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DISCORDANT PATTERNS OF MORPHOLOGICAL VARIATION IN GENETICALLY DIVERGENT POPULATIONS OF ORNATE SHREWS (*SOREX ORNATUS*)

JESÚS E. MALDONADO,* FRITZ HERTEL, AND CARLES VILÀ

Department of Organismic Biology, Ecology, and Evolution, University of California, 621 Charles E. Young Drive South, Los Angeles, CA 90095-1606, USA (JEM, FH, CV)
Present address of JEM: Genetics Program, National Museum of Natural History, Washington, DC 20008, USA
Present address of FH: Department of Biology, California State University, Northridge, CA 91330-8303, USA
Present address of CV: Department of Evolutionary Biology, Uppsala University, S-752 36 Uppsala, Sweden

Although the ornate shrew (*Sorex ornatus*) is widely distributed throughout California and northern Baja California, genetic analyses have shown that it is phylogeographically structured into 3 genetically differentiated regions (southern, central, and northern) within its distribution. These genetic groups might have been separated for more than a million years. In the northern region, ornate shrews cannot be genetically differentiated from their sister taxon, the wandering shrew (*S. vagrans*). Therefore it has been suggested that northern ornate shrews might have been misclassified. However, by analyzing skull morphology we show that ornate and wandering shrews, as well as the closely related montane shrew (*S. monticolus*), are well differentiated. Shrews from the northern region have a morphology similar to ornate shrews and not to wandering or montane shrews. Within the ornate shrews, populations across the range differ in morphology. However, morphological differentiation is not concordant with the deep tripartite pattern of genetic differentiation. Our results imply that skull shape differences among populations could be the result of local adaptation, whereas the long history of isolation might have contributed little to morphological differences between species. In addition, these results suggest that wandering shrews might be derived from the postglacial northward expansion of an ancestral population of northern ornate shrews.

Key words: biogeography, cranium, genetic differentiation, morphometrics, subspecies, *Sorex vagrans*, skull

The range of the ornate shrew (*Sorex ornatus*) extends from central California south to northern Baja California (Mexico) with a relictual population in Sierra de la Laguna, at the tip of Baja California Sur (Fig. 1). Currently, 9 subspecies are recognized, and a number of populations presumably have existed in small, isolated areas for long periods of time, such as those in montane meadows in southern California, in small coastal salt marshes in northern Baja California, and on Santa Catalina Island. Other populations have existed in widespread habitats, such as the large coastal marshes of the Los Angeles Basin and San Joaquin Valley (Williams 1986). Recently, some of these habitats have been altered by development, resulting in extensive habitat fragmentation. Three subspecies included in the list of mammalian species of special concern in California, and the Buena Vista Lake shrew (*S. o. relictus)* recently have been listed as endangered (USFWS 2002) due to loss of habitat through urban development.

* *Correspondent: maldonadoj@nzp.si.edu*

The systematics of this group are poorly studied. Past subspecific descriptions of ornate shrews often were based on body size and pelage coloration of only 1 or 2 specimens (Owen and Hoffmann 1983). Ornate shrews show a great degree of variation in size and pelage coloration and some populations exhibit differing degrees of melanism (i.e., *S. o. sinuosus, S. o. salarius,* and *S. o. relictus*); however, size and pelage coloration have been shown to be ecophenotypically plastic characters in small mammals (Patton and Brylski 1987) and other species of shrews evince melanism in salt marsh environments. The taxa *S. o. juncensis, S. o. sinuosus, S. o. lagunae,* and *S. o. willetti* sometimes are considered species (cf. Hall 1981) but commonly are considered as subspecies of *S. ornatus* (Brown and Rudd 1981; Junge and Hoffmann 1981; Williams 1979). Near San Francisco Bay, California, a complex and poorly understood situation exists. It is thought that *S. o. californicus* occurs in the uplands surrounding the bay, whereas the marshlands are occupied by *S. o. sinuosus* and a subspecies of wandering shrew (*S. vagrans halicoetes*). Populations of *S. o. sinuosus* are nearly black in color; however populations of *S. v. halicoetes* are equally dark (Junge and Hoffmann 1981). Rudd (1955) described some salt marsh

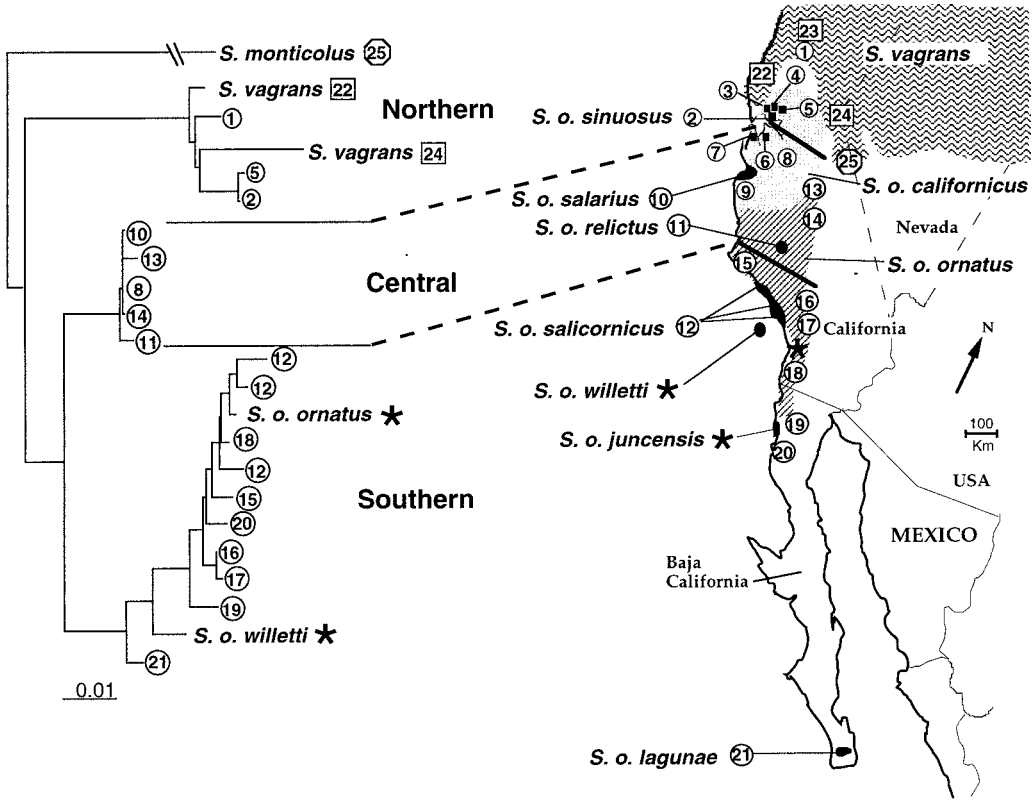

FIG. 1.—Map of southwestern United States and northwestern Mexico showing locations of populations sampled in this study (see Table 1 for details). Distribution of 9 subspecies of ornate shrew (*Sorex ornatus*) is indicated (adapted from Owen and Hoffman 1983). Thick lines indicate subdivisions based on genetic analyses (neighbor-joining tree based on average sequence divergence between populations, from Maldonado et al. 2001). Asterisks mark populations not sampled for morphometric study. Boxes indicate populations of wandering shrews and circles indicate populations of ornate shrews. The montane shrew population used as an outgroup is indicated with an octagon.

shrews from the northern shore of the San Francisco Bay as hybrids between *S. o. sinuosus* and wandering shrews (*S. vagrans*) on the basis of intergradation in color and external measurements.

The validity of the 9 named subspecies of ornate shrews has never been confirmed using univariate and multivariate statistical analyses of cranial measurements. However, in a recent molecular genetic analysis of this species using mtDNA and allozymes, Maldonado et al. (2001) found that the ornate shrew phylogeographically is separated into 3 clades representing southern, central, and northern localities (Fig. 1). Clades have a high genetic divergence (4.2–4.9% cytochrome *b* sequence divergence) that suggests a relatively long evolutionary independence from one another. Based on molecular data, populations in the northern clade diverged from the central and southern populations >1 million years ago and are genetically more similar to neighboring populations of wandering shrews. Results of the genetic study suggested that northern populations of the ornate shrew might be a unique lowland form of the wandering shrew that has converged independently on the morphology of southern and central California ornate shrews.

In this study, our aim was to determine whether a detailed morphological analysis, involving larger sample sizes than used in previous studies and encompassing the entire range of the species, shows a more congruent relationship between genetics and morphology than was suggested by traditional subspecies definitions. We also determined the degree to which the 9 subspecies of ornate shrews represent evolutionary units as espoused by systematists (Barrowclough 1982; Crandall et al. 2000; Moritz 1994). In addition, cranial morphometrics were used to examine patterns of morphologic variation among ornate shrew populations and their divergence with neighboring wandering and montane shrews (*S. monticolus*).

MATERIALS AND METHODS

Four hundred and fifty-five ornate shrew skulls from 21 populations, 37 representing 3 populations of wandering shrews, and 10 montane shrews from 1 population were examined (Table 1; Appendix I; Fig. 1). Specimens were from California, Nevada (near border with California), and Baja California, Mexico. Due to the confusing species affiliation of presumed ornate shrews in northern California, multiple populations were sampled around the San Francisco Bay area (Fig. 1). Additionally, 15 shrews from a population in Dye Creek, California (population 1; Table 1; Fig. 1) were included. Although it is outside the recognized species range, Maldonado et al. (2001) suggested this population corresponded to ornate shrews from northern California, based on external morphology. Finally, 15 specimens from Tolay Creek, California (population 4) corresponding to the presumed ornate-wandering shrew hybrids (Rudd 1955), were examined. Individuals were assigned to subspecies following the distribution suggested by Owen and Hoffmann (1983).

TABLE 1.—Sampling localities of samples used in the morphometric analyses for ornate (*Sorex ornatus*), wandering (*S. vagrans*), and montane shrews (*S. monticolus*) in California, Nevada, and Baja California, Mexico. Locality numbers correspond to numbers in Fig. 1. n = sample size. Column headed Molecular marker denotes localities examined with molecular markers by Maldonado et al. 2001.

Subspecies	Locality #	Locality	County	State	n	Molecular markers
Ornate shrews						
S. ornatus (unnamed)	1	Dye Creek Ranch	Tehema	California	15	M
S. o. sinuosus	2	Grizzly Island Wildlife Refuge	Solano	California	17	M
S. o. californicus	3	Petaluma	Sonoma	California	9	
S. o. californicus	4	Tolay Creek	Solano	California	18	
S. o. californicus	5	Rush Ranch	Solano	California	13	M
S. o. californicus	6	Berkeley and vicinity	Alameda	California	72	
S. o. californicus	7	Stanford	Santa Clara	California	13	
S. o. californicus	8	Los Banos	Merced	California	14	M
S. o. californicus	9	Monterey, Soledad	Monterey	California	15	
S. o. salarius	10	Mouth of the Salinas River	Monterey	California	23	M
S. o. relictus	11	Kern Lake Preserve	Kern	California	9	M
S. o. salicornicus	12	Point Mugu	Ventura	California	2	M
S. o. salicornicus	12	Rancho Palos Verdes	Los Angeles	California	25	M
S. o. salicornicus	12	Bolsa Chica–Newport	Orange	California	3	M
S. o. ornatus	13	El Portal	Mariposa	California	26	M
S. o. ornatus	14	Jose Basin	Fresno	California	58	M
S. o. ornatus	15	Santa Barbara	Santa Barbara	California	39	M
S. o. ornatus	16	San Bernardino Mountains	San Bernardino	California	21	M
S. o. ornatus	17	Santa Margarita Mountains	Riverside	California	8	
S. o. ornatus	18	San Diego	San Diego	California	19	M
S. o. ornatus	19	San Pedro Mountains		Baja California, Mexico	10	M
S. o. ornatus	20	Mouth of El Rosario River		Baja California, Mexico	17	M
S. o. lagunae	21	Sierra de la Laguna Mountains		Baja California, Mexico	9	M
Wandering shrews						
S. v. vagrans	22	Bodega Bay	Sonoma	California	19	M
S. v. vagrans	23	Shasta Mountain	Shasta	California	5	M
S. v. vagrans	24	Sweetwater Mountains	Mono	Nevada	13	M
Montane Shrews						
S. m. monticolus	25	Big Pine Creek, Sierra Nevada	Inyo	California	10	M

Seventeen cranial and mandibular measurements (Fig. 2) were recorded from each specimen using digital calipers and an ocular micrometer mounted on a Bausch & Lomb binocular microscope. Specimens were assigned to 1 of 3 age categories based on tooth wear (juvenile, subadult, or adult) and gender also was recorded. All measurements were recorded by 1 person (JEM) to ensure measurement consistency. The selection of morphometric characters was based on those that other investigators determined useful for distinguishing various taxa of shrews (Carraway 1990; George and Smith 1991; Kirkland 1977; van Zyll de Jong 1980), as well as characters that did not exhibit size dependence (Pimentel and Smith 1986). All measurements were recorded to the nearest 0.01 mm and were taken between identifiable landmarks to insure homology (sensu Strauss and Bookstein 1982).

Standard descriptive statistics (mean, range, *SD*, *SE*, and coefficient of variation) were calculated (Collins and George 1990). Skewness and kurtosis tests were performed to indicate whether any variables departed from normality. Because no significant differences were observed, and because size for different species and populations was similar, variables were used in multivariate analyses without transformation.

Multivariate analysis of variance (MANOVA) was used to study the effect of sex and age on morphological variability within populations, as well as divergence among subspecies or populations of ornate shrews. When these differences were significant, discriminant function analysis (DFA) was performed, as well as univariate *F*-tests, in order to characterize the variables responsible for divergence of groups. DFA was used to assess the effectiveness of the selected variables in predicting the different group memberships (Morrison 1967). This analysis calculates linear combinations of variables that maximize differences among groups determined a priori. Variables with the highest loadings contribute most in determining separation among groups. DFA also provides a classification of unknowns by determining the group having the highest assignment probability. For each of the samples included in the DFA, probability of classification to a group was estimated based on distance to the center of the distribution for each group in a multi-dimensional space resulting from the analysis. Samples of ornate shrews from northern California, including presumed ornate shrews from Dye Creek, and presumed hybrids from Tolay Creek, were excluded from the tests of species divergence, but later were classified using the classification probabilities.

The proportion of correct classifications obtained with DFA, compared to the proportion of correct classifications that would be expected if each individual were randomly assigned, was used to evaluate how well different groupings of individuals explained morphological variability of ornate shrews. The groupings tested corresponded to subspecies (Fig. 1), to regions suggested by genetic analyses (Maldonado et al. 2001; Fig. 1), and to sampled populations.

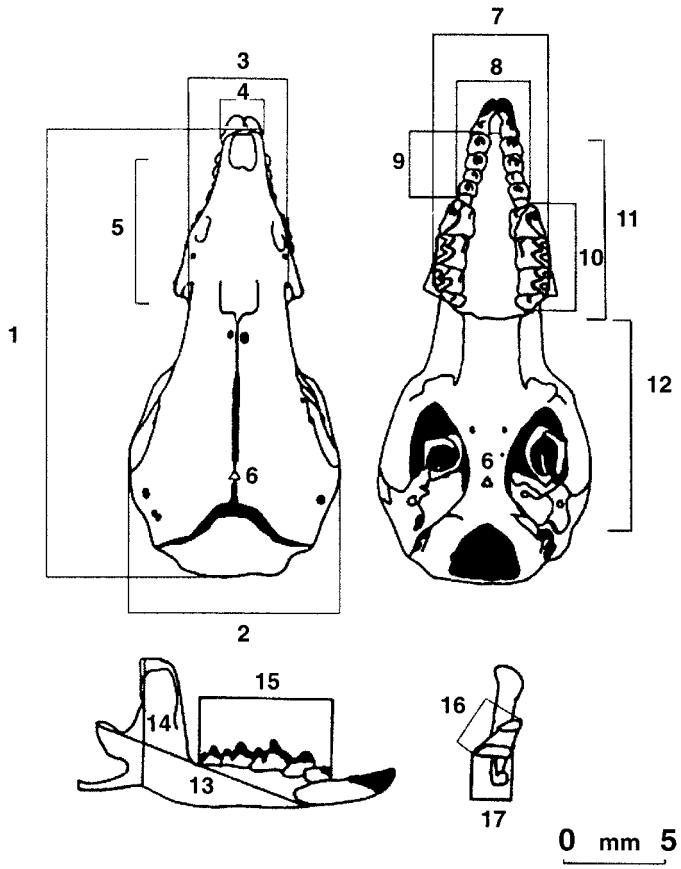

FIG. 2.—Diagrammatic views of skull and mandible of a *Sorex* illustrating skull dimensions measured (after Carraway 1990: figure 4): 1) greatest cranial length; 2) cranial breadth; 3) interorbital width; 4) width across incisors I1–I1; 5) length of nasals; 6) cranial depth; 7) width across molars; 8) width across unicuspids U4–U4; 9) length of unicuspid tooth row; 10) length of molariform tooth row; 11) palatal length; 12) post-palatal length; 13) length of the mandible; 14) height of coronoid process; 15) length of mandibular tooth row; 16) greatest condylar depth; and 17) width of condylar facet.

A neighbor-joining tree of all populations was built based on the between-group F-matrix from the DFA using PAUP* 4.0b software (Swofford 2002). Divergence by distance was assessed by plotting pairwise F values obtained in the DFA against geographical distance. The significance of the association was determined by applying Mantel's permutation test (Mantel 1967). A significant association between F and geographical distance indicates geographic structure, a pattern that would be consistent with historic patterns of migration between neighboring populations or clinal selection on environmentally related traits. All computations were done using SYSTAT (Wilkinson 1988).

RESULTS

Sources of intrapopulation variability.—In order to identify the effect of sex and age differences as sources of variability within populations, we performed a 2-way multivariate analysis of variance (MANOVA) for populations with the largest sample sizes. For samples from the Jose Basin area in Fresno County (population 14 in Fig. 1; $n = 58$) and the southwestern Bay area in Alameda County (population 6; $n = 41$), both the effect of age (adult, subadult) and sex, as well as their interaction, were not significant ($P > 0.05$). Consequently, we pooled all individuals from each locality independently of sex to study differences among populations. Seventeen juveniles were excluded from the analysis.

Divergence among ornate, wandering and montane shrews.—To assess divergence among ornate shrews and the partially sympatric wandering and montane shrews, a MANOVA was used with all morphological variables. Samples of ornate shrews from northern populations were excluded from this analysis. The analysis indicated that the 3 species are morphologically divergent (Wilks' Lambda = 0.351, $F = 12.824$, $d.f. = 34, 634$, $P < 0.001$). In univariate F-tests, most of the measurements that did not show significant differences among species are measurements of some aspect of skull length (Table 2), suggesting that skulls of the different species differ primarily in shape. A DFA was performed to identify variables responsible for the divergence among species. For the 1st discriminant function, variables with the highest loading factors (canonical discriminant functions standardized by within variances) were cranial depth (loading factor = 0.752), height of coronoid process (0.486), width across incisors (−0.416), and length of molariform tooth row (-0.401). For the 2nd function, the highest loading factors were interorbital width (0.655), length of mandibular tooth row (−0.569), and width across incisors (0.409). Hence the 1st discriminant function differentiated ornate from wandering shrews (Fig. 3), with the latter having relatively deeper crania and mandibles, narrower incisors, and a shorter molar toothrow. The 2nd function separated montane shrews from the others, as a result of a greater interorbital and incisor width and a shorter mandibular toothrow. These discriminant functions correctly classified 94% of the shrews (Table 3). Only 1 of each of the 47 wandering and montane shrews was misclassified as an ornate shrew.

The above discriminant functions were used to classify 3 sets of samples of controversial affiliation. The 1st group of controversial samples corresponded to presumed ornate shrews collected in northern California. However, 91% (95 of 104) of these samples were classified as ornate shrews (Table 3), a percentage similar to the correct classification for southern ornate shrews. The distribution of probabilities was biased toward high values as were the ornate shrews from southern and central California. These results confirmed that the cranial morphology of these shrews corresponded to the morphology of ornate shrews and not to that of wandering shrews.

The 2nd set of controversial samples was the shrews from Dye Creek (population 1) in northern California. Although this usually is considered to be outside the range of the ornate shrew, external morphology of those shrews suggests that they were *S. ornatus* (Maldonado et al. 2001). As with the other ornate shrews from northern California, these could not be distinguished genetically from neighboring wandering shrews. Only 40% (6 of 15) of the shrews from this locality were classified as ornate shrews (Table 3) and appear to have an intermediate morphology. Consequently, the cranial morphol-

TABLE 2.— Mean ± *SD* for 17 skull measurements for ornate, wandering, and montane shrews, and comparison of means with *F*-tests (asterisk indicates $P < 0.05$). Ornate shrews from northern California were not included (see text).

	Ornate ($n = 306$)		Wandering ($n = 37$)		Montane ($n = 10$)		
	$\bar{X}$	*SD*	$\bar{X}$	*SD*	$\bar{X}$	*SD*	*F*
Greatest cranial length	16.25	0.53	16.42	0.28	16.87	0.41	*
Cranial breadth	8.02	0.27	8.11	0.19	8.45	0.22	*
Cranial depth	4.10	0.26	4.61	0.26	4.73	0.41	*
Interorbital width	3.07	0.17	2.99	0.15	3.42	0.13	*
Length of nasals	5.22	0.28	5.30	0.15	5.40	0.25	*
Length of molariform tooth row	4.01	0.15	3.92	0.11	4.12	0.20	*
Length of unicuspid tooth row	2.14	0.13	2.05	0.16	2.18	0.09	*
Width across incisors	1.50	0.10	1.33	0.09	1.54	0.10	*
Width across unicuspids	2.19	0.15	2.09	0.09	2.25	0.13	*
Width across molars	4.44	0.15	4.36	0.15	4.50	0.16	*
Palatal length	6.55	0.27	6.44	0.17	6.61	0.10	
Post-palatal length	7.60	0.26	7.58	0.21	7.70	0.16	
Length of the mandible	8.28	0.29	8.32	0.23	8.49	0.10	
Length of mandibular tooth row	4.65	0.19	4.62	0.17	4.62	0.24	
Height of coronoid process	3.70	0.15	3.80	0.09	3.95	0.07	*
Greatest condylar depth	1.99	0.12	2.05	0.10	2.09	0.06	*
Width of condylar facet	1.20	0.09	1.24	0.08	1.22	0.04	

ogy of this population is sufficiently divergent that it was not considered with other ornate shrew populations.

Finally, the 3rd set of samples corresponds to animals from Tolay Creek, California (population 4). The intermediate morphology and variability of these animals were interpreted as corresponding to hybrid individuals between ornate and wandering shrews (Rudd 1955). The DFA supports this intermediate position and only 61% (11 of 18) of the animals were classified as ornate shrews (Table 3). This population also was excluded from analyses of variation in ornate shrews. The distribution of probabilities of classification as ornate shrews for the animals from Dye Creek and Tolay Creek showed that many have a morphology uncommon for either ornate or wandering shrews.

Morphological variability in ornate shrews.—To analyze the origin of variability in skulls of ornate shrews, we compared 3 partitions across the range of the species. These partitions were defined according to subspecies (7 groups; Fig. 1), genetic regions described by Maldonado et al. (2001) (3 groups; Fig. 1); and sampled populations (19 groups). All 3 partitions produced significant differences in MANOVAs: partitioned according to subspecies, Wilks' lambda = 0.190, $F = 5.879$, *d.f.* = 119, 245, $P < 0.001$; according to genetic regions, Wilks' lambda = 0.659, $F = 5.104$, *d.f.* = 34, 748, $P < 0.001$; or to populations, Wilks' lambda = 0.049, $F = 4.049$, *d.f.* = 306, 4489, $P < 0.001$. DFA resulted in similar proportions of correct classifications of the samples: 53% with the 1st partition, 55% with the 2nd, and 45% with the 3rd. However, these results do not imply that partitions are equivalent. In a random assignment of individuals from the 7 subspecies, a correct classification in 14% of the instances (1 of 7) was expected. The results obtained for this group (53%) were 3.8 times higher than expected from a random assignment. In the partition by genetic regions, results were only slightly higher than a random assignment (1.7 times). When samples were partitioned into 19 populations, the correct classification was 8.8 times more often than expected for a random assignment.

A neighbor-joining tree of all populations was obtained based on the between-groups *F*-matrix (*d.f.* = 17, 358) in the DFA corresponding to the last partition (populations; Fig. 4). However, this method does not allow for testing consistency of the tree topology. Populations from the 3 regions suggested from genetic studies did not form different clusters in the tree.

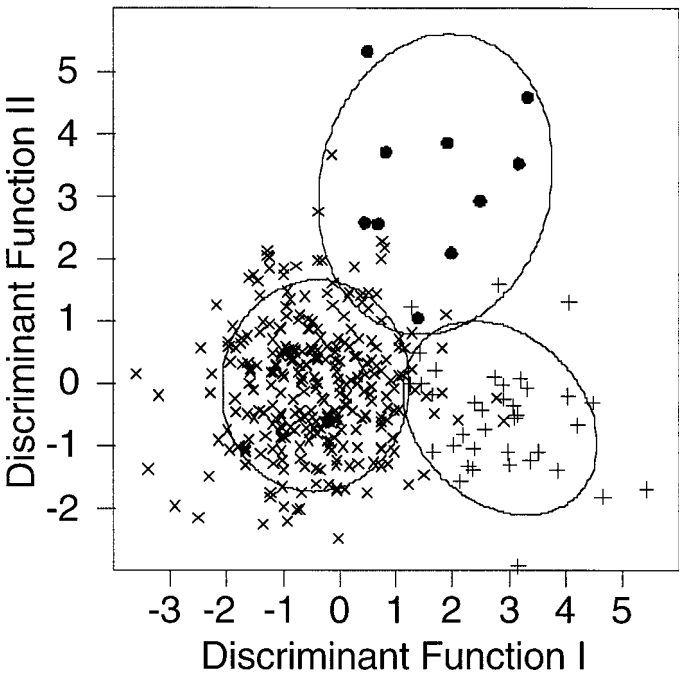

FIG. 3.—Discriminant function analysis of 17 cranial measurements for wandering (+), montane (•), and ornate shrews (×). Ornate shrews from northern California were not included. Ninety-five percent confidence ellipses for the samples are indicated.

TABLE 3.—Classification matrix resulting from the discriminant function analysis for montane, ornate, and wandering shrews and for 3 sets of samples of controversial affiliation.

	Montane	Ornate	Wandering	% Correct
Montane shrews	9	0	1	90
Ornate shrews	6	272	11	94
Wandering shrews	2	1	34	92
Total	17	273	46	94
Northern California	4	95	5	
Dye Creek (population 1)	0	6	9	
Tolay Creek (population 4)	2	11	5	
Total	6	112	19	

Similarly, populations pertaining to neighboring subspecies were not located in the same or neighboring branches. However, for the 2 widely distributed subspecies (*S. o. ornatus* and *S. o. californicus)*, populations corresponding to the same subspecies clustered in the same branches. Of the 5 populations corresponding to subspecies with limited distributions, 3 formed a cluster separated from representatives from the widely distributed subspecies and appear morphologically divergent (*S. o. lagunae, S. o. salarius,* and *S. o. relictus*). The other 2 populations clustered with the populations of the more widespread subspecies. However, *S. o. sinuosus* was divergent from the neighboring populations of *S. o. californicus* and was similar to *S. o. ornatus*, whereas the opposite is true for *S. o. salicornicus*. A DFA including 317 specimens identified as either *S. o. ornatus* or *S. o. californicus* correctly classfied 90% of the individuals.

For individual populations, some appear to have particularly long branches in the tree (Fig. 4), suggesting deep divergence from all other populations. These populations correspond to most of those for which the percentage of correct classifications was high. For instance, populations 10, 18, 19, and 21 had percentages ranging from 69 to 100% and were significantly divergent from all the others (MANOVA, F values; $P < 0.05$).

To assess whether degree of morphological variability was associated with degree of genetic variability in the different ornate shrew populations, the coefficient of variation for each of the 17 cranial measurements was examined for correlation with heterozygosity and percentage polymorphism values observed in allozymes in the genetic study (Maldonado et al. 2001). None of the 34 correlations were significant ($P > 0.05$ in all cases) for 17 cranial variables with the 2 genetic variables (heterozygosity and percentage polymorphic loci).

Finally, to ascertain whether morphological divergence among populations corresponded to geographic distance along a north-south cline in morphological characters, the pairwise F values were plotted against geographical distance. A Mantel's permutation test showed no significant association between these variables ($r = 0.145$, $P = 0.160$).

DISCUSSION

We found that 3 closely related species of California shrews (ornate, wandering, and montane) could be distinguished by morphological characteristics of their skull (in 90–94% of the instances). When ornate shrews from northern California were examined, we found that they were more similar in morphology to ornate shrews from central, southern California and Baja California, than to wandering shrews. This contrasts with the genetic results obtained by Maldonado et al. (2001), wherein ornate shrews from northern California were more closely related to wandering shrews. In that study, the authors suggested that ornate shrews from northern California could be wandering shrews that were misidentified as a result of a certain degree of convergence in morphological traits. Although some interspecific convergence of pelage coloration and functionally

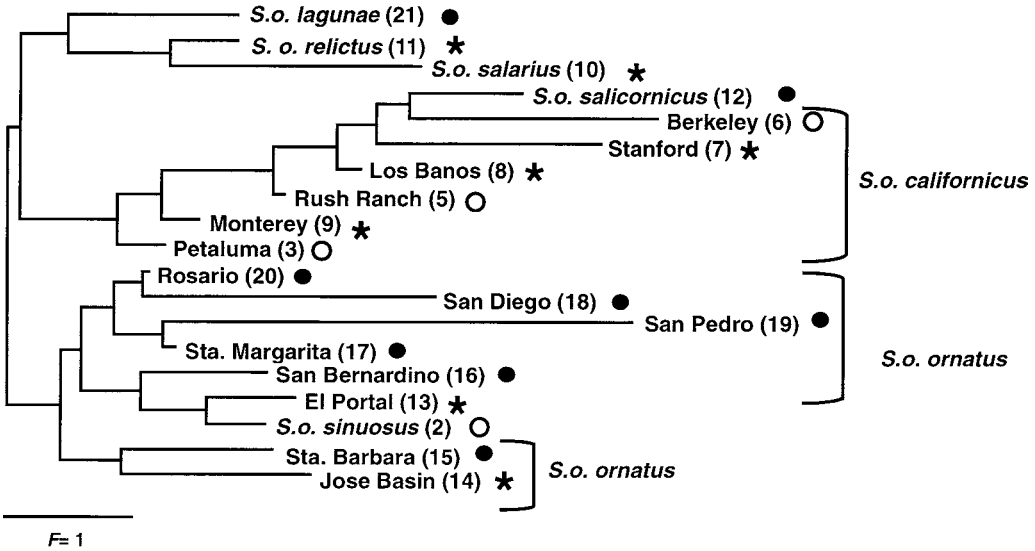

FIG. 4.—Neighbor-joining tree based on between-groups F-matrix ($d.f. = 17, 358$) derived from a discriminant function analysis of 19 populations of ornate shrews. Symbols denote geographic assignment of the populations based on genetic data as follows: southern •, central ∗, and northern ○ regions. Locality numbers are in parentheses and correspond to localities in Fig. 1.

significant cranial traits might have occurred in response to environmental selection, such an extreme convergence of a large set of measurements to the extent of producing similar morphologies has never been demonstrated. Our analyses suggest that high similarities in morphology of northern compared with central and southern ornate shrews probably is not just the result of convergence between genetically divergent species (as suggested by Maldonado et al. 2001).

An alternative explanation for the similarity between wandering shrews and ornate shrews from northern California could be that wandering shrews were derived from the ancestor of these northern ornate shrews (Willmann 1986). Three genetically different groups of ornate shrews were observed by Maldonado et al. (2001; Fig. 1), indicating divergences >1 million years old. It is possible that with the retreat of the ice sheet following the last glaciation, a population of northern ornate shrews expanded northward to occupy the new habitats available. An ancestral northern group of ornate shrews could have given rise to the wandering shrew. Because ornate and wandering shrews cannot be differentiated (Carraway 1995) in the scarce fossil record available (Carraway 1990; Kurtén 1967; Kurtén and Anderson 1980; Lundelius et al. 1983; Repenning 1967), the hypothesis that wandering shrews were derived from a recent expansion of 1 of the northern populations of ornate shrews cannot be tested by studying the morphology of fossils. However, if it is true that wandering shrews were derived from ornate shrews, a lower genetic variability is expected for wandering shrews than for ornate shrews across their entire range, and all wandering shrews should be paraphyletic to ornate shrews from northern California. In a genetic study of North American *Sorex* shrews, Demboski and Cook (2001) sequenced a fragment of the mitochondrial cytochrome *b* gene in vagrant shrews from Montana and British Columbia. The sequences obtained differed by only 1 base pair (bp) from 1 of the sequences (699 bp in length; sequence divergence of 0.1%) obtained by Maldonado et al. (2001) in northern California. The variability observed across the range of wandering shrews is very limited compared with the extensive variability observed for ornate shrews (>6% sequence divergence—Maldonado et al. 2001). This result supports the hypothesis that wandering shrews could be the result of a northward expansion of northern ornate shrews since the last glaciation, although further sampling across the distribution range of wandering shrews is needed to test this hypothesis.

Two populations of presumed ornate shrews in northern California deserve special attention. Individuals from Tolay Creek (population 4) were identified as possible hybrids by Rudd (1955). Our analysis shows that they have an intermediate morphology between ornate and wandering shrews. A similar result is apparent for shrews from Dye Creek (population 1), suggested to be a new, perhaps isolated, population of ornate shrew outside its known range (Maldonado et al. 2001). However, our analyses are inconclusive regarding their specific status. Neither of these populations can be identified as *S. ornatus* thus, further research is required.

Previous studies have suggested that morphological variation in shrew populations is limited. Carraway (1990) studied the *S. vagrans* group and after removing size variation found no significant geographic variation. Van Zyll de Jong and Kirkland (1989) reported that geographic variation of the cranium in the *S. cinereus* group involved mostly size differences and only slight shape differences. Studies of *S. granarius* in the Iberian Peninsula in Europe found few intraspecific differences (Gisbert et al. 1988) and only a general trend of larger size of the mandible from north to south was found in *S. coronatus* (Casteig and Escala 1988). However, the ornate shrew represents an exception to this trend; there are significant morphological differences among populations. Additionally, these differences are not restricted to size, but are also manifested in the shape of the skull. These differences also do not correspond to the 3 phylogeographic partitions that were identified with genetic markers and that presumably have been diverging for >1 million years (Maldonado et al. 2001). In addition, these differences do not correspond to a pattern of divergence with geographic distance. The subspecific partitioning suggested from the study of reduced numbers of samples seems to portray the patterns of morphological variation better than the genetic data. If we consider only the 2 most widespread and largely sampled subspecies (*S. o. ornatus* and *S. o. californicus*), 90% of the specimens were correctly identified in a DFA. The population level analysis also suggested that the differences among populations are great and that the isolation among them might be an important mechanism of divergence.

Some studies have shown concordant patterns of morphologic differentiation correlated with genetic differentiation (González et al. 2002; Miller-Butterworth et al. 2003; Polly 2001). Others have shown little genetic differentiation among morphologically differentiated populations or species (Paxinos et al. 2002; Talbott and Shields 1996; Waits et al. 1997) and vice versa (Barratt et al. 1997; Roca et al. 2001). These results normally have been explained as a consequence of fast morphological differentiation between recently isolated populations (Losos et al. 1997), or by lack of selective pressures that could induce morphological differentiation among long-isolated populations. However, the existence of discordant patterns of differentiation in morphologic and genetic analyses is difficult to explain. If our hypothesis on the origin of the wandering shrew from the ornate shrew is correct, the morphological differentiation between these 2 species might have arisen in a relatively short time (from an evolutionary perspective). In contrast, the 3 clades genetically differentiated and presumably isolated for over a million years do not show strong morphologic differentiation. There does not appear to be a correlation between degree of morphological variation (as shown by the coefficient of variation for each of the 17 cranial measurements) and that of genetic variation (as shown by measures of percentage polymorphic loci and heterozygosity values from the allozyme data). The different morphotypes might have arisen after populations became genetically differentiated. Patton and Brylski (1987) have shown that size in *Thomomys bottae* is an ecophenotypically plastic character, whereas shape differences are the products of long-term

evolutionary divergence. However, in this example, changes in cranial shape seem to be the result of local adaptation.

The genetic study by Maldonado et al. (2001) suggested a deep tripartite subdivision of ornate shrew populations. Apparently, those subdivisions corresponded to an ancient fragmentation of ancestral ornate shrew populations. According to Moritz (1994:373), each of the subdivisions identified in the genetic study should be considered an evolutionarily significant unit (ESU): ''a set of populations that has been historically isolated and, accordingly, is likely to have a distinct potential.'' However, our results indicate that this genetic divergence is not coupled with morphological divergence. In fact, the morphological variability is partitioned in a different way. The 2 subspecies with a wider distribution, *S. o. ornatus* and *S. o. californicus*, show a very distinct morphology (Fig. 4), and the limit of their distribution does not correspond with the genetic partition (Fig. 1).

Crandall et al. (2000) suggested a new definition for ESUs considering evolutionary processes. These authors propose that both ecological and genetic exchangeability should be considered to define conservation units. Genetic divergence should not be used solely to define units for management because morphology might indicate other significant patterns of ecological divergence. Our results represent a complex situation. Populations that seem genetically exchangeable might not be exchangeable at the morphological level, and vice versa. Consequently, in addition to the separate management of the different genetic lineages (southern, central, and northern), our results also suggest that the 5 subspecies with restricted distribution analyzed in this study are morphologically divergent, which implies ecological adaptation and therefore should be managed separately. In particular, *S. o. lagunae, S. o. salarius* and *S. o. relictus* appear morphologically divergent from *S. o. ornatus* and *S. o. californicus*, whereas *S. o. sinuosus* and *salicornicus* do not resemble the surrounding subspecies that are in close proximity. Additionally, the 2 subspecies not included in this study, *S. o. willetti* and *S. o. juncensis* deserve further study as they are small and fragmented and have a high probability of extinction (Maldonado 1999).

Resumen

A pesar de que las musarañas *Sorex ornatus* tienen una amplia distribución que incluye California, E.U. y Baja California, México, análisis genéticos han mostrado que sus poblaciones están estructuradas en 3 regiones genéticamente diferenciadas (sur, centro, y norte) dentro de su distribución. El tiempo de separación de las poblaciones de los tres grupos se ha estimado en mas de un millón de años. En la región del norte, *S. ornatus* no se puede diferenciar genéticamente de su especie hermana *S. vagrans*. Por consiguiente, se sugirió que las musarañas del norte pudieron haber sido clasificadas incorrectamente. Sin embargo, al analizar la morfología craneal, observamos que tanto *S. ornatus* y *S. vagrans*, así como otra especie cercana, *S. monticolus*, están bien diferenciadas entre sí. Las musarañas de la región norte tienen una morfología similar a las poblaciones de *S. ornatus* del centro y sur de su distribución, mientras que *S. vagrans* y *S. monticolus* son muy diferentes. Dentro de *S. ornatus*, las poblaciones muestran diferencias morfológicas. Sin embargo, esta diferenciación morfológica no es concordante con el patrón de diferenciación genética. Nuestros resultados sugieren que las diferencias en la forma del cráneo entre las poblaciones pueden ser el resultado de adaptación local, mientras que la larga historia de aislamiento geográfico pudo haber contribuido poco a las diferencias morfológicas entre especies. Además, estos resultados sugieren que *S. vagrans* pudo haber derivado de una expansión pos-glacial hacia el norte a partir de una población ancestral norteña de *S, ornatus*.

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APPENDIX I

List of specimens examined.—The 500 specimens examined in this study representing the 9 subspecies currently recognized are listed below with location, sample size, and specimen numbers. Museum acronyms follow Hafner et al. (1997). Acronyms: CM—Carnegie Museum of Natural History; CSULB—California State University, Long Beach; LACM—Los Angeles County Museum of Natural

History; MVZ—Museum of Vertebrate Zoology; SBMNH—Santa Barbara Museum of Natural History; SDNHM—San Diego Natural History Museum; MWFB—Museum of Wildlife and Fisheries Biology, University of California, Davis; UCLA—University of California, Los Angeles; USNM—National Museum of Natural History (Smithsonian Institution). JEM denotes specimen collector numbers by Jesús Maldonado, and LAF denotes specimen numbers in the frozen tissue collection located at LACM. All sampling localities are from the United States unless noted otherwise. Forty-one specimens were excluded from the population analysis due to missing data. In addition, specimens from *S. o juncencis* ($n = 1$) and *S. o. willeti* ($n = 3$) were measured but were not included in the population analysis due to the small sample sizes. Morphometric and locality data available upon request.

Sorex ornatus californicus (n = 168).—California: Alameda County: West slope Strawberry Canyon, Berkeley, 16 (CMNH 12197, MVZ 29959—29960, 66416, 81120—81121, 101662, 102076—102079, 108937, 181437—181438, USNM 32756, UCLA 16042); Calaveras County: 2.3 miles [3.7 km] S 0.3 miles [0.4 km] W West Point, 2 (CMNH 71063—71064); Contra Costa County: 5 miles [8 km] N Concord, 1 (UCLA 7009), LaFayette, 1 (MVZ 104561), Martinez Salt Marsh, 8 (MVZ 123638, 123640—123643, 123646, 123648—123649), Orinda, 6 (MVZ 98940, 141184, 122407, 112876—112877, 135345), Point Isabel, 5 (MVZ 115517—115520, 115586), Salt Marsh, 14 (MVZ 74572, 122074, 119041, 119118, 121286, 121287, 123790, 123631—123637), Tilden Park, 19 (MVZ 114121, 115099, 115111—115117, 115120—115122, 115124—115129, 115131), Walnut Creek, 4 (USNM 32578, 32580, LACM 5057—5058); Lake County: Clear Lake, 1 (MVZ 109354); Madera County: San Joaquin Experimental Range, 2 (CMNH 84120, MVZ 114549), W. Fork, San Joaquin River, Soda Creek, 2 (LACM 52266—52267); Merced County: Los Banos Wildlife Area, 14 (LACM [LAF] 1206—1210, 1212, 1214—1221), San Luis National Wildlife Refuge, 1 (CMNH 60957); Monterey County: Arroyo Seco, 1 (MVZ 107794), Carmel, 1 (MVZ 107796), Chalk Peak, 1 (MVZ 30119), Chualas Canyon, 1 (MVZ 97947), Hastings, 7 (MVZ 17731—17732, 140064, 140071, 140081, 140082, 149663), Monterey, 5 (USNM 32003, UCLA C-131, C-151–152, C166), Paraiso Springs, 1 (USNM 117845), Soledad, 3 (MVZ 30120, 100731–100732); Placer County: Auburn, 1 (USNM 118909), 1.5 miles [2.4 km] N 1.5 miles [2.4 km] W Forest Hill, 2 (CMNH 71093–71094); Sacramento County: Rio Vista, 1 (MVZ 15612); San Benito County: San Benito Peak, 2 (MVZ 101466–101467), Paicines, 1 (MVZ 124027), Pinnacle National Monument, 2 (SBMNH 3344, 3394); San Mateo County: Dunbarton Bridge, 8 (MVZ 115142–115145, 115148–115149, 115154–115155), Palo Alto and Redwood City, 2 (CMNH 12343, 12345), San Bruno, 1 (MVZ 115155); Santa Clara County: Alviso, 1 (MVZ 126074), Pacheco Pass, 2 (USNM 150440–150441), San Francisco Bay, 1 (CMNH 12345), Stanford University, 1 (USNM 107918); Solano County: 1 mile [1.6 km] E Fairfield, 1 (CMNH 50321), 6 miles [9.7 km] S 5 miles [8 km] E Fairfield, 8 (LACM [LAF] 1241, 1243, 1244, 1247, 1248, 1250–1252), 1 mile [1.6 km] E Suisun, 2 (CMNH 50322,50323); Sonoma County: Petaluma, 8 (MVZ 90471, 115572–115577, USNM 4427), 3 miles [4.8 km] S Petaluma, 1 (CMNH 16311), Rio Vista, 1 (MVZ 97856); Stanislaus County: Del Puerto Canyon, 3 (CMNH 84078–84080).

Sorex ornatus juncensis (n = 1).—Mexico: Baja California Norte: 15 miles [24.1 km] S San Quintin, El Socorro, 1 (USNM 139594).

Sorex ornatus lagunae (n = 12).—Mexico: Baja California Sur: Sierra de la Laguna, La Laguna, 1 (USNM 147119), La Laguna Chica 11 (LACM [JEM] 1190, 1192–1194, 1197–1198, 1200–1201, 1203–1205).

Sorex ornatus ornatus (n = 246).—California: Fresno County: 0.9 miles [1.5 km] W Balsam Creek, 1 (CMNH 71065), 1 mile [1.6 km] W Spilway, Huntington, 1 (CMNH 71284), Dawn Meadow area, 7 (CMNH 84081, 71066–71071), Elk Creek, 8 (CMNH 84082–84083, 70968–70969, 71072–71075), Jose Basin, 17 (CMNH 84101, 84107, 84090–84100, 71078–71081, LACM [LAF] 1258), Jose Creek, 6 (CMNH 84108–84112, 71082), Flume Peak, 8 (CMNH 84087–84089, 71076–71077, 84084–84086), Mendota, 1 (USNM 150439), Musick Mountain, 9 (CMNH 71083–71084, 84113–84119); Kern County: Bakersfield, 1 (MVZ 14644), 4 miles [6.4 km] NE Caliente, 1 (MVZ 122207), Fort Tejon, 1 (MVZ 6923), Kelso Valley, 1(MVZ 59962), 0.5 miles [0.8 km] E Miramonte, 1 (MVZ 55031), Piute, 1 (USNM 159416), Rankin Ranch, 3 (MVZ 59956, 59960–59961), Rip-Rap Mine, 1 (LACM 978), San Emigdio Canyon, Mount Pinos, 4 (USNM 31333, UCLA 18412, 18413, 18416), Tehachapi, 1 (USNM 135947), 10 miles [16 km] S Oak Creek, 1 (LACM 36978), Walker Basin, 4 (MVZ 59951, 59953–59954, UCLA 9586); Kings County: Lemoore, 1 (USNM 149816); Los Angeles County: Big Pine Mountain, 2 (USNM 129693, UCLA 9639), El Monte, 2 (MVZ 5283, 6922), Ice House Canyon, San Gabriel Mountains, 1 (UCLA 50735), Mulholland Drive, 1 (LACM 52271), Sepulveda and Sunset Avenue, 1 (MVZ 125641), Whittier, Turnball Canyon, 1 (LACM 33712), Wrightwood, San Gabriel Mountains, 1 (CSULB 6423); Mariposa County: N Fork of Merced River, Bower Cave, 20 (CMNH 71085–71092, 71060–71062; LACM [LAF] 1262–1263, 1267–1271, 1274, 1276), El Portal, 9 (MVZ 21523–21525, 21528, 21530, 21532–21533, 21535–21536,); Orange County: Laguna Beach, 1 (CSULB 3800), Trabuco Canyon, 1 (MVZ 2378), Starr Ranch, Bell Canyon, 1 (CSULB 10458); Riverside County: Santa Ana Mountains, 2 (CSULB 5986, 9690), Santa Margarita Mountains, 2 (SDMNH 22891, 22943), Strawberry Valley, 1 (MVZ 2090), Tahquitz Valley, 1 (MVZ 2150); San Bernardino County: Big Bear Valley, 1 (UCLA C-89), 1.5 miles [2.4 km] S 1.5 miles [2.4 km] W Big Bear Lake, 10 (LACM [LAF] 398–399, LACM [JEM] 1224, 1229–1230, 1234–1238), Lytle Creek 3 (USNM 127976–127977, SDMNH 50), San Bernardino Peak, Bluff Lake, 13 (USNM 56558–56561, 56682, LACM 10313, 19556, MVZ 6919–6920, 5285, UCLA H-277, H-289, H-310), Camp Baldy, 3 (UCLA G-73, G-74, 7731), Lake Arrowhead, 1 (CSULB 4766), Summit, 1 (USNM 55550); San Diego County, Adobe Falls, 1 (SDMNH 8089), Dulzura, 5 (MVZ 2942–2944, UCLA E-268–269), 3 miles [4.8 km] SE Dulzura, 1 (CMNH 7327), El Cajon, 1 (SDMNH 18678), Julian, 1 (SDMNH 21563), La Jolla, 1 (UCLA 9670), Mission Gorge, 1 (SDMNH 8088), Murray Dam, 1 (SDMNH 10802), San Diego Bay, 1 (MVZ 3261), San Diego, Kearny Mesa, 1 (SDMNH 18695), San Marcos, 1 (SDMNH 22897), Rancho Santa Fe, 2 (LACM 39669, 43755), Santa Ysabel, 1 (USNM 73772), W Sycamore Canyon, Santee, 3 (SDMNH 22998–23000), Torrey Pines, 1 (SDMNH 10587); San Luis Obispo County: Morro Bay, 1 (MVZ 8788), Piedras Blancas Point, 1 (USNM 530330); Santa Barbara County: Buellton, 6 miles [9.7 km] S Hancock Ranch, Mendoza Canyon, 2 (LACM 20638, 20656), Carpinteria, 1 (SBMNH 3273), Goleta, Mills Way, 2 (SBMNH 7036, 5579), Montecito, Hidden Valley, 10 (SBMNH 372, 445, 774, 807, 809–812, 865, 3149), Nojogai Falls Park, 1 (LACM 56167), Santa Barbara, 17 (SBMNH 318, 808, 933, 2380, 2528–2533, 2551, 2718,2719, 2720, 2912, 2913, UCLA 10104), Summerland, 2 (SBMNH 3388–3389), Vandenburg Air Force Base, 6 miles [9.7 km] E of Mouth of Santa Ynes River, 9 (SBMNH 2210, 2603, SDMNH 23332, 23090–23092, 23304–23306); Tulare County: Orosi, 1 (USNM 149815); Ventura County: Fillmore, 1 (LACM 56166), Ventura River, 1 (USNM 32017);

Mexico: Baja California Norte: El Rosario de Abajo, El Rosario River Mouth, 9 (SDMNH 21562, 4788, 4836, 4859, LACM [JEM]

1214–1216, 1220–1221), San Ramon, 2 (MVZ 35394, 36164), San Telmo, 6 (MVZ 35397–35401, 35403).

Sorex ornatus relictus (n = 10).—California: Kern County: Buena Vista Lake, 3 (MVZ 51414–51416), Kern Lake Preserve, 7 (LACM 74317, 85715–85716, LACM [JEM] 1209–1211, 1211B).

Sorex ornatus salarius (n = 19).—California: Monterey County: Salinas River Wildlife Management Area, 19 (LACM [LAF] 1222–1224, 1226–1238, MVZ 81548, 107799–107800).

Sorex ornatus salicornicus (n = 30).—California: Los Angeles County: Ballona Creek, 0.25 miles [0.4 km] SW Lincoln Boulevard, 1 (LACM [JEM] 1207), Bolsa Chica, 1 (LACM [LAF] 267), Long Beach, 2 (LACM 30236–30237), Newport Bay, 2 (MVZ 63322–63323), Palos Verdes, 4 (CSULB 111, LACM 36833, 74312–74313), Playa Del Rey, 14 (CMNH 12336–12342, LACM 1195, 1215, 20454, 30727, 67382, UCLA 9880,MVZ 74679), Seal Beach Naval Station, Bolsa Road, 3 (LACM 67430–67431, CSULB 5811); Ventura County: Point Mugu, 2 (LACM 3435, 8118); Orange County: Huntington Beach, 1 (CSULB 11078).

Sorex ornatus sinuosus (n = 11).—California: Solano County: Cordelia, 1 (UCLA E-547), Grizzly Island, 10 (LACM 5059, LACM [LAF] 1239, 1240, 1242, 1245, 1253–1256, MVZ 16470).

Sorex ornatus willetti (n = 3).—California: Los Angeles County: Santa Catalina Island, Avalon Canyon, 1 (LACM 7400), 1 km E Cottonwood Canyon, 1 (LACM 74316), Cherry Cove, 1 (LACM [LAF] 437).