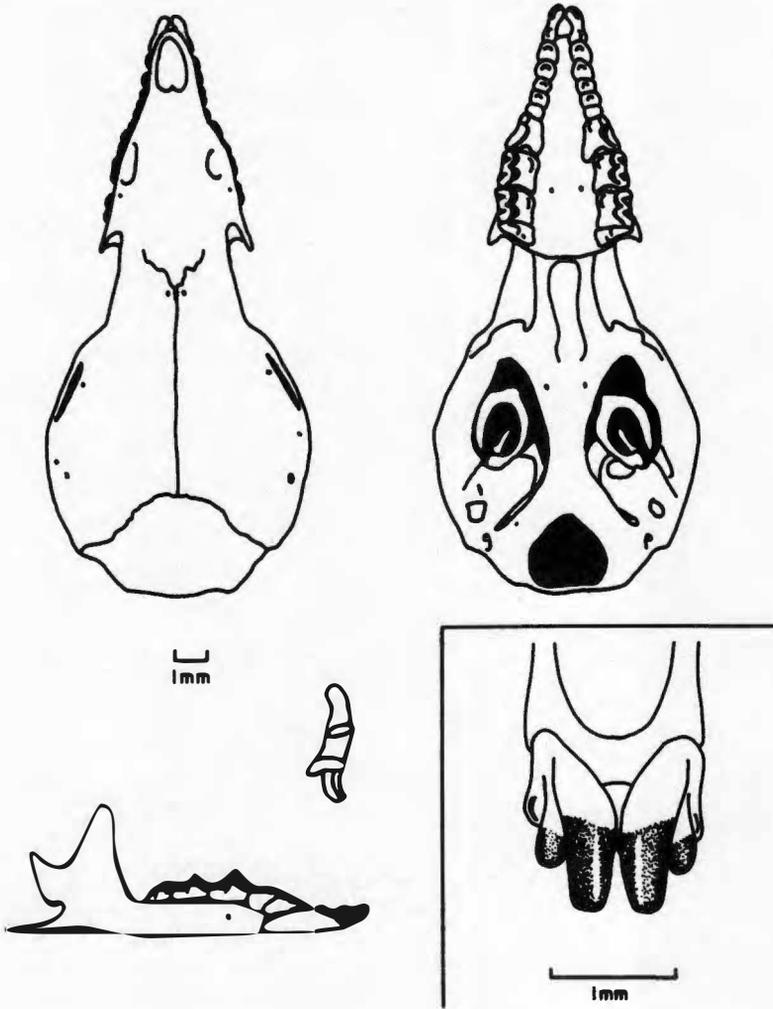
FIG. 22.—Camera-lucida tracings of dorsal and ventral views of skull, lateral and posterior views of mandible, and anterior view of I1 of an adult female *Sorex monticolus setosus* (PSM 2075) from Kalalock, Jefferson Co., Washington.

resulted in two well-defined groups with 98 percent correct classification (Figs. 11 and 12). These groups correspond to *S. monticolus* occurring primarily in Washington and *S. bairdii* occurring in Oregon. All of the 14 misclassified specimens (Fig. 12) were from Oregon; of these, seven were taken in northern Hood River County and eastern Multnomah and Clackamas counties from the Columbia River south to Parkdale (Fig. 23). These seven specimens had high probabilities (69 to 88 percent) of
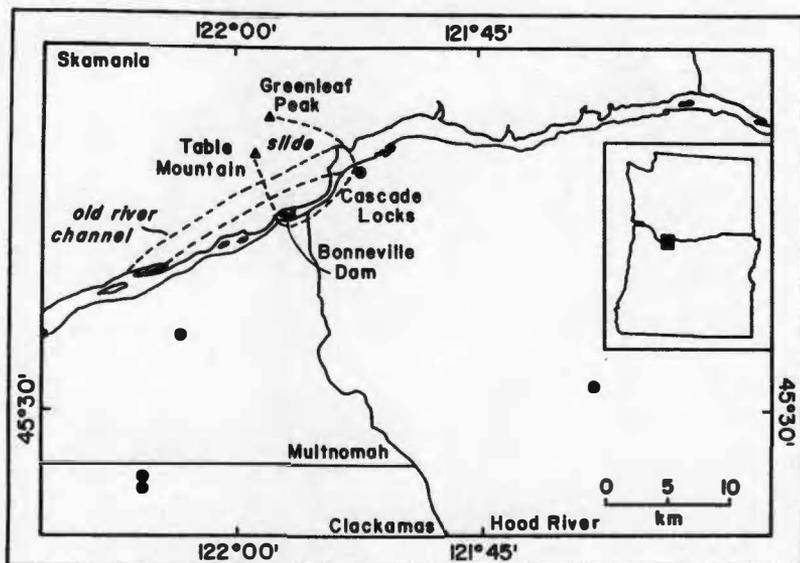
FIG. 23.–Map of northern Hood River County, and eastern Multnomah and Clackamas counties, Oregon, and southern Skamania County, Washington, with the area of the Table Mountain-Greenleaf Peak landslide (locally referred to as Bridge-of-the-Gods) illustrated relative to the former and present-day channels of the Columbia River (after Lawrence and Lawrence, 1958:35, fig. 4). Localities from which *Sorex monticolus setosus* was collected in Oregon are respresented by solid circles. All five localities are within 27 kilometers of the middle of the slide.

being members of the western Washington group and were referred to *S. m. setosus*. Although the remaining seven misclassified specimens had probabilities less than 61 percent of being members of the western Washington group, they were so widely scattered geographically that their misclassification was judged erroneous and they were referred to *S. b. bairdii*.

The morphologic and morphometric separation of *S. monticolus* and *S. bairdii*, and the absence of specimens referrable to either taxon on islands in the Columbia River (Hinschberger, 1978; G. Kirk, 1976; J. J. Kirk, 1976), led to the inference that the Columbia River is a barrier to gene flow between these two taxa. Therefore, the geographic distribution of *S. m. setosus* (Fig. 19) extending south of the Columbia River into Oregon requires explanation.

About 1700 years ago, the basalt-cap extension of Table Mountain, Skamania County, Washington, was undercut sufficiently to allow a sudden landslide (McKee, 1972) into the Columbia River (Fig. 23) "that carried millions of tons of rock and soil into the channel, across the floor of the gorge (to a depth of 61 to 92 meters), and even a little distance up the south wall, completely damming the river" (Lawrence and Lawrence, 1958:35). Because the subsequent channel of the Columbia

TABLE 4.—*Mean (±SE), range, and CV of measurements (in mm.) of skull and skin characters for female and male Sorex monticolus in Washington.*

| | Sorex monticolus obscurus | | | | | | Sorex monticolus setosus | | | | | |
| | Females (n = 32) | | | Males (n = 18) | | | Females (n = 96) | | | Males (n = 80) | | |
Character	x̄±SE	Range	CV	x̄±SE	Range	CV	x̄±SE	Range	CV	x̄±SE	Range	CV
Greatest length of skull	17.06±0.06	16.29-17.76	2.12	17.19±0.09	16.30-17.67	2.19	17.53±0.04	16.78-18.42	1.97	17.53±0.04	16.42-18.35	2.18
Cranial breadth	8.36±0.04	7.86-8.68	2.46	8.46±0.06	7.97-8.83	2.78	8.59±0.02	8.07-9.18	2.66	8.61±0.03	7.81-9.15	2.98
Maxillary breadth	4.81±0.03	4.26-5.13	3.19	4.82±0.03	4.47-5.05	2.75	5.02±0.02	4.59-5.37	3.09	5.04±0.02	4.52-5.47	3.78
Least interorbital breadth	3.33±0.03	2.87-3.63	4.33	3.33±0.04	3.04-3.65	4.53	3.49±0.01	3.09-3.91	3.57	3.52±0.02	2.98-3.96	4.65
Cranial depth	5.00±0.05	4.29-5.57	5.65	5.02±0.08	4.47-5.66	6.68	5.13±0.03	4.38-5.77*	5.76	5.04±0.03*	4.31-5.61	5.55
Breadth at M2-M2	4.38±0.02	4.01-4.61	3.18	4.41±0.04	3.91-4.63	3.76	4.59±0.02	3.98-5.04	3.52	4.60±0.02	4.12-4.91	3.29
Length of unicuspid toothrow	2.41±0.02	2.23-2.67	3.63	2.41±0.02	2.20-2.57	3.67	2.48±0.01	1.43-2.67	5.53	2.47±0.01	2.13-2.63	3.69
Length of complex toothrow	4.24±0.03	3.88-4.62	4.06	4.30±0.04	3.89-4.63	4.21	4.36±0.01	3.94-4.71	3.32	4.39±0.02	4.00-4.72	3.38
Width across I1-I1	1.45±0.01	1.37-1.57	3.40	1.46±0.01	1.37-1.53	5.01	1.53±0.01	1.37-1.70	4.29	1.53±0.01	1.33-1.73	4.76
Breadth of zygomatic plate	1.09±0.03	0.80-1.43	13.77	1.10±0.03	0.80-1.33	12.49	1.19±0.01	0.83-1.50	11.00	1.18±0.02	0.90-1.50	12.04
Length of mandibular toothrow	4.85±0.02	4.40-5.01	2.79	4.88±0.03	4.62-5.04	2.28	5.01±0.01	4.61-5.33	2.74	5.02±0.02	4.50-5.37	2.86
Length of mandible	7.21±0.04	6.60-7.51	3.08	7.31±0.04	6.95-7.55	2.17	7.46±0.02	6.95-7.92	2.69	7.46±0.02	6.75-8.08	2.76
Height of coronoid process	3.85±0.03	3.53-4.26	4.04	3.88±0.02	3.60-4.01	2.63	3.98±0.01	3.45-4.25	3.01	3.97±0.01	3.58-4.25	3.33
Coronoid process-condylar length	2.74±0.02	2.47-2.99	4.14	2.79±0.03	2.48-2.98	4.33	2.83±0.01	2.50-3.18	5.05	2.84±0.02	2.40-3.14	4.76
Greatest condylar depth	1.97±0.02	1.50-2.23	6.18	1.99±0.01	1.90-2.10	2.94	2.04±0.01	1.77-2.30	4.09	2.05±0.01	1.87-2.33	4.33
Width of lower condylar facet	1.16±0.02	0.80-1.47	9.00	1.16±0.01	1.03-1.23	4.68	1.18±0.01	1.03-1.30	4.78	1.19±0.01	1.03-1.37	5.77
Width of upper condylar facet	0.85±0.02	0.67-1.13	11.09	0.83±0.01	0.73-0.90	5.01	0.85±0.01	0.70-1.00	7.87	0.85±0.01	0.73-1.07	8.18
Total length	115.19±1.43	100-134	7.04	115.22±1.81	97-131	6.66	118.35±0.73	105-134	6.02	119.08±0.90	95-142	6.77
Tail length	50.47±0.86	35-58	9.65	49.22±0.92	39-56	7.93	53.80±0.43	36-62	7.98	53.78±0.54	42-70	8.92
Length of hind foot	13.25±0.16	12-15	6.64	13.11±0.21	12-15	6.87	13.56±0.10	11-16	6.92	13.65±0.11	10-15	6.91

* Means of the variable for the two sexes within a taxon are significantly different (P < 0.05).

River was recut through the dam (locally referred to as the Bridge-of-the-Gods) somewhat to the north of the end of the slide (Lawrence and Lawrence, 1958), the slide with its inoculum of shrews served as a fortuitous route of dispersal for *S. m. setosus* into Oregon.

At the present time, there is no evidence that *S. monticolus* and *S. bairdii* are sympatric in Oregon; the ranges of these taxa are separated by at least 27 kilometers (Fig. 19). If *S. bairdii* occurred in the region of the landslide when a sample of *S. m. setosus* was injected into that population, and the two taxa were not reproductively isolated, then introgression should have been such that *S. m. setosus* was swamped. However, either *S. bairdii* was not present and *S. m. setosus* has not been able to expand farther than 27 kilometers from the point of injection (Fig. 23), or *bairdii* was present (and still is there) and reproductive isolation has been maintained. The key to understanding the relationship between *S. monticolus* and *S. bairdii* undoubtedly lies in the region adjacent to the Bridge-of-the-Gods slide.

Specimens examined.—OREGON (7).—*Clackamas Co.*: 4.5 mi. N Alder Creek, T1S, R6E, sec. 29/32, 1 (OSUFW 8586); 6 mi. N Alder Creek, T1S, R6E, sec. 29, 1 (OSUFW 8514). *Hood River Co.*: 1 mi. E Cascade Locks, Oxbow Fish Hatchery, 1 (PSM 6893); 2 mi. W Parkdale, 1500 ft., 1 (USNM 231670). *Multnomah Co.*: 2 mi. S, 2.5 mi. E Multnomah Falls, 3 (OSUFW 8393, 8556, 8565).

WASHINGTON (266).—*Clallam Co.*: 3 M Soleduck River, Canyon Creek, 1 (USNM 241978*, 241980); 3 mi. S Solduck River, Canyon Creek, 3550 ft., 1 (USNM 241820); headwaters Cat Creek, 4500 ft., 2 (USNM 241985, 241986); Deer Lake, Olympic National Park, 2 (PSM 2164, 2166); Happy Lake, 4900 ft. [T29N, R8W], 1 (USNM 241965*); Heart of the Hills, 1 (PSM 19264); Heart o' the Hills campground, Olympic National Park [T29N, R6W, sec. 2], 4 (PSM 21049, 21050, 21052, 26393); road to Hurricane Ridge, Olympic National Park, 1 (PSM 2427); La Push, 2 (USNM 89153, 89159); Moose Lake, Olympic National Park, 1 (PSM 26396); Neah Bay, 12 (USNM 88497, 88519, 88522, 88523, 88527, 88529, 88530, 88536-88538, 186679, 186680); Olympic National Park, 1 (PSM 25775); Sand Point Trail, Ozette Lake, Olympic Pennisula, 4 (PSM 1404, 1412*, 1421, 1422); Sol Duc Park, Olympic National Park, 3 (PSM 2890*, 3153*, 3155); Sol Duc Hot Springs, 1700 ft., 1 (KU 10718). *Clark Co.*: 10 mi. E Amboy, 1 (UCD 4682). *Cowlitz Co.*: Gilbert Lookout, 4500 ft., T10N, R4E, sec. 28, 4 (PSM 11879, 11882, 11884, 11885). *Grays Harbor Co.*: Aberdeen, 2 (USNM 24326, 24342); Cedarville, 2 (USNM 230999, 231001); 3 mi. S Copalis, 2 (PSM 1428, 1439); Elma, 1 (USNM 275798); Oakville, 1 (USNM 230996); Quinault Lake [T23N, R9/10W], 2 (USNM 242389, 242390); Quiniaielt [= Quinault] Lake [T23N, R9/10W], 8 (USNM 89635, 89636, 89639, 89645*, 89647, 89655, 89660, 89662). *Jefferson Co.*: Brinnon, 1 (PSM 19146); headwaters Dosewallips River, Olympic Mts., 4500 ft., 2 (USNM 241818*, 241970*); Duckabush, 1 (USNM 231633); Elwha Basin, 1 (USNM 241972); Kalalock [= Kalaloch], 3 (PSM 2071, 2072, 2075); Marmot Lake, Olympic National Park, 2 (PSM 3850, 3851); headwaters north fork Quinault River, 1 (USNM 241976); Rainbow Forest Camp [T26N, R2W, sec. 3], 1 (PSM 3297). *King Co.*: [no specific locality given], 2 (UWBM 31728, 31844*); Baldi, 1 (PSM 10654); Cascade tunnel [T26N, R13E, sec. 22/23], 1 (USNM 230127); Enumclaw, 1 (USNM 234281); Lester, 1 (PSM 10636); Little Eagle Lake [T21N, R8E, sec. 14], 1 (PSM 13851*); Lynn Lake [T20N, R8E, sec. 21/22], 1 (PSM 10639); T22N, R7E, sec. 16, 11 (UWBM 32356, 32357*, 32358, 32360, 32361, 32367-32371, 32373); T22N, R7E, NE¼ sec. 20, 1 (UWBM 32359); T22N, R8E, sec. 32, 3 (UWBM 32362, 32363, 32365*). *Lewis Co.*: 8 mi. W Chehalis, 1 (USNM 230183); 1 M. Rainier Park, Mt. Rainier, Meslers Ranch, 2000 ft., 4 (USNM 233607, 233608, 233610, 233611). *Mason Co.*: Detroit, 3 mi. SW Allyn, 1 (PSM 984); Lake Cushman, Olympic Mts. [T23N, R4/5W], 2 (USNM 66176*, 66186*). *Pacific Co.*: 1 mi. N Bear River on Willapa Bay, 2 (MSB 8942*,

8943*); Ft. Canby State Park, 2 (PSM 26573*, 26574); Ilwaco, 1 (USNM 230184); Long Beach, 1 (USNM 273124); Long Beach, Gile Rd., 2 (PSM 1447, 1475); Shoalwater Bay, Tokeland, 1 (USNM 230194). *Pierce Co.*: Bench Lake, Rainier National Park, 4500 ft., 2 (PSM 16458, 16459); C. L. Pack Experimental Forest, 3 (UWBM 33964, 33965, 33967); 5 mi. S, 4 mi. E Carbon River entrance, Mt. Rainier National Park, Spray Park, 2 (UWBM 30681, 30801); Chrystal [= Crystal] Mt., 5000 ft., 1 (PSM 11936); Corral Pass campground [T18N, R11E, sec. 30], 1 (PSM 19266); Kautz Creek [headwaters], Rainier National Park [T14N, R7E, sec. 1], 3 (PSM 4279-4281); 1.5 mi. NW La Grande, 760 ft., 1 (UWBM 33962); 2 mi. NW La Grande, 640 ft., 1 (UWBM 33961*); 2 mi. NW La Grande, 740 ft., 1 (UWBM 33963*); 5 mi. NW La Grande, 660 ft., 1 (UWBM 33960); Longmire, Mt. Rainier, 2700 ft., 4 (USNM 233603-233606); Mountain Meadows, Mt. Rainier, 4000 ft., 1 (USNM 233081); 1.5 mi. up from Nisqually gate [T15N, R7E, SE¼ sec. 33], 1 (PSM 16380*); Ohanaprecosh Springs, Mt. Rainier, 2000 ft., 3 (USNM 232850, 232851, 232853); Paradise Park, Mt. Rainier, 5400 ft., 1 (USNM 233598); headwaters north fork Puyallup River, Rainier National Park, 3500 ft., 1 (PSM 5971); Tacoma, 1 (PSM 13852*); Tahoma Creek, Rainier National Park, 1 (PSM 4282); White River campground, Mt. Rainier National Park, 1 (UWBM 31490*); 2 km. NW White River ranger station, Mt. Rainier National Park, 1 (UWBM 31188); 1 km. SW White River ranger station, Mt. Rainier National Park, 1 (UWBM 31467*). *Skagit Co.*: Hamilton, 1 (USNM 24311); Mt. Vernon, 10 (USNM 24309*, 76317, 76318, 76490, 76491, 88808, 88809, 88817, 88824, 88833); Rockport, 1 (USNM 234512). *Skamania Co.*: 4 mi. N, 7 mi. W Carson, 12 (USNM 558145, 558146, 558148, 558149, 558152-558154, 558157-558159, 558164, 558380); 4.5 mi. N, 7.5 mi. W Carson, 6 (USNM 558165, 558366, 558376-558378, 558381); 5 mi. N, 6.3 mi. W Carson, 16 (USNM 558166, 558167*, 558168, 558169, 558173, 558174*, 558175-558177, 558178*, 558181, 558394, 558400, 558403, 558405, 558407); 7 mi. N, 7.4 mi. W Carson, 3 (USNM 558182, 558428, 558429); 7 mi. N, 8.3 mi. W Carson, 2 (USNM 558186, 558190); 8.4 mi. N, 7.5 mi. W Carson, 7 (USNM 558216, 558217, 558223, 558228, 558502, 558506, 558507); 8.5 mi. N, 1.5 mi. W Carson, 19 (USNM 558191*, 558194, 558196, 558198, 558201, 558202, 558207, 558210, 558450, 558452, 558460, 558461, 558469-558474, 558476); 10 mi. N, 1.3mi. W Carson, 19 (USNM 558238, 558239*, 558240-558244, 558246, 558247*, 558250, 558252, 558253, 558255, 558530, 558546, 558550, 558551, 558553, 558743); 15 m[i]. N Carson, Government Springs, 2 (USNM 230208, 230211); Council Pass, 4356 ft. [T9N, T9E, sec. 14], 1 (PSM 1396); Mt. St. Helens, 2 (USNM 90715, 90716*); 8 mi. S St. Helens, 1 (USNM 231018); Spirit Lake, Mt. St. Helens, 3200 ft., 3 (USNM 273134, 273135*, 273138). *Snohomish Co.*: 4 mi. E Everett, 1 (USNM 229882); Granville, 1 (USNM 89651). *Thurston Co.*: Tenino, 1 (USNM 89649*). *Whatcom Co.*: Glacier, 900 ft., 3 (USNM 234290*, 234292, 234875); northeast side Mt. Shuksan, Nooksack Cirque, North Cascades National Park, 8 (UWBM 30870, 30963, 30974, 30985, 30989*, 30996*, 31000, 31001); U.S. Cabin, Whatcom River [T39N, R10E, sec. 1], 1 (USNM 234877*). *Yakima Co.*: Conrad Meadows [T12N, R12E, sec. 26/27], 1 (USNM 227235*).

Sorex monticolus obscurus Merriam

1891. *Sorex vagrans similis* Merriam, N. Amer. Fauna, 5:34, July (name preoccupied by *Sorex similis* Hensel, 1855).

1895. *Sorex obscurus* Merriam, N. Amer. Fauna, 10:72, December (a renaming of *Sorex vagrans similis*).

1955. *Sorex vagrans obscurus*, Findley, Univ. Kansas Publ., Mus. Nat. Hist., 9:43, December.

1977. *Sorex monticolus obscurus*, Hennings and Hoffmann, Occas. Papers Mus. Nat. Hist., Univ. Kansas, 68:14, July.

Holotype.—Adult female, skin and skull, cranium broken; USNM 23525/30943; "Salmon River Mountains [Timber Creek, Lemhi Mountains], [Lemhi County], Idaho"; obtained on 26 August 1890 by B. H. Dutcher, original number 1670. Holotype examined and measured.
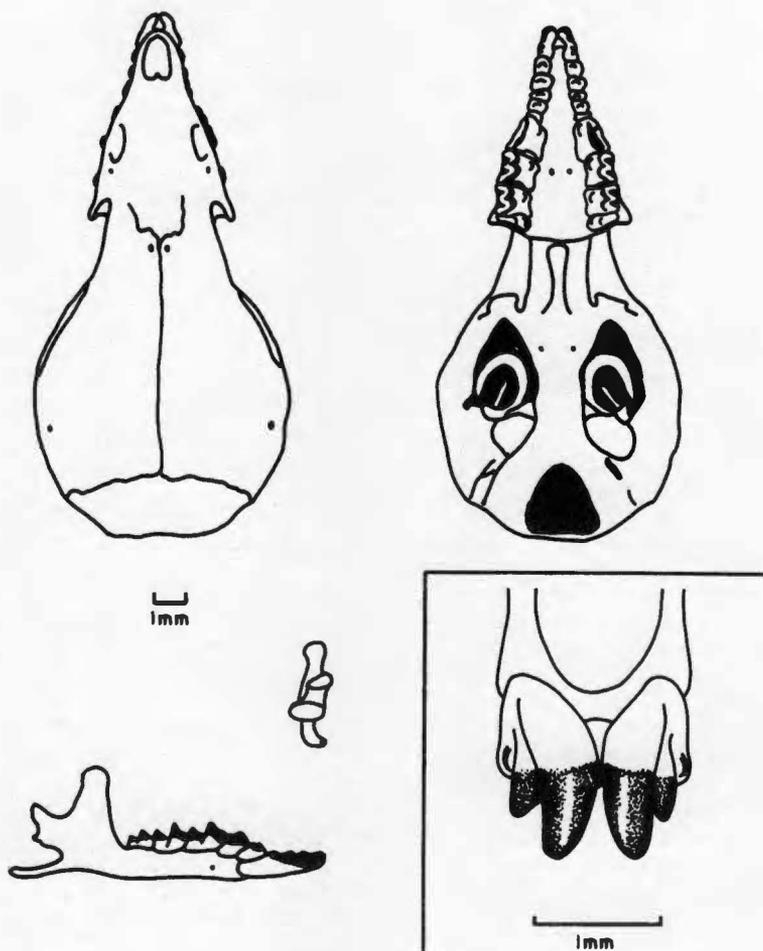
Fig. 24.—Camera-lucida tracings of dorsal and ventral views of skull, lateral and posterior views of mandible, and anterior view of I1 of an adult of unknown sex of *Sorex monticolus obscurus* (OSUFW 6063) from Wenatchee Lake, Chelan Co., Oregon.

Distribution.—*Sorex monticolus obscurus* occurs east of the crest of the Cascade Mountains in Washington, except in the southeastern scablands (Fig. 19), and beyond the limits of the study area to the north and east.

Description.—This taxon is composed of individuals distributed east of the crest of the Washington Cascade Mountains classified as morphotypes 9-11. The dorsal and ventral pelages of three specimens collected in July and September are medium brown (7.5YR 4/2—Munsell Color, 1975) to medium yellowish-brown (7.5YR 4/4) and white (5YR 8/1), respectively.

Bases of the hairs on the dorsum are neutral very dark-gray (7.5YR 3/0) and on the venter neutral dark-gray (7.5YR N4/0). In *S. m. setosus* the dorsal pelage is brown black and the ventral pelage is light brown. The tail is indistinctly bicolored, medium brown above and white below. Flank glands of two adult males collected in July are covered with white bristles.

Sorex monticolus obscurus (Fig. 24, Table 4) is smaller than *S. m. setosus* (Fig. 22, Table 4). The foramen on the zygomatic plate (Fig. 5) in 57.6 percent of individuals examined is immediately posterior to the metacone of M1 (Fig. 9h).

Measurements.—No variables were significantly different between the sexes (Table 4).

Remarks.—Although *S. m. setosus* and *S. m. obscurus* seem morphometrically similar (Fig. 13), the present classification is retained because I did not examine specimens from throughout the geographic ranges of the two taxa. Of the 45 misclassified specimens (Fig. 13), six had high probabilities of being members of the eastern Washington group and 39 members of the western Washington group and were considered referable to *S. m. obscurus* and *S. m. setosus*, respectively. Because most of the misclassified specimens were collected at the boundary between the geographic distributions of these two taxa, they may represent intergrades. Geographic variation present within *S. monticolus* may be a fruitful topic for further research.

Specimens examined.—ARIZONA (1).—*Coconino Co.*: San Francisco Mt., 11000 ft., 1 (USNM 17599—holotype of *Sorex monticolus*).

IDAHO (1).—Salmon River Mts., 1 (USNM 23525—holotype of *Sorex obscurus*).

WASHINGTON (66).—*Chelan Co.*: Wenatchee Lake, 1 (OSUFW 6063). *Douglas Co.*: head of Lake Chelan [T27N, R23E, sec. 29], 2 (USNM 42244, 42603); Wenatchee, 1 (USNM 91044). *King Co.*: Carroll Cyn., Mt. Baker, 3000 ft., T26N, R12E, sec. 35, 10 (UWBM 31791, 31804*, 31812*, 31833, 32625, 32632, 32641, 32656, 32662, 32739); Lester, 1 (PSM 10634); Little Eagle Lake, 1 (PSM 10646); McCain Creek [T20N, R10E, sec. 11/15], 1 (USNM 229880). *Kittitas Co.*: 2 mi. E Cle Elum, 1 (MSB 8953); Easton, 5 (USNM 29544, 29546, 29548, 29549, 29554); Hells Crossing, American River, T17N, R12E, NE¼ sec. 18, 1 (MMNH 9739*); 2 mi. S, 0.5 mi. W Roslyn, 2 (MSB 43422, 43423). *Klickitat Co.*: 1 mi. E Bingham, 1 (PSM 6154). *Lewis Co.*: Bear Prairie, Mt. Rainier, 2 (USNM 233085*, 233086); 1 mi. W Packwood, 1 (UWBM 30682); Ohanapecosh ranger station, Mt. Rainier National Park [T14N, R10E, sec. 4], 5 (UWBM 31459*, 31460, 31465, 31473, 31476); 2 mi. N, 4 mi. W Ohanapecosh, Mt. Rainier National Park, 1 (UWBM 30677); Paradise Creek, Mt. Rainier, 1 (USNM 89577); *Okanogan Co.*: Bauerman Ridge, 6800 ft., 1 (USNM 235205); W fork Pasayten River [headwaters], 1 (USNM 235120*). *Pierce Co.*: 4 mi. S, 3 mi. E Carbon River entrance, Mt. Rainier National Park [T17N, R7E, sec. 24], 1 (UWBM 30497); Chrystal [= Crystal] Mt., 5000 ft., 2 (PSM 11934, 11935); Corral Pass [T18N, R11E, sec. 30], 2 (PSM 25777, 26388); 5 mi. N, 1 mi. E Ohanapecosh entrance, Mt. Rainier National Park [T15N, R10E, sec. 10], 1 (UWBM 30496); Owyhigh Lake, near outlet, Rainier National Park, 1 (PSM 5941); 2 km. NW White River ranger station, 1 (UWBM 31486). *Skamania Co.*: 4 mi. N, 7 mi. W Carson, 5 (USNM 558142, 558155, 558160, 558162, 558163); 7 mi. N, 7.4 mi. W Carson, 1 (USNM 558183); 8.5 mi. N, 1.5 mi. W Carson, 3 (USNM 558197, 558199, 558209); 10 mi. N, 1.3 mi. W Carson, 4 (USNM 558256, 558545, 558547, 558552). *Snohomish Co.*: Chiwawa Mt. Fork, Suiattle River [T31N, R15E, sec. 24], 2 (USNM 230220, 230224); 3 mi. up Rapid River from Beckler River, 2000 ft., 1 (PSM

14146). *Whatcom Co.*: Barron, 5000 ft., 1 (USNM 234974); Bonte Mine, Barron, 5000 ft., 1 (USNM 235010). *Yakima Co.*: 1 mi. N, 2 mi. E Chinook Pass, 1 (UWBM 30371).

Sorex pacificus pacificus Coues
Pacific Shrew

1877. *Sorex pacificus* Coues, Bull. U.S. Geol. Geogr. Surv. Terr., 3:650, March.
1918. *Sorex yaquinae* Jackson, Proc. Biol. Soc. Washington, 31:127, July. Holotype from "Yaquina Bay, Lincoln County, Oregon"; obtained on 29 November 1895 by B. J. Bretherton. Holotype examined and measured.
1936. *Sorex pacificus yaquinae*, Bailey, N. Amer. Fauna, 55:364, June.
1955. *Sorex vagrans pacificus*, Findley, Univ. Kansas Publ., Mus. Nat. Hist., 9:34, December.
1955. *Sorex vagrans yaquinae*, Findley, Univ. Kansas Publ., Mus. Nat. Hist., 9:34, December.

Holotype.—Adult sex unknown, damaged anterior half of skull inside flat skin; USNM 3266; "Fort Umpqua [mouth Umpqua River, Douglas County], Oregon"; obtained before 1861 by E. P. Vollum. Holotype examined, but not included in analyses.

Distribution.—*Sorex pacificus pacificus* occurs from Cascade Head, Tillamook County, southward to Coos Bay, Coos County, thence eastward to Philomath, Benton County, Cottage Grove, Lane County, and northwest of Sutherlin, Douglas County, all in Oregon (Fig. 25).

Description.—This taxon is composed of individuals distributed in the Oregon Coast Range classified as morphotype 2. The dorsal pelage, based on 15 specimens collected in June, August, September, and October, is dark brown (between 7.5YR 3/2 and 7.5YR 3/4—Munsell Color, 1975); the ventral pelage is pinkish light-brown (between 7.5YR 6/4 and 7.5YR 5/4). Bases of hairs on both dorsum and venter are neutral dark--gray (7.5YR N4/0). The tail is indistinctly bicolored, dark brown (7.5YR 3/2) above and white (5YR 8/1) below. Flank glands of two adult males collected in June and October are covered with pinkish light-brown bristles.

The first upper incisors have a ridge at the posteriomedial edge visible in anterior view through the gap between the incisors (Fig. 26). The foramen on the zygomatic plate (Fig. 5) in 82.1 percent of individuals examined is either immediately posterior to or directly in line with the metacone of M1 (Fig. 9c); in *S. s. sonomae* the foramen usually is anterior to the metacone of M1 (Fig. 9b). There is a small ridge anteriolaterally on the cranium (Fig. 26). The zygomatic processes of the maxillary are finely pointed (Fig. 26), not rounded as in *S. s. sonomae*.

Sorex pacificus (Table 5) can be distinguished from *S. s. sonomae* (Fig. 17, Table 2) by the projection on the medial edge of the first upper incisors, shallower coronoid process, and shorter length of the unicuspid toothrow. It can be distinguished from *S. bairdii* (Fig. 20, Table 3) by its larger size, longer than wide unicuspids, shape and position of the projection on the medial edge of the first upper incisors, and darker pelage color.

Measurements.—No variables were significantly different between the sexes (Table 5). Length of unicuspid toothrow for the holotype is 3.70 millimeters.

Remarks.—George (1984, 1988) reported data for 25 electromorphs, mean heterozygosity, and percent polymorphism for specimens referrable to *Sorex pacificus* within my study area; however, it is unknown if the specimens used were respresentative of morphotype 1 or 2. Therefore, these data are not used in descriptions of *S. pacificus* or *S. sonomae*.

Individuals classified in morphotype 2 form a distinct morphologic (Figs. 26 and 27) and morphometric (Fig. 6) unit characterized by the presence of a ridge at the posteriomedial edge of the first upper incisors. Holotypes of both *S. yaquinae* and *S. p. pacificus* possess this morphologic character and thus are synonomized. The latter name has priority.

Specimens examined.—OREGON (30).—*Benton Co.*: 1 mi. S, 6 mi. W Alpine, 1 (OSUFW 3141); 10 mi. W Alsea, 1 (OSUFW 3107); Mary's Peak, 4 (OSUFW 4836-4838, PSM 3334); 5 mi. SW Philomath, 1 (USNM 233629); T12S, R7W, sec. 14, 1 (USNM 561139); *T12S, R7W, sec. 17/20*, 1 (USNM 561142); T12S, R7W, sec. 24/25, 1 (USNM 561145); T13S, R8W, sec. 20, 1 (USNM 561152*). *Coos Co.*: Marshfield [= Coos Bay], 1 (FMNH 9632); Delmar, 9 mi. S Marshfield, 1 (MVZ 63461). *Douglas Co.*: Ft. Umpqua, 1 (USNM 3266—holotype of *Sorex pacificus* Coues, 1877); Oxbow Burn, 300 ft., 3 (PSM 11892, 11895, 11899); 4 km. N, 12.1 km. W Sutherlin, 1 (USNM 560080). *Lane Co.*: Mapleton, 1 (USNM 205270); T15S, R8W, sec. 11, 2 (USNM 561164, 561165); T15S, R12W, sec. 12, 1 (USNM 561161). *Lincoln Co.*: Alsea Bay, 1 (PSM 9700); Newport, 2 (SDNHM 17042, 17044); Taft, 1 (SDNHM 17036); Yaquina Bay, 1 (USNM 73051—holotype of *Sorex yaquinae* Jackson, 1918); T12S, R10W, sec. 13/24, 2 (USNM 561128, 561129). *Tillamook Co.*: Cascade Head, 1 (PSM 4417).

Sorex pacificus cascadensis new subspecies

Holotype.—Adult female, skin and skull, left angle of jaw missing; USNM 204479; "McKenzie Bridge, [Lane County], Oregon"; obtained on 5 July 1914 by V. Bailey, original number 9650. Holotype examined and measured.

Distribution.—*Sorex pacificus cascadensis* occurs from northeastern Linn County, southward to southern Jackson County, Oregon (Fig. 25).

Diagnosis.—Overall, *S. p. cascadensis* is smaller and more reddish than *S. p. pacificus* (Figs. 26 and 27, Table 5). The dorsal pelage, based on the holotype, is medium reddish-brown (between 7.5YR 4/2 and 7.5YR 4/4 of Munsell Color, 1975; Sepia of Ridgeway, 1912); the ventral pelage is light brown (7.5YR 6/4). Bases of the hairs of the dorsum and venter are neutral very dark-gray (7.5YR N3/0). The tail is indistinctly bicolored, medium reddish-brown above and light brown below. I was unable to examine skins of unquestionably male animals, thus the color of the bristles cannot be reported. In contrast, the dorsal and ventral pelages of *S. p. pacificus* are dark brown and pinkish light-brown, respectively.

Description.—This taxon is composed of individuals distributed in the Oregon Cascade Mountains classified as morphotype 2. The first upper
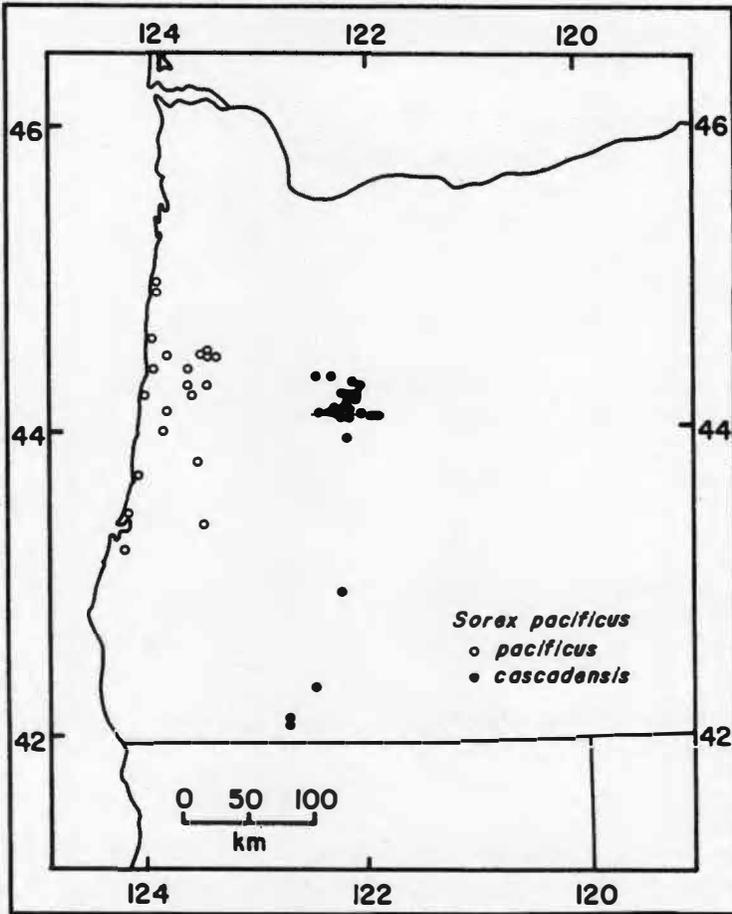
FIG. 25.–Localities in Oregon at which museum specimens of *Sorex pacificus pacificus* (open circles, 22 localities, 21 localities plotted, *n* = 30) and *S. p. cascadensis* (closed circles, 41 localities, 26 localities plotted, *n* = 116) used in this research were collected.

incisors have a ridge at the posteriomedial edge that is visible in anterior view through the gap between the incisors (Fig. 27). The foramen on the zygomatic plate (Fig. 5) in 94.9 percent of individuals examined is located either immediately posterior to, or directly in line with, the metacone of M1 (Fig. 9d). There is a small ridge present anteriolaterally on the cranium (Fig. 27). The zygomatic processes of the maxillary are finely pointed (Fig. 27), not rounded as in *S. sonomae* (Figs. 17 and 18).

In addition to the differences in morphology of the first upper incisor (Figs. 18 and 27), *S. p. cascadensis* can be distinguished from *S. s. tenelliodus* by the striking differences in pelage coloration. The former has a reddish dorsum and light brown venter, whereas the latter has a medium brown dorsum and pinkish-white venter (Munsell Color, 1975).
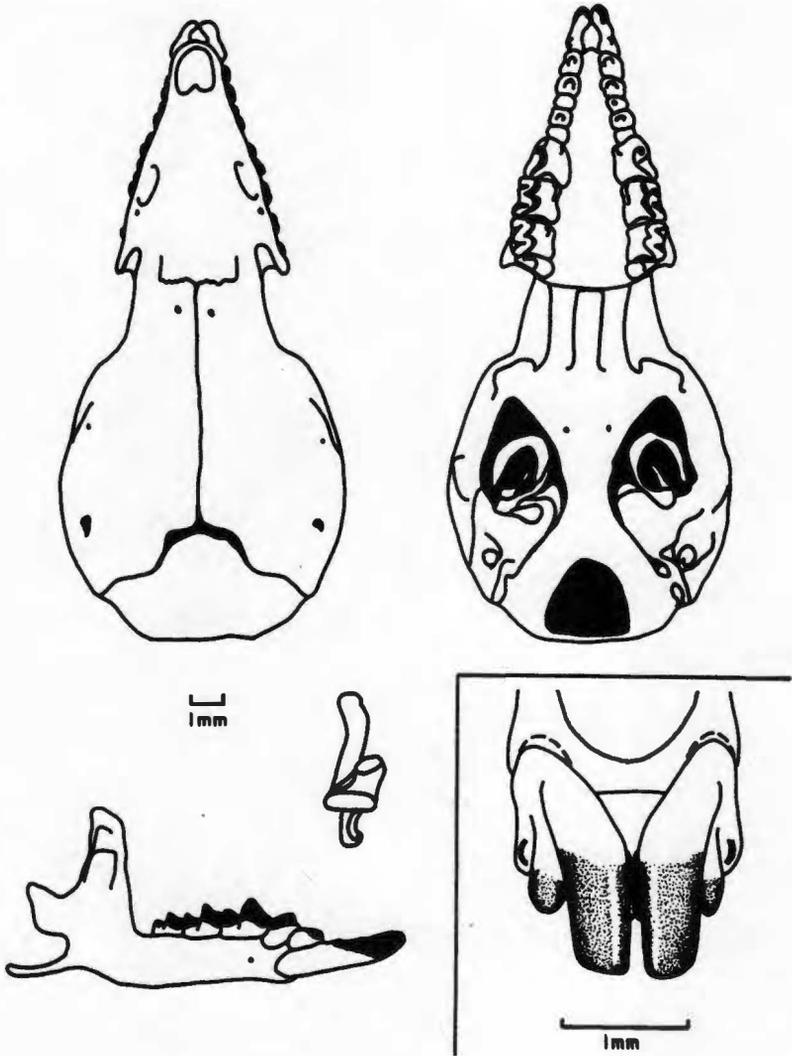
FIG. 26.—Camera-lucida tracings of dorsal and ventral views of skull, lateral and posterior views of mandible, and anterior view of I1 of an adult female (?) *Sorex pacificus pacificus* (OSUFW 4837) from 3 mi. S, 6 mi. W, Philomath, Benton Co., Oregon.

Measurements.—Only one of 20 variables was significantly different between the sexes (Table 5). Measurements of the holotype are: greatest length of skull, 19.32; cranial breadth, 9.14; maxillary breadth, 5.58; least interorbital breadth, 3.73; cranial depth, 5.62; breadth at M2-M2, 5.23; length of unicuspid toothrow, 2.77; length of complex toothrow, 4.64; width across I1-I1, 1.83; breadth of zygomatic plate, 1.30; length
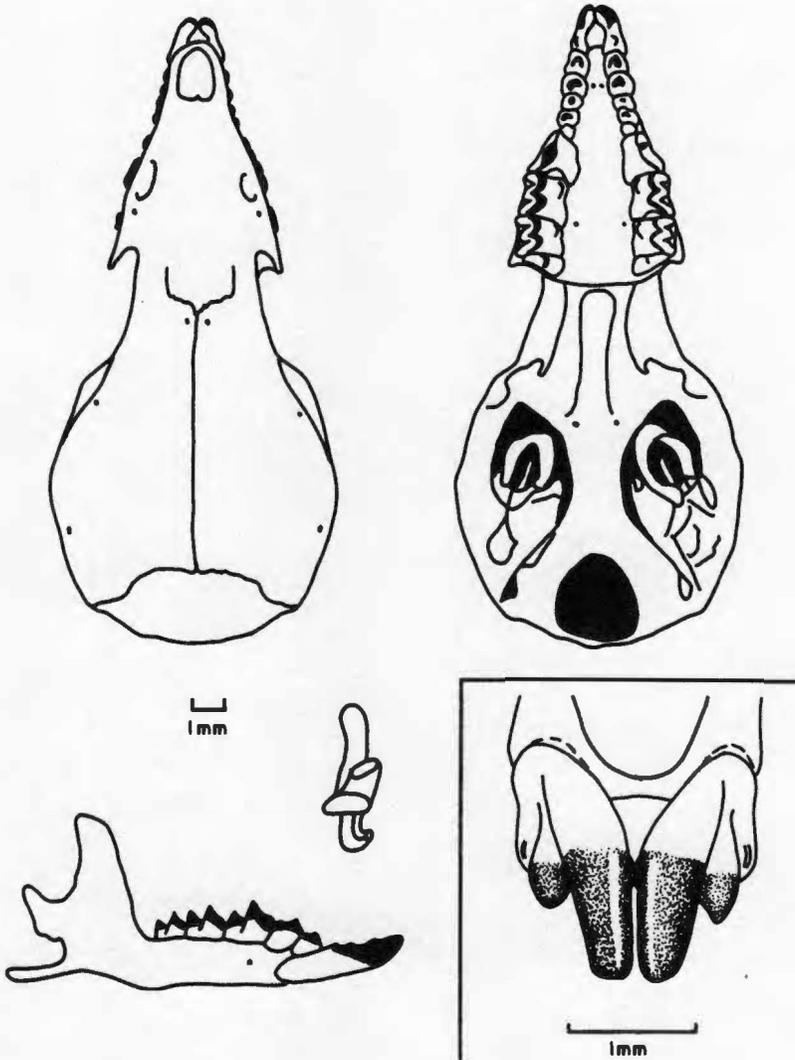
FIG. 27.—Camera-lucida tracings of dorsal and ventral views of skull, lateral and posterior views of mandible, and anterior view of I1 of an adult female *Sorex pacificus cascadensis* (USNM 204479) from McKenzie Bridge, Lane Co., Oregon.

of mandibular toothrow, 5.43; length of mandible, 8.53; height of coronoid process, 4.92; coronoid process-condylar length, 3.18; greatest condylar depth, 2.37; width of lower condylar facet, 1.43; width of upper condylar facet, 0.97; total length, 124.0; length of tail, 55.0; and length of hind foot, 15.0.

Etymology.—The subspecific name is from the Cascade Mountains in which this shrew is found.

Remarks.—The nominate subspecies and *S. p. cascadensis* are separated geographically (Fig. 25) and are morphometrically distinct (Fig. 10).

The superficial similarity between *Sorex sonomae tenelliodus* and *S. pacificus* seemingly is responsible in part for confusion regarding the taxonomic status of shrews of the "*Sorex vagrans* species complex" in the Pacific Northwest. Some researchers (Black and Hooven, 1974; Borrecco *et al.*, 1979; Findley, 1955; Forsman and Maser, 1970; Gashwiler, 1959, 1967, 1970*a*, 1970*b*; Hooven and Black, 1976; Hooven *et al.*, 1979; Silovsky and Pinto, 1974) failed to recognize the morphological differences and considered them conspecific. Hennings and Hoffmann (1977:19) considered specimens; in a zone extending from northern Lincoln County, through Benton County, and H. J. Andrews Experimental Forest, Lane County, to the crest of the Cascade Mountains, Oregon, "with traces of medial tines" on the first upper incisors as possible hybrids between *S. bairdii* and *S. sonomae*. Junge and Hoffmann (1981) reiterated the suggestion. *S. bairdii* has a tine on the anteriomedial edge of the first upper incisors and *S. sonomae* has no projections on the medial edge. The intermediate morphology of the projection on the first upper incisors of *S. p. pacificus* and *S. p. cascadensis* makes Hennings and Hoffmann's (1977) suggestion seem logical. However, the distribution of the geographic races of *S. pacificus* as described herein (Fig. 25) extend far beyond the zone in which hybridization could possibly occur (Figs. 16, 19, and 25) between *S. bairdii* and *S. sonomae*.

Specimens examined.—OREGON (116).—*Jackson Co.*: Upper Ashland Research Natural Area, 2 (SOSC 1054, 1657); *0.6 mi. N jct. FSR 3903 and E. Fork Ashland Cr.*, 1 (SOSC 917); 6 mi. S Ashland, 1 (SOSC 221); T37S, R3E, SW¼sec. 20, 1 (SOSC 1699). *Klamath Co.*: Sphagnum Bog, Crater Lake Nat. Park, 2 (SOSC RAM31, RAM62). *Lane Co.*: 5.5 mi. NE Blue River, 1500 ft., 1 (PSM 15705); 6 mi. W Blue River, 1 (OSUFW 8306*); Cougar Creek, T16S, R5E, sec. 32, 1 (OSUFW 8562); Elk Creek, McKenzie Bridge, 1 (USNM 204479); *Elk Creek, T16S, R4E, sec. 19*, 2 (OSUFW 8574, 8581); Hagan Cr., T16S, R3E, sec. 22, 2 (OSUFW 8558, 8578); Lookout Creek, T15S, R6E, sec. 30, 1 (OSUFW 8613); Mack Creek Tributary, T15S, R5E, sec. 35, 1 (OSUFW 8398); Swamp Creek, T16S, R5E, sec. 20, 9 (OSUFW 8362, 8399, 8532, USNM 556648, 556649, 556651, 556653, 556654, 557787); Upper Lookout Creek tributary, T15S, R5E, sec. 24, 1 (OSUFW 8389); *T15S, R5E, sec. 25*, 13 (USNM 556605, 556607-556610, 556616, 556699, 556701, 556704, 556888, 557756, 557757, 557765); *2000 ft., T15S, R5E, NW ¼ sec. 28*, 1 (PSM 19696); *1650 ft., T15S, R5E, NE ¼ sec. 32*, 3 (PSM 19844, 19846, 19855); *2000 ft., T15S, R5E, NE ¼ sec. 32*, 1 (PSM 19688); *T15S, R5E, sec. 32*, 4 (USNM 556623, 557767, 557774, 557775); *2500 ft., T15S, R5E, SW ¼ sec. 33*, 3 (PSM 19770, 19772, 19775); 1800 ft., T16S, R4E, NE¼sec. 19, 6 (PSM 19717, 19718, 19722*, 19725, 19727, 19734); 1400 ft., T16S, R4E, NE¼sec. 24, 6 (PSM 19654, 19739, 19753, 19754, 19757, 19762); T16S, R5E, sec. 3, 8 (USNM 556635, 556640, 556644, 556734, 557050, 557431, 557734, 557778); *T16S, R5E, sec. 6*, 1 (USNM 556646); *T16S, R5E, sec. 7*, 1 (USNM 557782); T16S, R5E; sec. 25, 2 (USNM 556655, 557795*); *T16S, R5E, sec. 26*, 5 (USNM 556657, 556659, 556761, 556762, 557797); T16S, R6E, sec. 35, 7 (USNM 556662, 556663, 556766, 557802-557805); T16S, R7E, sec. 32, 7 (USNM 556669, 556671, 556771, 556773, 556774, 557807, 557810); *T16S, R7E, sec. 33*, 6 (USNM 556675, 556677, 557811, 557815-557817); 3000 ft., T18S, R5E, sec. 23, 1 (PSM 12033). *Linn Co.*: 7 mi. E Cascadia, 1 (UCD 4667); 4400 ft., T14S, R6E, NE¼sec. 20, 1 (PSM 19819); 4600 ft., T14S, R6E, NE¼sec. 28, 1 (PSM 19863); T15S, R5E, sec. 1, 4 (USNM 556585, 556682, 556683, 557744); T15S, R5E, SE¼sec. 11, 1 (PSM 19834); *3000 ft., T15S, R5E,*

TABLE 5.—*Mean (±SE), range, and CV of measurements (in mm.) of skull and skin characters for female and male Sorex pacificus.*

| | Sorex pacificus cascadensis | | | | | | Sorex pacificus pacificus | | | | | |
| | Females (n = 48) | | | Males (n = 63) | | | Females (n = 14) | | | Males (n = 13) | | |
Character	x̄±SE	Range	CV	x̄±SE	Range	CV	x̄±SE	Range	CV	x̄±SE	Range	CV
Greatest length of skull	19.12±0.07	17.55-20.67	2.62	18.94±0.05	17.86-19.91	2.30	20.26±0.25	18.69-22.09	4.68	20.03±0.24	17.92-21.23	4.35
Cranial breadth	9.35±0.03	8.49-9.75	2.54	9.29±0.03	8.69-10.00	2.51	9.69±0.11	9.29-10.47	4.24	9.75±0.09	9.23-10.42	3.44
Maxillary breadth	5.56±0.03	4.83-6.05	3.90	5.51±0.02	4.90-5.93	3.34	5.99±0.07	5.68-6.55	4.23	5.92±0.08	5.52-6.42	4.94
Least interorbital breadth	3.78±0.03	3.18-4.16	4.93	3.74±0.02	3.22-4.01	4.75	4.03±0.05	3.78-4.38	4.81	4.00±0.04	3.70-4.25	3.98
Cranial depth	5.51±0.04	4.91-6.14	5.21	5.44±0.03	4.87-6.03	4.24	5.49±0.09	4.72-6.01	6.32	5.59±0.09	5.11-6.50	6.28
Breadth at M2-M2	5.01±0.03	4.38-5.38	4.09	4.95±0.02	4.40-5.35	3.65	5.42±0.06	5.14-5.82	3.82	5.40±0.06	5.11-5.82	4.20
Length of unicuspid toothrow	2.90±0.01*	2.67-3.13	3.39	2.84±0.01*	2.63-3.07	3.36	3.15±0.05	2.77-3.50	6.04	3.21±0.04	2.90-3.47	4.46
Length of complex toothrow	4.70±0.03	3.98-5.04	4.52	4.68±0.02	4.15-5.20	3.91	4.96±0.07	4.50-5.47	5.38	4.99±0.06	4.76-5.30	4.03
Width across I1-I1	1.81±0.01	1.67-1.97	4.41	1.81±0.01	1.63-1.97	4.46	1.95±0.04	1.73-2.27	8.15	1.94±0.04	1.70-2.13	6.63
Breadth of zygomatic plate	1.35±0.02	1.07-1.63	8.76	1.35±0.02	1.07-1.77	10.15	1.45±0.03	1.20-1.63	8.78	1.39±0.05	1.00-1.63	13.90
Length of mandibular toothrow	5.41±0.03	4.77-5.74	3.54	5.36±0.02	4.88-5.66	2.97	5.81±0.12	4.60-6.48	7.61	5.84±0.07	5.60-6.42	4.37
Length of mandible	8.24±0.04	7.55-8.83	3.31	8.18±0.03	7.40-8.62	3.23	8.88±0.13	8.16-9.91	5.66	8.77±0.09	8.14-9.38	3.67
Height of coronoid process	4.96±0.03	4.31-5.38	4.24	4.89±0.02	4.33-5.21	3.55	5.33±0.13	4.71-6.27	9.09	5.20±0.07	4.80-5.74	5.15
Coronoid process-condylar length	3.36±0.03	2.93-3.81	6.40	3.28±0.03	2.81-3.67	6.26	3.64±0.09	3.14-4.39	9.53	3.55±0.04	3.30-3.83	4.47
Greatest condylar depth	2.37±0.02	2.20-2.63	4.80	2.35±0.01	2.20-2.93	4.69	2.48±0.05	2.17-2.83	7.26	2.48±0.03	2.27-2.67	4.58
Width of lower condylar facet	1.45±0.01	1.27-1.63	5.10	1.42±0.01	1.27-1.57	5.51	1.51±0.04	1.27-1.77	8.96	1.50±0.02	1.40-1.67	5.74
Width of upper condylar facet	1.03±0.01	0.87-1.30	7.88	1.02±0.01	0.87-1.63	10.43	1.06±0.03	0.90-1.27	10.28	1.13±0.03	1.03-1.33	8.24
Total length	120.13±0.97	104-132	5.59	118.37±0.74	104-132	4.96	135.36±1.60	127-149	4.43	132.00±1.81	119-140	4.94
Tail length	53.00±0.49	47-63	6.43	51.84±0.41	44-60	6.31	61.00±2.30	55-89	14.09	59.92±1.08	53-67	6.52
Length of hind foot	14.29±0.09	13-15	4.78	14.49±0.07	13-16	4.09	16.07±0.29	15-18	6.67	15.77±0.17	15-17	3.80

* Means of the variable for the two sexes within a taxon are significantly different ($P < 0.05$).

SW ¼ sec. 13, 1 (PSM 19799); T15S, R5E, sec. 14, 3 (USNM 556592, 556686, 556690); 4,300 ft., T15S, R6E, NE¼sec. 7, 1 (PSM 19705); 5000 ft., T15S, R6E, NW ¼ sec. 7, 1 (PSM 19827).

Sorex vagrans Baird
Vagrant Shrew

1858. Sorex vagrans Baird, Mammals, in Explorations and surveys for a railroad route from the Mississippi River to the Pacific Ocean. Mammals, 8(1):15, July.

1858. Sorex suckleyi Baird, Mammals, in Explorations and surveys for a railroad route from the Mississippi River to the Pacific Ocean. Mammals, 8(1):18, July. Holotype from Steilacoom, Pierce Co., Washington. Holotype not examined.

1891. Sorex dobsoni Merriam, N. Amer. Fauna, 5:33, July. Holotype from Alturas or Sawtooth Lake, about 7200 ft., E base Sawtooth mountains, Blaine Co., Idaho. Holotype not examined.

1895. Sorex amoenus Merriam, N. Amer. Fauna, 10:69, December. Holotype from near Mammoth, 8800 ft., head Owens River, E slope Sierra Nevada, Mono Co., California. Holotype not examined.

1895. Sorex nevadensi Merriam, N. Amer. Fauna, 10:71, December. Holotype from Peese River, 6000 ft., Nye-Lander County line, Nevada. Holotype not examined.

1899. Sorex shastensis Merriam, N. Amer. Fauna, 16:87, October. Holotype from Wagon Camp, Mt. Shasta, 5700 ft., Siskiyou Co., California. Holotype not examined.

1922. Sorex trigonirostris Jackson, J. Washington Acad. Sci., 12:264, June. Holotype from Ashland, 1975 ft., Jackson County, Oregon; obtained on 5 May 1914 by L. J. Goldman. Holotype examined and measured.

1936. Sorex ornatus trigonirostris, Bailey, N. Amer. Fauna, 55:366, June.

Holotype.—Adult male, in alcohol; USNM 1675; ''Shoalwater Bay, W. T.'' (= Willapa Bay, Pacific Co., Washington); obtained by J. G. Cooper. Holotype examined, but not measured.

Distribution.—Vagrant shrews occur throughout Washington, except in the southeastern scablands, west of the Cascade Mountains to the Pacific Coast in Oregon, and southward along the Pacific Coast to Abalone Point, Marin County, California (Fig. 28); they also are found beyond the limits of the study area to the north and east.

Description.—This taxon is composed of all individuals classified as morphotypes 3-8 (Fig. 4). It (Fig. 29, Table 6) is larger than *S. m. obscurus* (Fig. 24, Table 4), but smaller than all other taxa under consideration. The dorsal and ventral pelages of 14 specimens collected in March, May, June, July, August, October, and December, are light medium-brown (7.5YR 5/2—Munsell Color, 1975) and white (Ridgeway, 1912; no comparable Munsell color), respectively. The pelage on the sides is light pinkish-gray (7.5YR 7/2). Bases of hairs on the dorsum, venter, and sides are neutral very dark-gray (7.5YR N3/0). Adults have an indistinctly bicolored tail, light medium-brown above and white below; juveniles have a sharply bicolored tail, dark brown (7.5YR 3/2) above and white below. Flank glands on nine adult males collected in March, June, July, August, and December are covered with dark pinkish-gray (7.5YR 6/2) bristles. No more than four pairs of friction
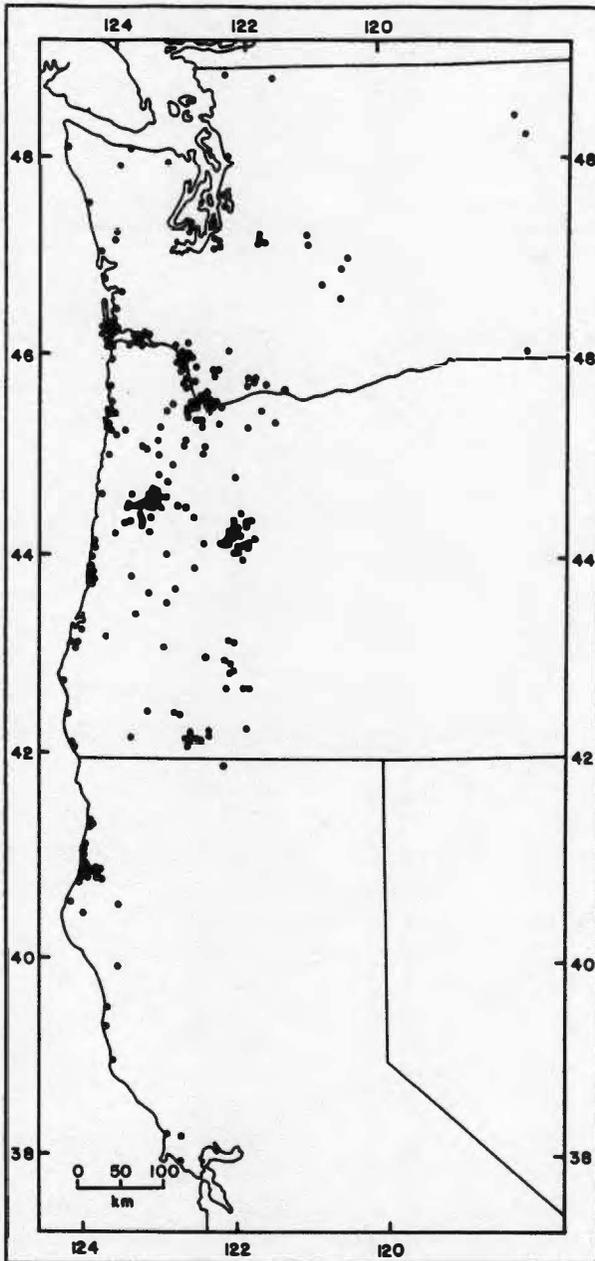
FIG. 28.–Localities in Washington, Oregon, and northern California at which museum specimens of *Sorex vagrans* (closed circles, 313 localities, 270 localities plotted, n = 931) used in this research were collected.
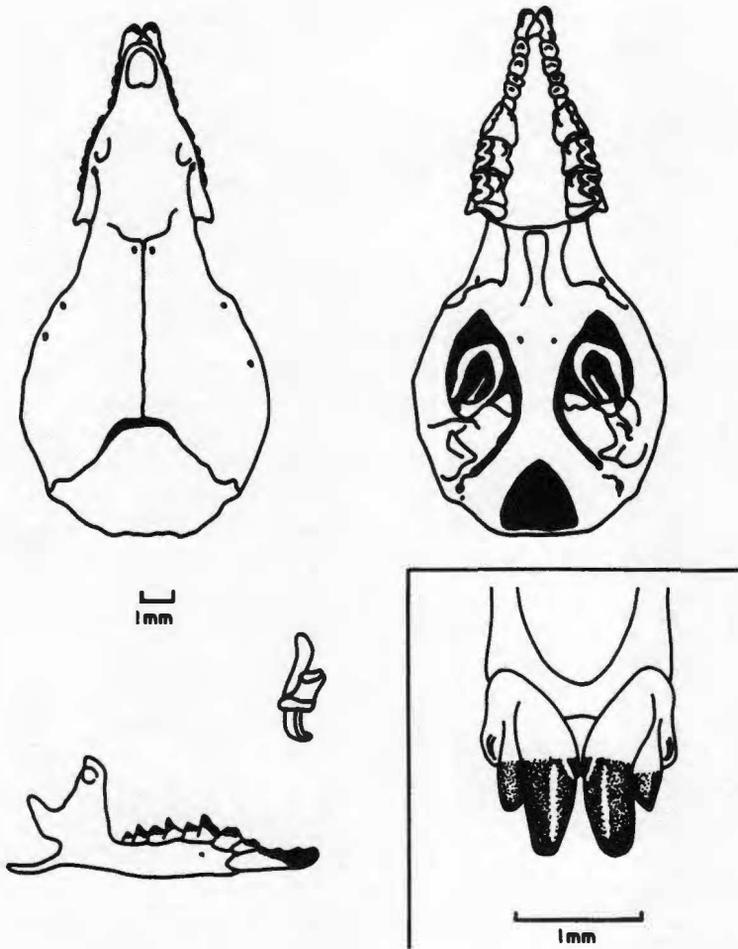
Fig. 29.—Camera-lucida tracings of dorsal and ventral views of skull, lateral and posterior views of mandible, and anterior view of I1 of an adult male *Sorex vagrans* (OSUFW 3033) from Albany, Linn Co., Oregon.

pads occur on the second to fourth toes of the hind feet; *S. monticolus* has more than four pairs (van Zyll de Jong, 1982).

The body of the first upper incisors is straight and only slightly divergent (Carraway, 1987: fig. 1; Fig. 29). Cranially, *Sorex vagrans* can be distinguished from all other taxa conidered herein by the presence on the anteriomedial edge of the first upper incisors of a small tine with pigment that does not occur above the dorsal level of the tine (Fig. 29); commonly there is a white or pale-colored area between the tine and the body of the

tooth. The foramen on the zygomatic plate (Fig. 5) in 95.6 percent of individuals examined is either immediately posterior to, or directly in line with, the metacone of M1.

Measurements.—Only eight of 20 variables were significantly different between the sexes (Table 6).

Remarks.—Individuals classified in morphotypes 3-8 form a distinct morphologic (Fig. 29) and morphometric (Fig. 6) unit characterized by the presence of a tine on the medial edge of the first upper incisors with pigment not extending above the dorsal level of the tine.

Morphotypes 3-8 illustrate the plasticity of the median tine and pigment characters on the first upper incisors (Fig. 4) within *S. vagrans*. Morphometric analyses (Fig. 6) gave no indication of distinct subunits within the 931 specimens measured as illustrated by the complete overlap of the 95 percent confidence ellipses about the group centroids within the canonical-variates plot of the six morphotypes. Analyses by minimum-spanning tree and coefficients of correlation to the first and second canonical-variate axes supported the determination of only one discrete unit among the six morphotypes. Also, each of these morphotypes is distributed geographically throughout Washington, Oregon, and California in no discernable pattern.

In canonical space, specimens formerly referred to as *S. trigonirostris*, from southwestern Oregon, are spread thoughout most of the canonical distribution of *S. vagrans* with no evidence of clumping. Thus, the subsuming of *S. trigonirostris* into *S. vagrans*, first proposed by Hennings and Hoffmann (1977), is affirmed.

Specimens examined.—CALIFORNIA (81).—*Humboldt Co.*: Arcata, 8 (HSU 122, 204, 596, 597, 753, 1664, 1782, MVZ 11828); *Arcata, Jacoby Creek*, 1 (HSU 60); Arcata, Fickle Hill, 1 (HSU 1109); 1 mi. W Arcata, 1 (HSU 594); *2 mi. W Arcata*, 2 (HSU 592, 595); *east Arcata*, 1 (HSU 745); 3 mi. E Arcata, 1 (HSU 902); 20 mi. E Arcata, 1 (HSU 143); Bayside, 1 (HSU 770); Big Lagoon, 6 (MVZ 113010-113013, 113015, 113016); Blue Lake, 1 (HSU 3845); Bucksport, 1 (HSU 589); Clam Beach, 1 (HSU 993); 7 mi. N Dinsmore, 1 (HSU 3847); Eureka, 1 (HSU 198); Ferndale, 2 (MVZ 11830, 11832); Gold Bluff Beach, Prairie Creek, 1 (HSU 329); Gunther Island, Humboldt Bay, 1 (HSU 46); 1 mi. SE Korbel, 1 (HSU 2050); Lanphere Dunes, 2 (HSU 3785, 3845); 1 mi. N jct. Mad River at Maple Creek, 1 (MVZ 99510); McKinleyville, 3 (HSU 587, 1152, 1423); *McKinleyville Airport*, 7 (HSU 749, 750, 757-759, 761, 813); 4 mi. N Orick, 50 ft., 1 (MVZ 106419); across Eel R. from Scotia, 2 (MVZ 90385, 90386); just above S [southern] Prairie Creek [Redwoods] State Park [T12N, R1E, SEC. 30/31], 2 (UCD 4703, 4704); Trinidad, 1 (HSU 1299); 3 mi. N Trinidad, 300 ft., 2 (MVZ 97405, 97407). *Marin Co.*: 3 mi. NW Bolinas, Abalone Point, Arroyo Honda, 3 (MVZ 134591-134593); W end Elk Valley, 10 ft., 5 (MVZ 101232-101234, 101287, 101289); White Gulch, Tomales Point, 5 ft., 2 (MVZ 101282, 101283). *Mendocino Co.*: 3.5 mi. N Ft. Bragg, Mill Creek, 4 (MVZ 101801-101803, 101805); Point Arena, 4 (MVZ 107728-107731); Russian Gulch State Park, 40 ft., 6 (MVZ 95625, 95626, 95628-95630, UCD 1751); Russian Gulch State Park, 200 ft., 1 (MVZ 95631); 11.5 mi. N Hwy. 101, Golden Ram sportsman club [along road from Cummings], 1 (HSU 3843). *Siskiyou Co.*: Tule Lake sump, 1 (OSUFW 906).

OREGON (625).—*Benton Co.*: Alsea, 1 (PSM 5808); 9 mi. E Alsea, 1 (MSB 40786); 4 mi. S Blodgett, 1 (OSUFW 7091); Corvallis, 12 (KU 63198, MVZ 101055, OSUFW 1307, 1308, 2862, 3504, 4741, 4744, 4769, 4794, 4827, PSM 15700); *north edge of Corvallis*, 1 (OSUFW 1312); *0.25 mi. N Corvallis*, 1 (OSUFW 3030); *1 mi. N Corvallis*, 1 (OSUFW 4757); 2 mi. N Corvallis, 250 ft., 3

TABLE 6.—*Mean (± SE), range, and CV of measurements (in mm.) of skull and skin characters for female and male Sorex vagrans in Washington, western Oregon, and Western California.*

Character	Females (n = 401)			Males (n = 357)		
	x̄ ± SE	Range	CV	x̄ ± SE	Range	CV
Greatest length of skull	16.35 ± 0.02*	14.93-19.50	2.89	16.46 ± 0.03*	15.46-19.34	2.87
Cranial breadth	8.08 ± 0.01*	7.36-9.69	3.18	8.16 ± 0.01*	7.55-9.41	3.16
Maxillary breadth	4.64 ± 0.01*	3.97-5.99	4.71	4.68 ± 0.01*	4.15-5.81	4.64
Least interorbital breadth	3.12 ± 0.01	2.67-3.91	4.82	3.14 ± 0.01	2.81-4.12	5.17
Cranial depth	4.76 ± 0.01	3.91-5.94	6.58	4.80 ± 0.01	4.15-5.53	5.36
Breadth at M2-M2	4.19 ± 0.01	3.57-5.28	4.52	4.20 ± 0.01	3.77-5.29	4.49
Length of unicuspid toothrow	2.27 ± 0.00	2.03-3.00	4.14	2.28 ± 0.01	2.00-2.87	4.40
Length of complex toothrow	4.01 ± 0.01	3.53-4.76	4.04	4.03 ± 0.01	3.55-4.91	4.05
Width across I1-I1	1.37 ± 0.00*	0.97-1.93	5.78	1.40 ± 0.00*	1.23-1.90	5.55
Breadth of zygomatic plate	1.05 ± 0.01*	0.73-1.40	11.04	1.07 ± 0.01*	0.70-1.53	11.93
Length of mandibular toothrow	4.58 ± 0.01	3.49-5.79	4.29	4.59 ± 0.01	4.11-5.67	3.95
Length of mandible	7.03 ± 0.01*	6.29-8.81	3.64	7.08 ± 0.01*	6.43-8.43	3.82
Height of coronoid process	3.64 ± 0.01	3.03-4.97	4.55	3.66 ± 0.01	3.22-5.13	5.06
Coronoid process-condylar length	2.65 ± 0.01	2.07-3.45	6.35	2.67 ± 0.01	2.28-3.45	6.62
Greatest condylar depth	2.02 ± 0.01*	1.63-2.50	5.36	2.05 ± 0.01*	1.80-2.47	5.34
Width of lower condylar facet	1.17 ± 0.00	0.97-2.10	7.70	1.18 ± 0.00	1.00-1.47	6.14
Width of upper condylar facet	0.83 ± 0.00	0.63-1.07	8.43	0.84 ± 0.00	0.70-1.10	8.64
Total length	98.64 ± 0.38	80-130	7.70	99.69 ± 0.38	83-128	7.26
Tail length	39.68 ± 0.20*	23-55	10.05	40.52 ± 0.21*	25-58	9.83
Length of hind foot	12.15 ± 0.05	10-18	7.75	12.23 ± 0.05	10-18	7.78

* Means of the variable for the two sexes are significantly different (P < 0.05).

(OSUFW 1299, PSM 11938, 12009); 7 mi. N Corvallis, 800 ft., 2 (PSM 12848, 12849); 1 mi. N, 2 mi. W Corvallis, 1 (OSUFW 1652); *1 mi. N, 3 mi. W Corvallis*, 2 (OSUFW 4221, 4225); *2 mi. N, 1 mi. W Corvallis*, 2 (OSUFW 4222, 4223); 2 mi. N, 4 mi. W Corvallis, 3 (OSUFW 2914, 7380, 7393); 2.5 mi. N, 1.5 mi. W Corvallis, 1 (OSUFW 1311); *3 mi. NW Corvallis*, 1 (OSUFW 4793); *1 mi. W Corvallis*, 4 (OSUFW 4770, 4772, 4775, 4792); *1.25 mi. W Corvallis*, 1 (OSUFW 4773); *2 mi. W Corvallis*, 4 (OSUFW 1600, 1601, 3023, 4795); 3 mi. W Corvallis, 1 (OSUFW 3048); 5 mi. N, 5 mi. E Corvallis, 200 ft., 3 (CM 65052-65054); 4 mi. NE Corvallis, 1 (OSUFW 4759); 2 mi. S Corvallis, 7 (PSM 12840-12846); *3 mi. S Corvallis*, 1 (PSM 10327); *Corvallis Airport*, 1 (OSUFW 1314); 4.5 mi. SW Corvallis, 1 (OSUFW 4779); 10 mi. S Corvallis, W. L. Finley National Wildlife Refuge [T13S, R5W, sec. 21/27/28], 35 (OSUFW 8360, 8374, 8376, 8387, 8391, 8392, 8396, 8502-8506, 8510-8513, 8515, 8516, 8541-8544, 8552, 8554, 8557, 8594, 8597-8599, 8602-8604, 8607, 8610, 8615); 12 mi. S Corvallis, 200 ft., 2 (PSM 12016, 12069); Lewisburg, 1 (OSUFW 4743); 0.5 mi. S, 3 mi. W Corvallis, 1 (OSUFW 1650); Greasy Creek on Beaver Creek Rd., 1 (OSUFW 4755); Missouri Bend [T14S, R8W, sec. 8], 1 (OSUFW 3171); 2 mi. S, 13 mi. W Philomath, 1 (OSUFW 3170); 1.5 mi. E Philomath, 1 (OSUFW 2196); 5 mi. SW Philomath, 4 (USNM 231654, 231660, 231661, 231663); 0.5 mi. S, 3 mi. E Wren, 2 (OSUFW 4437, 4439); T10S, R4W, SE¼ sec. 30, 1 (PSM 12851); T11S, R5W, sec. 20, 1 (OSUFW 4781); 650 ft., T11S, R7W, SW¼ sec. 8, 1 (PSM 22617); 200 ft., T12S, R5W, SE¼sec. 3, 2 (PSM 12870, 12872); T12S, R7W, sec. 10, 16 (USNM 561615, 561618-561632); T12S, R7W, NW¼sec. 21, 2 (OSUFW 4791, 4805). *Clackamas Co.*: Camp Millard [T2S, R4E, sec. 31], 1 (KU 10140); Jennings Lodge, 2 (MVZ 71214, SDNHM 17020); 8 mi. SE Mollala, 4 (PSM 6236-6239); Oak Grove, 1 (PSM 1914); Oregon City, 1 (USNM 56900); Oswego, 1 (PSM 8069); Lake Oswego, 1 (OSUFW 2152); Wilhoit Springs, 1 (PSM 6235). *Clatsop*

Co.: Old Ft. Clatsop, 100 ft., 18 (MVZ 94086, 94088-94091, 94094-94100, 94102, 94104-94107, 94109, 94110); Seaside, 1 (PSM 8633); Welsh Island, T9N, R6W, N½ sec. 19, 2 (PSM 26675, 26676); T8N, R8W, sec. 16/20, 1 (PSM 26678); T8N, R10W, NW¼ sec. 6, 2 (PSM 26663, 26667); T8N, R11W, E½ sec. 35, 1 (PSM 26674). *Columbia Co.*: 2 mi. W Deer Island, 250 ft. [T5N, R2W, sec. 12], 2 (PSU 334, 338); 0.5 mi. E Deer Island, 300 ft. [T5N, R1W, sec. 8], 1 (PSU 327); 7 mi. SE Rainier, 100 ft., 12 (MVZ 95879, 95880, 95882, 95884-95886, 95888-95892, 95894); Reed Island, T6N, R1W, NW¼ sec. 18, 2 (PSM 26639, 26640); T4N, R1W, W½ sec. 22, 1 (PSM 26653); T4N, R1W, N½ sec. 34, 3 (PSM 26654, 26655, 26658); *T4N, R1W, NE ¼ sec. 34*, 2 (PSM 26646, 26649); T6N, R1W, SW¼ sec. 7, 5 (PSM 26635, 26636, 26641, 26643, 26644); T6N, R2W, E½ sec. 13, 1 (PSM 26659); *T6N, R2W, E ½ sec. 13*, 3 (PSM 26622, 26631, 26632); *T6N, R2W,. NW ¼ sec. 12*, 1 (PSM 26620); T7N, R2W, SE¼ sec. 26, 2 (PSM 26628, 26633). *Coos Co.*: 1.75 mi. E Bandon, 5 (PSM 13702-13704, 14549, 15748); 2 mi. SE Bandon, 1 (PSM 11939); T27S, R10W, sec. 17/20, 1 (USNM 561641); Delmar, 9 mi. S Marshfield [= Coos Bay], 3 (MVZ 63463, 63464, 63472); Marshfield [= Coos Bay], 1 (FMNH 9614); 1 mi. N Two Mile, 1 (PSM 15747). *Curry Co.*: Brookings, 1 (PSM 4075); Gold Beach, 7 (FMNH 9669-9671, PSM 5895, 5896, USNM 68161, 166972); 0.25 mi. N Harris Beach St. Park [T40S, R14W, sec. 35], 1 (SOSC 989); Port Orford, 1 (SDNHM 17008). *Douglas Co.*: Diamond Lake [T27S, R6E, sec. 32], 2 (PSM 8634, SDNHM 17012); north end Diamond Lake near outlet [T27S, R51/2E, sec. 31], 3 (OSUFW 1550, 1552, 1554); Drain, 1 (USNM 69809), 4 km. W Drain, 1 (USNM 560094); Gardiner, 2 (MVZ 81059, 81061); 6 mi. N Gardiner, 1 (MVZ 120440); 1.3 mi. E Gardiner, 5 (MVZ 120435-120439); Louis Creek, T28S, R3W, SE¼SE¼ sec. 30, 1 (SOSC 1690); Oxbow Burn, 300 ft., T20S, R7W, sec. 19, 2 (PSM 11950, 15745); T25S, R7W, sec. 1, 1 (USNM 561640); T29S, R3E, NE¼SE¼ sec. 33, 1 (SOSC 1682); T29S, R3E, SE¼NE¼ sec. 35, 1 (SOSC 1681). *Hood River Co.*: 9 mi. ENE Mt. Hood, Brooks Meadow, 4300 ft. [T2S, R10E, sec. 11], 4 (MVZ 87004, 87005, 87009, 87012); 2 mi. W Parkdale, 1500 ft., 1 (USNM 231671). *Jackson Co.*: Ashland, 5 (SOSC 566, 1193, 1718, 1873, USNM 203608—holotype of *Sorex trigonirostris* Jackson, 1922); near Ashland, 1 (SOSC 1882); 4.5 mi. N, 12.8 mi. E Ashland, 1 (SOSC 1423); *5 mi. N, 13 mi. E Ashland*, 1 (SOSC 107); 1 mi. E Ashland, 1 (PSM 22611); 2 mi. E Ashland, 9 (PSM 22612-22614, 22616, 24142-24146); Lower Ashland Natural Research Area, T39S, R1E, SW¼ sec. 28, 1 (SOSC CK17); Ashland, Senic Hills Memorial Park [T39S, R1E, sec. 11], 4 (SOSC 565, 632-634); *Senic Hills cemetery*, 1 (SOSC 886); Bear Creek at junction with Mt. Ave., Ashland, 1 (SOSC 1886); Denman Game Management Area [T36S, R1W, sec. 30], 2 (SOSC 1420, 1422); Emmigrant Lake, Neil Creek Rd. [T39S, R2E, SW¼], 1 (SOSC 792); Adjacent to Howard Prairie Dam Rd. on Hyatt Lake Rd. [T39S, R3E, sec. 2], 1 (SOSC 1107); Medford, 1 (SOSC 751); T36S, R2W, NW¼ sec. 14, 1 (SOSC 662); T39S, R7W, SW¼ sec. 18, 2 (SOSC 749, 750). *Klamath Co.*: Sphagnum Bog, Crater Lake National Park [T30S, R5E, sec. 4/5], 13 (SOSC RAM35, RAM42, RAM43, RAM57, RAM60, RAM64, RAM65, RAM67, RAM68, RAM78, RAM79, RAM119, RAM120); *Panhandle Crater Lake National Park*, 1 (SOSC RAM81); Crater Lake headquarters [T31S, R6E], 1 (OSUFW 195); 2 mi. S Park headquarters, Crater Lake National Park [T31S, R6E, sec. 20], 9 (SOSC RAM82-RAM84, RAM94, RAM95, RAM97, RAM98, RAM100, RAM103); Crater Lake National Park, Munson Creek, 2 (SOSC RAM105, RAM112); Ft. Klamath, 5 (OSUFW 1036, 1053, 1054, 1061, 1063); 8 mi. NW Klamath, 1 (OSUFW 54); Seven Lakes Basin, North Lake [T33S, R05E], 2 (SOSC 1110, 1111). *Lane Co.*: 5 mi. N Alpha, 1 (OSUFW 4601); 5 mi. N, 6 mi. W Alpha, 3 (OSUFW 6883, 6884, 6898); ½ mi. S, 5 mi. E Cottage Grove, 1 (OSUFW 7534); 15 mi. S Cottage Grove, 2 (PSM 15749, 15750); Cushman, north bank Siuslaw River, 2 (CM 74233, 74236); Eugene, 3 (OSUFW 1046, USNM 204438, 204468); 9 mi. N, 1 mi. W Gardiner, 4 (PSM 14551, 14552, 15752, 15753); Heceta, 1 (OSUFW 2636); *Heceta, Cape Creek* [T16S, R12W, sec. 22], 1 (OSUFW 2637); 10 mi. W Junction City, 400 ft., 2 (PSM 12071, 12072); *10 mi. W Junction City, 450 ft.*, 1 (PSM 12871); 1 mi. S, 4 mi. E Lowell, 2 (OSUFW 8538, 8551); McKenzie Bridge, 3 (OSUFW 1044, 6060, USNM 204442); 2.6 km. S McKenzie Bridge, 1 (USNM 557958); 10 mi. SE McKenzie Bridge, 2 (USNM 204443, 204444); Mercer [= Florence], Dowell Ranch [T17S, R12W, sec. 25], 1 (SDNHM 17005); *Mercer* [= Florence], *Grass Mt. Refuge*, 1 (OSUFW 4768); north base Three Sisters, 5000 ft., 1 (USNM 204469); *north slope Three Sisters Mts., 7000 ft.*, 2 (SDNHM 17017, 17018); Upper Horse Lake meadow [T18S, R7½ E, sec. 22], 1 (OSUFW 4758); Vida, 1 (USNM 204439); T15S, R5E, sec. 25, 2 (USNM

557366, 557952); 1400 ft., T15S, R6E, sec. 26, 1 (USNM 557368); T16S, R4E, NE¼, sec. 24, 1 (PSM 19656); T16S, R5E, sec. 3, 1 (USNM 557369); T16S, R5E, sec. 20, 2 (USNM 557955, 557956); T16S, R5E, sec. 25, 1 (USNM 557957); *T16S, R5E, sec. 26*, 2 (USNM 557378, 557379); T16S, R6E, sec. 35, 2 (USNM 557380, 557960); T16S, R7E, sec. 32, 8 (USNM 557382, 557383, 557386, 557389, 557961-557964); *T16S, R7E, sec. 33*, 36 (USNM 557392-557395, 557397-557399, 557401, 557404-557406, 557408, 557409, 557411-557413, 557416-557420, 557422, 557428-557430, 557965, 557967, 557968, 557971, 557973, 557975, 557976, 557978, 557979, 557981, 557982). *Lincoln Co.*: Cascade Head, 240 ft., 2 (PSM 13592, 13600); 5 mi. S Burnt Woods, 900 ft., 6 (PSM 12013-12015, 12084-12086); Newport, 4 (OSUFW 6049, 6056, SDNHM 16968, 16970). *Linn Co.*: 0.6 mi. S, 3 mi. E Corvallis, 1 (OSUFW 1310); 2 mi. S, 5 mi. E Corvallis, Peoria Rd., 1 (OSUFW 4830); Albany, 1 (OSUFW 3033); 5 mi. S, 7 mi. W Albany, 1 (OSUFW 4224); 0.5 mi. W Lebanon, 1 (OSUFW 3053); 1 mi. N, 28 mi. E Cascadia, 1 (CM 65055); Lost Prairie, Santiam Pass [T13S, R6E, sec. 27], 1 (OSUFW 4777); Big Lake, 4640 ft., T13S, R7½ E, SW¼ sec. 2, 1 (PSM 13345); Big Lake [T14S, R7½E, sec. 10/11], 1 (PSM 13346); *Big Lake, 4640 ft.* [T14S, R7½E, SW¼sec. 2], 1 (PSM 11944); 1½ mi. N Big Lake, 4800 ft., 7 (PSM 11941, 11943, 11946, 11949, 13327, 13328, 13347); 0.5 mi. N, 1.5 mi. W Sweet Home, 1 (OSUFW 5492); 1 mi. S, 2 mi. E Tangent, 1 (OSUFW 5102); 3.3 mi. N Waterloo, 1 (PSM 13348); 4400 ft., T14S, R6E, NE¼sec. 20, 9 (PSM 19622-19630); 4600 ft., T14S, R6E, NE¼sec. 28, 8 (PSM 19608, 19609, 19611, 19612, 19616-19619); 1020 m., T15S, R5E, sec. 1, 5 (USNM 556808, 557350-557352, 557945); T15S, R5E, sec. 14, 10 (USNM 557354, 557356-557359, 557361, 557362, 557949-557951); 5000 ft., T15S, R6E, NW¼sec. 7, 14 (PSM 19631-19634, 19637, 19638, 19641-19646, 19648, 19649). *Marion Co.*: 14 mi. N Detroit at Elk Lake, 1 (UCD 6002); Salem, 6 (MVZ 81053, SDNHM 17009, USNM 57112, 57116-57118); 1 mi. N, 1 mi. E Talbot, 2 (OSUFW 8548, 8550); Woodburn, 5 (PSM 8073-8077). *Multnomah Co.*: Government Island [T1N, R2/3E], 14 (PSU JJK766, JJK767, JJK770, JJK774, JJK785, JJK789, JJK790, JJK803, JJK805-JJK808, JJK819, JJK867); McGuire Island [T1N, R3E, sec. 18/19], 25 (PSU JJK768, JJK769, JJK772, JJK773, JJK777, JJK778, JJK780, JJK782-JJK784, JJK786-JJK788, JJK791, JJK793, JJK795, JJK797, JJK799, JJK801, JJK802, JJK809, JJK811, JJK813-JJK815); Oregon shore [T1N, R3E, sec.28], 7 (PSU JJK872, JJK874, JJK876-JJK880); Portland, 27 (AMNH 40193, MVZ 23645, 23647, 23648, 71198, 71204, 71205, 71213, 106565, OSUFW 1084, 4778, PSM 884, PSU 1594, SDNHM 16988, 16990, 16991, 16994, 16998, 17001-17003, SOSC 1541, USNM 142682, 142683, 161489, 204465, 205267); *1 mi. SE St. John's Bridge* [T1N, R1W, sec. 12], 1 (PSU 2096); T1N, R4E, NW¼sec. 20, 1 (PSM 26685); T3N, R1W, NW¼ sec. 26, 1 (PSM 26681). *Polk Co.*: McCoy, 1 (FMNH 9688); Independence, 1 (MVZ 143652). *Tillamook Co.*: Bayocean, 1 (SDNHM 17010); Blaine, 1 (MVZ 81052); Hebo Lake, 1 (PSM 8119); *Hebo Lake, 5 mi. E Hebo*, 1 (UCD 4684); Netarts, 9 (MVZ 81051, SDNHM 16975, 16978-16981, 16983-16985); Nehalem, 2 (OSUFW 4825, 4828); *1 mi. W Nehalem*, 3 (OSUFW 4820, 4821, 4824); Tillamook, 13 (KU 52549, OSUFW 6057, 6062, PSM 8046-8050, 8052, 8054-8057). *Washington Co.*: Beaverton, 2 (PSU 400, 1576); Hillsboro, 2 (MVZ 63467, 63470); Forest Grove, 1 (PSU 1865); 18.5 mi. NW Portland, 1 (MVZ 94111); 1.25 mi. W Sylvan [in Multnomah County], 2 (UWBM 20135, 20136); Tigard, 1 (PSU 1580). *Yamhill Co.*: 2 mi. S, 1 mi. W McMinnville, 1 (OSUFW 8252); Sheridan, 2 (USNM 69781, 69782); *0.5 mi. E Sheridan*, 2 (OSUFW 8243, 8244); 1.5 mi. E Yamhill, 1 (OSUFW 1313).

WASHINGTON (225).—*Clallam Co.*: 3 mi. NNE Joyce, 1 (MVZ 126281); Ozette, 1 (PSM 1019); 4 mi. SSW Sequim, Dungeness hatchery, 10 (MVZ 120446, 120447, 120449, 120629, 120632, 120634-120638); Sol Duc Hot Springs [T29N, R9W, sec. 32], 1 (CMNH 4339). *Clark Co.*: 0.75 mi. N, 1½ mi. E Amboy, 1 (MVZ 94081); 1½ mi. N, 3¼ mi. E Amboy, 2 (MVZ 94083, 94084); *1.25 mi. NE Amboy*, 1 (MVZ 94075); 2¼ mi. NE Amboy, 1 (MVZ 94073); 1¼ mi. ENE Amboy, 3 (MVZ 94076, 94079, 94080); Camas Slough,[T1N, R3E, sec. 15/16], 8 (PSU JJK824, JJK825, JJK829, JJK832, JJK850, JJK851, JJK863, JJK868); *Washington side of Camas Slough [T1N, R3E, sec. 15/16]*, 1 (PSU JJK855); *Lady Island [T1N, R3E, sec. 14/15]*, 20 (PSU JJK820-JJK823, JJK831, JJK833, JJK836-JJK838, JJK840, JJK841, JJK843-JJK845, JJK848, JJK849, JJK856-JJK858, JJK864); Reed Island T1N, R4E, W½sec. 22, 1 (PSM 26686); Upper Sand Island [T1N, R3E, sec. 17], 12 (PSU JJK827, JJK828, JJK830, JJK839, JJK842, JJK846, JJK852-JJK854, JJK859, JJK861, JJK866); 1.5 mi. W Yacolt, 1 (MVZ 94085); *T1N, R3E, N ½ sec. 14*, 3 (PSM 26593, 26594, 26608);

T1N, R4E, SE¼ sec. 17, 2 (PSM 26592, 26607); *T1N, R4E, NE ¼ sec. 21*, 1 (PSM 26603); *T1N, R4E, S ½ sec. 21*, 2 (PSM 26602, 26687); *T1N, R4E, W ½ sec. 22*, 1 (PSM 26597); T4N, R1W, NW¼sec. 35, 2 (PSM 26596, 26599). *Columbia Co.*: 19.4 road mi. SE Dayton, 3 (CM 60962-60964). *Cowlitz Co.*: mouth Kalama River, 6 (MVZ 95871-95873, 95875-95877); *1.5 mi. NNW mouth Kalama River*, 1 (MVZ 95870); 3 mi. E mouth Kalama River, 1 (MVZ 95878); 6 mi. NE Kelso, 1 (MVZ 83354); Longview, 1 (PSM 805); 3 mi. NE Woodland, 1 (PSM 7646). *Grays Harbor Co.*: Iron Springs, 3 mi. S Copalis, 2 (PSM 1427, 1438); Twin Harbor State Park, 1 (PSM 1259). *Jefferson Co.*: Kalalock [= Kalaloch], 2 (PSM 2087, 2088). *King Co.*: Baldi, 1 (PSM 10653); 1.5 mi. N Burton, Vashon Island, 2 (PSM 21043, 21045); Cedar River watershed, 1 (UWBM 31861); Humphrey Flats [= Humphrey], 2 (PSM 10642, 10643); Lester, 2 (PSM 10647, 10648); Little Eagle Lake [T21N, R8E, sec. 14], 1 (PSM 10644); Lynn Lake [T20N, R8E, sec. 21/22], 1 (PSM 10637); Renton, 1 (PSM 25778); Seattle, 17 (MVZ 134684-134690, PSM 2061, UWBM 9679, 9746, 9750, 9910, 12220-12222, 13766, 19183). *Kittitas Co.*: 2 mi. E Cle Elum, 2 (MSB 8954, 8955); 4.5 mi. N, 6.5 mi. E Easton, 1 (KU 57220); 5.5 mi. NNW Ellensburg, 1 (MSB 27942); 2 mi. S, 0.5 mi. W Roslyn, Cle Elum River, 1 (MSB 43424). *Klickitat Co.*: T3N, R12E, SE¼ sec. 33, 1 (PSM 26591). *Mason Co.*: Allyn, 1 (MSB 27939); Detroit, 1 (PSM 974); Grapeview, 1 (PSM 968). *Pacific Co.*: 1 mi. N Bear River on Willipa Bay, 4 (MSB 8941, 8947, 8949, 8950); 4 mi. N Chinook, 1 (MVZ 88855); 2.5 mi. NW Chinook, 4 (MVZ 94051, 94052, 94054, 94055); 4 mi. W Chinook, 4 (MVZ 88856, 88859, 88862, 88864); 2.5 mi. SE Chinook, 14 (MVZ 94053, 94056-94059, 94061-94069); Long Beach, 5 (PSM 1445-1459, 1466, 1467); Ft. Canby State Park, 7 (PSM 26609, 26610, 26612, 26614, 26615, 26617, 26619); 1 mi. S Nemah on Willapa Bay, 1 (MSB 8940); 3.5 mi. E Seaview, 2 (MSB 8945, 13510); South Bend, 1 (MVZ 81050); Willapa Harbor SW, 1 (PSM 1442). *Pierce Co.*: Fife, 1 (PSM 5834); Parkland, 1 (PSM 19145); 1.5 mi. NW Spanaway, 1 (MVZ 126282); Tacoma, 1 (PSM 928); 3.6 mi. S, 2.4 mi. E Tacoma, Clear Creek, 2 (MSB 43472, 43476). *Skamania Co.*: 5 mi. N, 6.3 mi. W Carson, 1 (USNM 558171); 8.5 mi. N, 1.5 mi. W Carson, 1 (USNM 558208); 10 mi. N, 1.3 mi. W Carson, 1 (USNM 558233); 4 mi. E Wind River, 2 (PSM 6157, 6158); 4 mi. W Little Wh. Salmon River, 1 (PSM 6155). Snohomish Co.: 0.5 mi. N, 7 mi. W Marysville, 3 (KU 34879-34881). Stevens Co.: Chewelah, 1 (KU 63197); 5 mi. S Colville, 1 (KU 63195). Wahhiakum Co.: Hunting Island [T9N, R6W, SW¼sec. 29], 1 (PSM 26688); 4 mi. E Skamokawa, 1 (MVZ 71196). Whatcom Co.: Nooksack, 1 (UWBM 13767); NE side Mt. Shuksan, Nooksack Cirque, North Cascades National Park, 800 m., 9 (UWBM 30964, 30965, 30968, 30978, 30981, 30983, 30984, 30986, 30998); NE side Mt. Shaksan, Nooksack Cirque, North Cascade National Park, 960 m. [T39N, R9/10E], 6 (UWBM 30960-30962, 30967, 30969, 30997). Yakima Co.: Cleman Mt. burn [T15N, R16E], 1 (PSM 8945); 2 mi. SW Ellensburg, 1 (UWBM 31863); Selah, 13 (UWBM 9748, 9753, 9759-9761, 9764-9771).

KEY TO THE SPECIES OF THE "*SOREX VAGRANS* SPECIES COMPLEX"
IN THE PACIFIC COAST REGION

Species included in this key are as described in the preceeding species accounts. Characters listed parenthetically may be useful in comparisons with taxa not in direct line in the key.

1a. Body size large; (four pairs of friction pads on second to fourth digits of hind feet); no projection on medial edge of I1, U5 usually rectangular, body of I1s completely abutting for length of pigment or at least at dorsal aspect of pigment, usually a gap between U5 and P4; zygomatic process of maxillary rounded (Figs. 17 and 18) . . . . *Sorex sonomae*

1b. Body size small to medium; a projection present on medial edge of I1, U5 triangular, body of I1s not touching, P4 overlapping U5; zygomatic process of maxillary pointed 2

2a. Ridge present at posteriomedial edge of I1 (Figs. 26 and 27); (five pairs of friction pads on second to fourth digits of hind feet) . . *Sorex pacificus*

2b. Tine present at anteriomedial edge of I1 3

3a. Tail distinctly bicolored in young individuals, indistinctly colored in adults; never more than four pairs, of friction pads on the second to fourth digits of hind feet (van Zyll de Jong, 1982); level of pigmentation at or below level of median tine on I1 (Fig. 29) . . . . *Sorex vagrans*

3b. Tail indistinctly bicolored in young and adult individuals; five or six pairs, of friction pads on second to fourth digits of hind feet (for *S. monticolus* van Zyll de Jong, 1982); level of pigmentation above level of median tine on I1 4

4a. Pelage dark brown; median tine on I1 usually small (Figs. 20 and 21) . . . . *Sorex bairdii*

4b. Pelage gray brown; median tine on I1 usually large and robust (Figs. 22 and 24) . . . . *Sorex monticolus*

RELATIONSHIPS AMONG THE SPECIES

The "*Sorex vagrans* species complex" as first conceived by Jackson (1928) included an array of poorly defined species that were difficult to distinguish. Since that time, various workers (Bailey, 1936; Findley, 1955; Hennings and Hoffmann, 1977; Junge and Hoffmann, 1981) recognized that much of the visible variation within the complex was not reflected in the taxonomy. However, by use of the differences of the medial-edge morphology on the first upper incisors, I was able to establish four distinct morphotypes that comprised five species: *S. sonomae, S. bairdii, S. monticolus, S. pacificus*, and *S. vagrans*. Of the four morphotypes, three had been recognized previously: no tine on the medial edge of the first upper incisors; a tine with pigment not extending above the dorsal edge of the tine; and a tine with pigment extending well above the dorsal edge of tine on the medial edge of the first upper incisors. I identified a fourth morphotype characterized by the presence of a ridge at the posteriomedial edge of the first upper incisors. For all except *S. vagrans*, I found a relationship between latitude and size of the projection on the medial edge of the first upper incisors. The relationship likely is related to the substantial differences in temperature, precipitation, and associated environmental factors over the 1250 kilometers from northern Washington south to San Francisco Bay, California. *Sorex monticolus*, primarily in Washington, has a large tine (Figs. 19, 22, and 24), *S. bairdii*, from northwestern Oregon, has a small tine (Figs. 19, 20, and 21), *S. pacificus*, from west-central Oregon, has only a ridge (Figs. 25, 26, and 27), and *S. sonomae*, from southwestern Oregon and northwestern California, has no projection (Figs. 16, 17, and 18) on the medial edge of the first upper incisors. This recognition of four morphotypes and the relationship of three of them to latitude (and the associated changes in precipitation and temperature) allowed me to propose a biologically and geographically meaningful explanation for much of the visible variation that has remained unresolved for 90 years.

There are no records of fossil shrews from western Oregon. However, the climatic conditions and accompanying boreal floral assemblage present in western Oregon, so unfavorable to fossil deposition in the Pleistocene (Detling, 1968), resemble the conditions that now, in montane regions of my study area (Detling, 1968), support a diversity of shrews of the genus *Sorex*. Thus, it is reasonable to infer that *Sorex* occurred within the boreal floral assemblage present in western Oregon during and before the Pleistocene (Detling, 1968; Heusser, 1983).

I propose that before Pleistocene glaciation there was a soricine taxon present in Washington, western Oregon, and northwestern California (and perhaps northward and eastward beyond the limits of my study area) that underwent speciation resulting in one taxon that was adapted for living in grassy and more open habitats and another that was adapted

for living in montane-forest habitats. The hypothetical ancestor ceased to exist when speciation occurred because a "parental species ceases to exist at the same moment in time" that a speciation event takes place, consequently "a biological species is delimited in time by two [simultaneous] speciation events" (Willmann, 1986:356). The shrew living in grass and open habitats evolved into *S. vagrans*, whereas the montane-forest shrew evolved into *S. monticolus*, *S. bairdii*, *S. pacificus*, and *S. sonomae* as described herein (Hawes, 1977; Terry, 1981; van Zyll de Jong, 1978). Therefore, I consider the concept of a "*Sorex vagrans* species complex" a misnomer, because the immediate ancestor to the montane-forest taxa and *S. vagrans* had a common ancestor. Consequently, *S. vagrans* could not have been the ancestor to the montane-forest taxa.

Along the Pacific Coast, periods of increasing aridity (interglacials) occurred during which the distribution of the original montane shrew was segmented by north-south disjunctions. These disjunctions likely occurred at the Columbia River, at about 44°50′N latitude (where a sharp drop in elevation occurs in the Coast Range and Cascade Mountains, Oregon), and at about 43°N latitude (where a sharp drop in elevation occurs in the Coast Range, Oregon). The combination of increasing aridity, higher temperatures, and reduced suitable habitat (causing populations to be restricted to refugia at higher elevations) provided the allopatric distributions necessary for speciation. The southward reduction and ultimate loss of the median tine combined with the progressive enlargement of skull characters—height of coronoid process, length of toothrows, and width of cranium (Fig. 6), and accompanying increase in size in the temporalis muscle (van Zyll de Jong, 1980)—associated with greater masticatory ability among taxa from northern Washington south to San Francisco Bay, California, strongly suggest a dietary function for the median tine. Thus, differences in relative hardness of the food resources of shrews in a southward direction in relation to increasing aridity and higher temperatures probably was the selective force responsible for reduction or loss of tines in southern taxa. In addition, if *S. sonomae* was restricted to the Klamath Mountains of Oregon and California (an area at the periphery of the distribution of the montane taxon) during interglacial periods, the arid environment and hardness of associated food resources available to shrews may have provided a stronger selective force for no tine than the wetter, cooler environments of Washington, with its hardness of the associated food resources, provided for enlargement of the tine. Consequently, modifications in the morphology of the medial edge of the first upper incisors could have proceeded at a progressively faster rate in populations of the montane taxa at lower latitudes.

Sorex bairdii, *S. pacificus*, and *S. monticolus* (species with pigment occurring above the dorsal level of a projection on the medial edge of the first upper

incisors) morphometrically are more closely related to each other than to *S. sonomae* (a species with no projection) or to *S. vagrans* (a species hypothesized to be related only distantly to the former group of species—Fig. 15). This relationship (Fig. 15) is in complete concordance with that portion of the distance-Wagner tree based on allozymic analyses of the same taxa presented by George (1988:452, fig. 3). However, the *S. pacificus* of George (1988) may have included both *S. sonomae* and *S. pacificus*, or only *S. sonomae*, as described herein. In addition, there appears to be a sizeable taxonomic distance between *sonomae* and *bairdii*, *pacificus*, and *monticolus*. However, if modifications in morphology of the medial edge of the first upper incisors of *sonomae* proceeded at a faster rate than in the other montane taxa, it is possible that the greater taxonomic distance (Fig. 15) is merely a reflection of stronger selective forces applied to *sonomae* rather than *sonomae* having evolved before *bairdii*, *monticolus*, and *pacificus*. Thus, when the periods of aridity were followed by periods of wetter, cooler conditions (glacials) the montane-forest shrews would have expanded from their refugia into the coastal lowlands and interior valleys. *S. sonomae* eventually would have expanded northward along the Oregon coast, southward along the California coast, and eastward through the Siskiyou Mountains, thence northward in the Cascade Mountains. During the wet, cool periods, populations of *bairdii* (*S. b. bairdii* and *S. b. permiliensis*) and *pacificus* (*S. p. pacificus* and *S. p. cascadensis*) in the Coast Range and Cascade Mountains would have reconnected (*bairdii* along the Columbia River and *pacificus* through the area of Spencer Butte and Coberg Hills, Lane County, Oregon). During the present interglacial period, the interior valleys are drier and warmer than during the last glacial, which may account for the current east-west break in the distribution of *pacificus* (Fig. 25). I hypothesize that in areas where *sonomae*, *pacificus*, and *bairdii* are presently sympatric (Figs. 16, 19, and 25) their ecological separation may be related to differences in temperature and precipitation similar to that observed for *S. araneus* and *S. coronatus* in Europe (Handwerk, 1987).

Although there seems to be a correlation between annual precipitation levels and geographic distribution for *S. sonomae* in the Cascade Mountains and Coast Range, and for *S. bairdii* in the Cascade Mountains (both occur in areas with 150 to 200 centimeters of annual precipitation), this environmental factor does not provide much information to explain the distributions of *S. bairdii* in the Coast Range or that of *S. pacificus*. Perhaps if more precise information were available regarding rainfall (and other environmental factors), for localities at which specimens of the various taxa under consideration were collected, a clearer relationship between annual precipitation levels and geographic distribution might be evident. However, areas of Washington, western Oregon, and northwestern California that contain the montane taxa

described herein have extremely varied topography (even over short distances—Baldwin, 1981), and the floral assemblages and climate (Baker, 1944; Zobel *et al.*, 1976) that affect faunal distributions are equally variable. Thus, a detailed approach will be required to correlate ecological factors, as related to topography, with geographic distributions of the taxa described.

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Address of author: *Department of General Science, Weniger Hall 355 and Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331. Received 20 May 1989, accepted 1 July 1989.*