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Source: American Museum Novitates, 2024(4018) : 1-24

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/4018.1

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AMERICAN MUSEUM NOVITATES

Number 4018, 24 pp. June 21, 2024

A Morphological Assessment of Osgood's 1918 Application of *Otognosis longimembris* Coues, 1875 (Rodentia, Heteromyidae), with the Proposal of a Neotype

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ABSTRACT

We review the current usage of the species-group names *Perognathus inornatus* Merriam, 1889, for the San Joaquin Pocket Mouse and *P. longimembris* (Coues, 1875) for the Little Pocket Mouse. Wilfred Osgood, in two papers published 18 years apart at the beginning of the 20th Century, provided conflicting applications of these names, with his second assignments in common use since 1918. Contrary to this prevailing usage, we show that the skull of the holotype of *longimembris* is best allocated to the San Joaquin form, as Osgood had originally concluded in 1900. To maintain stability and universality of current usage (International Code of Zoological Nomenclature: Article 75.6), we propose a neotype from the Antelope Valley of California as a replacement for Coues's holotype of *longimembris*.

INTRODUCTION

In his 1900 revision of the genus *Perognathus*, Wilfred Osgood organized species-group names then known and currently applied to members of the *longimembris* group (Williams et al., 1993; Patton, 2005; Hafner, 2016) into five species: the polytypic *P. panamintinus* Merriam, 1894 (included as subspecies *bangsi* Mearns, 1898; *arenicola* Stephens, 1900; and *brevinasus* Osgood, 1900), and the monotypic *P. nevadensis* Merriam, 1894; *P. pacificus* Mearns,

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ISSN 0003-0082

1898; *P. amplus*, Osgood, 1900; and *P. longimembris* (Coues, 1875). Osgood allocated Coues's *longimembris*, with its type locality at Fort Tejon in south-central Kern County, California, to specimens from the San Joaquin Valley that Merriam (1894) had earlier assigned to his new species *P. inornatus*. In Osgood's 1900 view, *P. longimembris* inhabited the San Joaquin Valley while *P. panamintinus* occupied the Mojave and western Sonoran deserts, *P. pacificus* the coast of southern California, and *P. nevadensis* the Great Basin Desert. Osgood (1900: 34) stated "the type of *longimembris* is immature, but its skull shows the narrow interorbital space peculiar to the San Joaquin Valley form." He further noted that "the only available topotype is fortunately a young adult which agrees perfectly with specimens from Fresno [type locality of *inornatus* Merriam] and other points in the San Joaquin Valley." Osgood included "Two young specimens from San Emigdio and Rose Station, both very near Fort Tejon [but on the adjacent floor of the San Joaquin Valley], are also clearly the same as those from Fresno," concluding that "the name *longimembris* should be applied to the animal recently called *inornatus* rather to the San Bernardino form."

In 1918, Osgood reevaluated his earlier equivalence of Coues's *longimembris* with Merriam's *inornatus*. On page 95, he wrote:

> the site of Fort Tejon…is within comparatively easy reach of several faunal districts. Recent collectors have failed to secure any pocket mice at the actual site of the old fort and it is, therefore, probable that the type [of *longimembris* Coues] did not come from there but from some of the surrounding country… there are two species inhabiting this surrounding country which as adults are easily distinguishable but which may be exceedingly similar when only partly mature. For convenience, these species may be referred to as the larger and the smaller, one having a range to the northward, principally in the San Joaquin Valley, and the other in the south and east….

He also noted that the majority of specimens taken in the vicinity of Fort Tejon were of the smaller species and that the larger species has been found in the region at but one locality, namely Rose Station…. As a result, Osgood concluded (p. 96) that "Geographical probabilities thus favor the supposition that the type [of *longimembris* Coues] was of the smaller species" and "the name *Perognathus inornatus* should be revived for the larger species of the San Joaquin region." He further concluded that both species occurred in the San Joaquin Valley and as far north as Marysville Buttes (Yuba County in the Sacramento Valley), at Fresno (the type locality of *inornatus* Merriam), and at Three Rivers (in Tulare County).

Although Osgood (1918) did not provide the voucher catalog numbers for specimens from the localities he referenced, at the time of his writing he had examined specimens only in the Biological Survey Collection at the National Museum of Natural History (USNM) and Field Museum of Natural History (FMNH). Thus, specimens currently housed in these two institutions make it possible to determine those that Osgood segregated into his large and small species. Herein we evaluate the two hypotheses Osgood posed in 1918, namely: (1) that he correctly applied the holotype of *longimembris* Coues, and thus that species-group name, to the Mojave Desert small species, and (2) that both species inhabit the floor of the San Joaquin Valley.

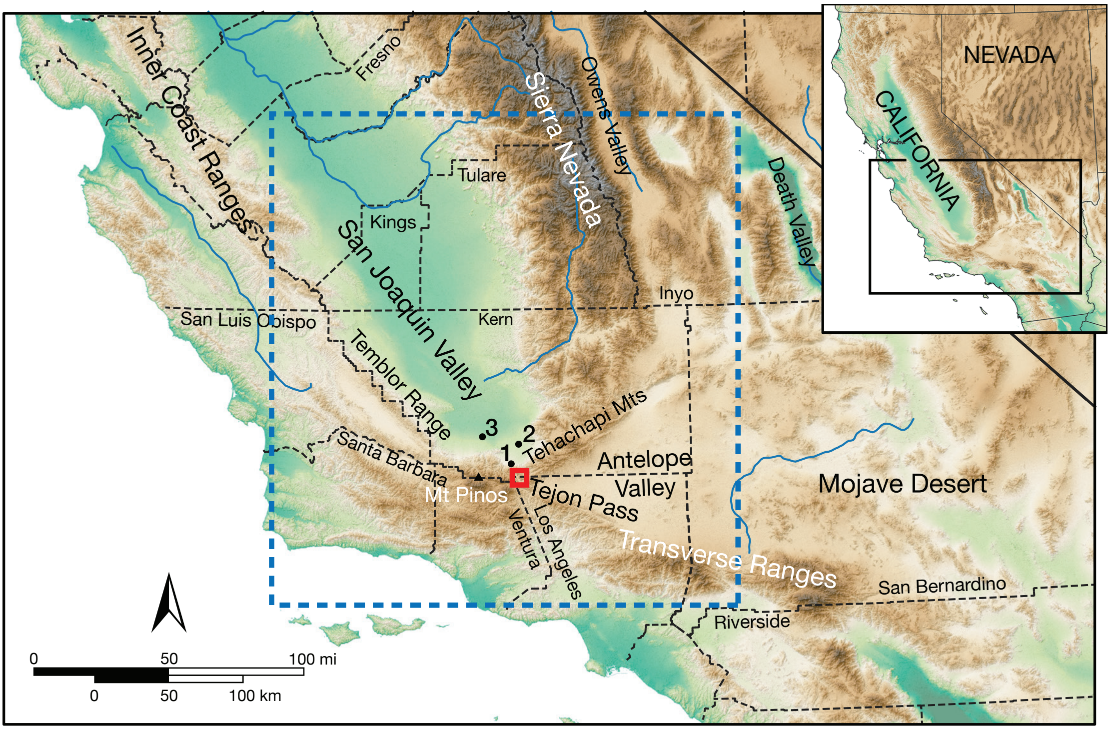

FIG. 1. Map of study area in south-central California with county names and geographic features provided. Numbered circles identify key localities: **1**. Fort Tejon, in the Cañada de las Uvas [Grapevine Canyon]; **2.** Rose Station, on the adjacent floor of the San Joaquin Valley; and **3.** San Emigdio, at the mouth of San Emigdio Canyon. The dotted blue box circumscribes the area mapped in figure 3A.

We map the general focal area of Osgood's separate treatments in south-central California in figure 1, providing key place names mentioned above for geographic context. Fort Tejon, a U.S. Army post operated from 1854 to 1864, is on the north side of Tejon Pass near the head of the Cañada de las Uvas (Grapevine Canyon, as known today) that ascends from the San Joaquin Valley floor south to Antelope Valley, the western extension of the Mojave Desert; the post was designed to protect this passage route. Rose Station is the site of an Overland Mail way station established in 1858 and operated until 1875 where it served as a stockman's headquarters, post office, and polling station. And San Emigdio was a Mexican land-grant ranch established in 1842 at the foot of San Emigdio Canyon on the El Camino Real, which connected the Spanish missions from Pueblo de Los Angeles in the south to Mission Santa Clara de Asis on San Francisco Bay.

MATERIALS AND METHODS

Specimens and Grouped Samples: To evaluate our two hypotheses, we examined all specimens we believe to have been available to Osgood for his 1900 revision and 1918 reconsideration of name applications. Among these are the holotype of *longimembris* Coues, 1875

(USNM 9856/37356), and a second specimen from Fort Tejon in the USNM (37501, skull only), likely the topotype mentioned by Osgood (1900: 34). We also examined, and included in the analyses, all adult specimens in the series of the small species Osgood (1918: 95) noted from "various places on all sides of the old fort"; the holotype (FMNH 11971) and type series (FMNH 11973–5, 11977, 11979) of *elibatus* Elliot, 1904, from Lockwood Valley; and FMNH 11914 from "Ft Tejon, Castac Lake," which is about 4 miles southeast of Fort Tejon, but also on the north side of Tejon Pass. Key samples of the large species were those from Fresno, Fresno County (USNM 13394/23790, the holotype of *inornatus* Merriam, and others from the same locality); Alila [= Earlimart], northern Kern County, and Delano, Tulare County; and the young specimens from San Emigdio and Rose Station mentioned by Osgood (1900: 34), both localities close to Fort Tejon but on the floor of the San Joaquin Valley in southern Kern County (USNM 31344/43209 and 31338/43203, respectively). Since by 1918 Osgood had access to specimens in the FMNH, we also included the small series (N = 7) collected by Edmund Heller in 1903, with locality designation "Ft. Tejon, Rose Station" even though all are young animals (FMNH 11951, 11955-6, 11958, 1960, 11962-3) and one specimen from "Piru Creek, Bailey's Ranch [Los Angeles County]" (FMNH 11913), also collected by Heller in 1903 but not explicitly mentioned by Osgood in his 1918 paper. We refer to this group of specimens (N = 54) as the Osgood Sample. Unfortunately, the specimen identified as *P. longimembris* collected by Luther J. Goldman from Tejon Canyon in 1903 (USNM 127819), mentioned by Osgood (1918: 96) as "although much older than the type, agrees with it very closely," has a damaged skull and was not included in our analyses.

Our second sample included the 54 Osgood specimens and 97 additional ones either then available in other collections, but not examined by Osgood, or collected at the same or nearby localities subsequent to his studies. We also included specimens of both species from Antelope Valley, the western arm of the Mojave Desert southeast of Fort Tejon. Osgood did not examine specimens from this area. These additional materials are housed in the Natural History Museum of Los Angeles County (LACM) and University of California Museum of Vertebrate Zoology (MVZ). We refer to this collective group of specimens (N = 151) as the Osgood Expanded Sample.

DATASETS: We evaluated two morphometric datasets, one based on digitized landmarks using geometric morphometric methodologies, and the second on linear measurements. For the first, we photographed the dorsal and ventral aspects of each skull using a Nikon D3200 or Nikon D850 digital camera fitted with AF-S AV Micro Nikkor 105 mm lens. Patton and Fisher (2023) provided definitions for landmarks (LM) and semilandmarks digitized (SL); we illustrate the dorsal set in figure 2A. Our analyses included all specimens examined by Osgood and added by us regardless of age as defined by toothwear (lower and upper wear stages for each of four age classes defined for the upper molar series of adult specimens illustrated in fig. 2B).

We used XYOM-CLIC (Dujardin and Dujardin, 2019) for digitization and MorphoJ (Klingenberg, 2011) to generate matrices of Procrustes coordinates, or residuals, that result from superimposition; principal components (PC scores) of the set of Procrustes residuals; canonical coefficients based on those principal component scores that compare predefined groups; and centroid size (a measure of geometric scale). We also used MorphoJ to construct wireframes

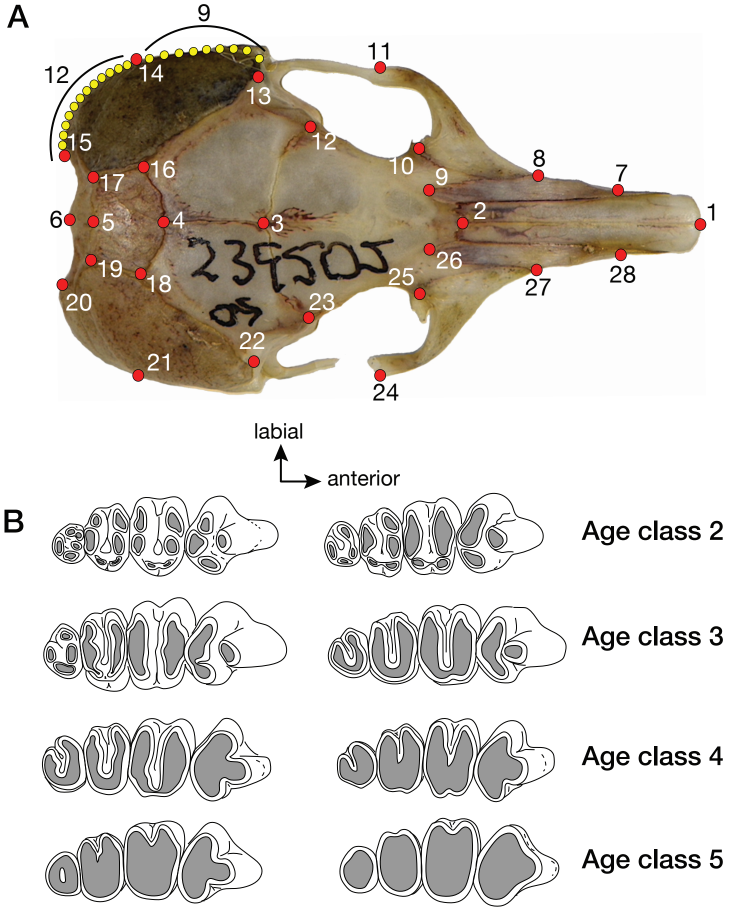

FIG. 2. **A.** Dorsal view of the skull of *Perognathus inornatus neglectus* (MVZ 239505; from 2.5 mi N McKittrick, Kern Co., California) illustrating the positions of 28 landmarks (LM, red circles) and 21 semilandmarks (SL, yellow circles) that define the outer margin of the epitympanic (9 SL, black arc) and mastoid (12 SL, black arc) portions of the auditory bulla. **B.** Lower and upper wear stages for each of four age classes defined for the upper molar series of adult specimens (see Patton and Fisher, 2023).

(sets of lines linking landmarks in a predetermined configuration) and deformation grids; both allow visualization of shape differences between groups. Finally, we used JMP Pro17™ (SAS Institute Inc., Cary, North Carolina) for univariate comparisons and multivariate analyses of the linear variables. We included each complete specimen in both the geometric and linear dataset analyses; specimens with damaged skulls were excluded.

Since each of the variables that Osgood mentioned in either 1900 or 1918 are dorsal measurements, we confined our linear dataset to 18 variables that included those mentioned by Osgood and others commonly employed for pocket mice (e.g., Williams, 1978). These we obtained from dorsal photographs of the skull using ImageJ (https: //imagej.nih.gov/ij/index.html). Measurements included: occipital-nasal length (ONL); distance along the midline for nasal length (NL), frontal length (FL), parietal length (PL); interparietal length (IPL); length of posterior premaxillary extensions (preMaxExtL), midline distance from nasal bones to distal tip of extension; rostral width (RW), the distance across the anterior rostrum; maxillary width (MW), the distance across the rostrum at the premaxillary-maxillary suture; outside width across premaxillary extensions (preMaxExtW); interorbital constriction (IOC), least width across the interorbital region; zygomatic breadth (ZB), greatest width across the zygomatic arches; width across anterior border of parietals (antParietalW), taken from the suture junction of the frontal, parietal, and squamosal bones; anterior width of the interparietal (IPW-ant), taken across the interparietal and the suture junction of the supraoccipital and parietal bones; posterior width of the interparietal (IPW-post), greatest distance between the postero-lateral margins of the interparietal; exoccipital width (exOccW), taken across the lateral-most extensions of the visible occiput; bullar width (BullarW), greatest width of skull across the auditory bullae; bulla length (BullaL), diagonal distance from anterior to posterior points encompassing both epitympanic and mastoid portions of the bulla; bulla width (BullaW), taken perpendicular to BullaL from junction of epitympanic and mastoid portions to medial border.

We map localities in the Osgood Sample and Osgood Expanded Sample in figure 3. We list locality, sample sizes, and museum voucher catalog numbers for all specimens examined in appendix 1. These are organized by a priori groups used in canonical analyses; the eight specimens not assigned to an a priori group we treated as unknowns. The Osgood Sample included four a priori groups, one of *P. longimembris* (Lockwood Valley) and three of *P. inornatus* (Fresno, Alila [=Earlimart] + Delano, and Rose Valley). The Osgood Expanded Sample included six a priori groups, the four of the Osgood Sample plus those of both species from the Antelope Valley. Specimens treated as unknowns in both datasets are from Fort Tejon and nearby sites as well as from San Emigdio.

As a final comparison, we employed linear measurement and shape datasets that included 561 and 563 specimens, respectively, of nine geographic sample sets for *P. inornatus* from its range in the San Joaquin Valley and peripheral regions and nine samples groups of *P. longimembris* from the western Mojave Desert. Whereas the full analyses will be published separately, herein we include the species assignments of the five key Osgood specimens based on the global analysis of this full dataset.

Molecular Identification of Holotypes: We destructively sampled the type specimens of both *P. longimembris* (USNM 9856/37356) and *P. inornatus* (USNM 13394/23790) upon approval from the NMNH Division of Mammals. Coues's holotype had been collected by John Xantus while he served as hospital steward at Fort Tejon between May 1857 and January 1859. The original preservative of the fluid specimen was ethyl alcohol, shipped to Xantus by Spencer Fullerton Baird, then Assistant Secretary of the Smithsonian Institution. As noted in Xantus' correspondence with Baird, faithfully transcribed and published in Swinger (1986), the alcohol was potentially compromised in two ways that could impact downstream DNA recovery. First, what began as 85% alcohol at the time of shipment may have been watered down to an unknown extent by the time of actual use. And, perhaps of greater importance, Xantus apparently used copper cans to ship his fluid specimens back to the Smithsonian. While copper absorption by a fluid-preserved specimen could have a negative effect through oxidative

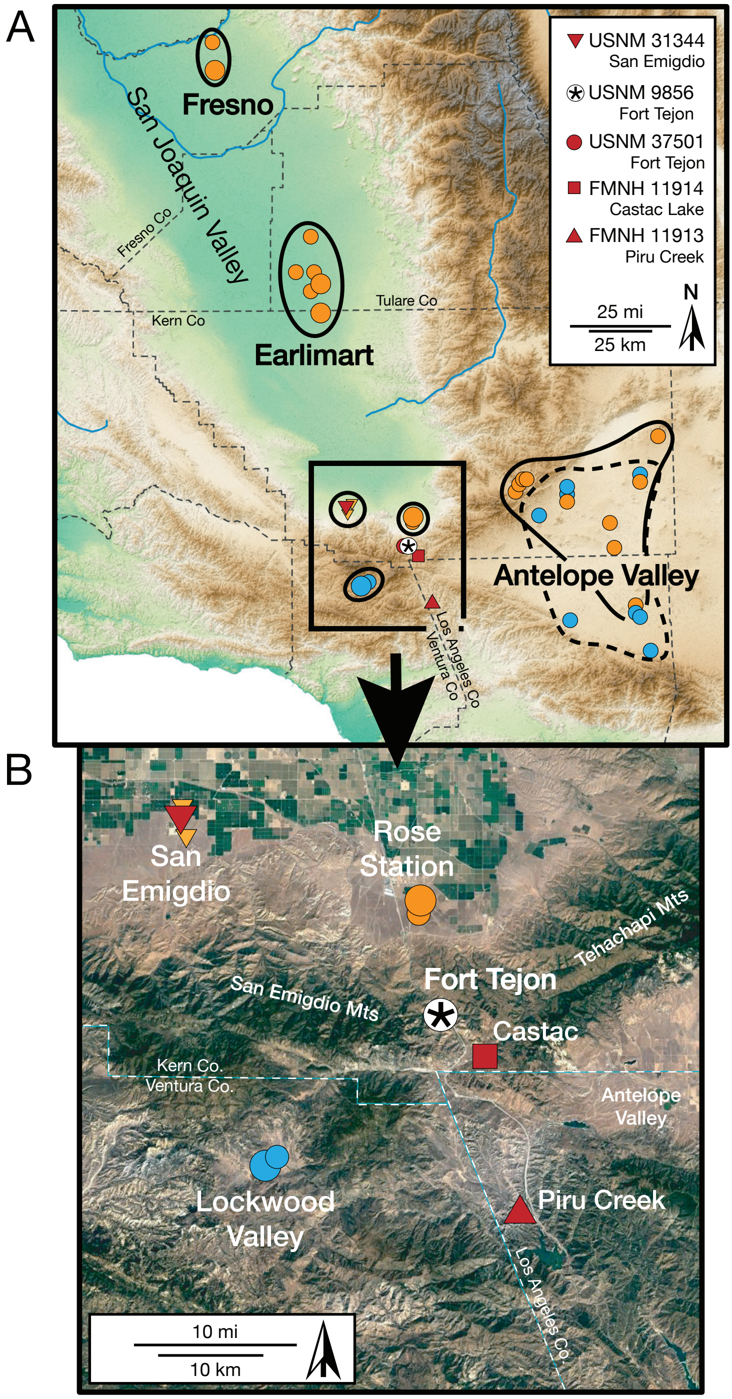

FIG. 3. **A.** Individual localities included in the Osgood Sample (large symbols) and those added in the Osgood Expanded Sample (small symbols). Orange circles depict localities of *Perognathus inornatus*, as currently understood; blue circles are those of *P. longimembris*; red symbols are localities of key specimens mentioned by Osgood in 1918; white circle with asterisk is the type locality (Fort Tejon) of *longimembris* Coues. **B.** Inset close-up map of the region around Fort Tejon illustrating the complex topography of the area; symbols as identified in A.

damage and/or DNA inhibition (e.g., Moreno and McCord, 2017), this did not appear to be the case in this instance.

We used established shotgun sequencing protocols for both specimens (see Hawkins et al., 2016a, 2016b, 2022)yet kit performance may influence the downstream processing of samples, particularly for samples which are degraded, and in low concentrations. Here we tested several commercial kits for specific use on commonly sampled mammalian museum specimens to evaluate the yield, size distribution, and endogenous content. Samples were weighed and had approximately equal input material for each extraction. These sample types are typical of natural history repositories ranged from 53 to 130 years old. The tested protocols spanned spin-column based extractions, magnetic bead purification, phenol/chloroform isolation, and specific modifications for ancient DNA. Diverse types of mammalian specimens were tested including adherent osteological material, bone and teeth, skin, and baleen. The concentration of DNA was quantified via fluorometry, and the size distributions of extracts visualized on an Agilent TapeStation. Overall, when DNA isolation was successful, all methods had quantifiable concentrations, albeit with variation across extracts. The length distributions varied based on the extraction protocol used. Shotgun sequencing was performed to evaluate if the extraction methods influenced the amount of endogenous versus exogenous content. The DNA content was similar across extraction methods indicating no obvious biases for DNA derived from different sources. Qiagen kits and phenol/chloroform isolation outperformed the Zymo magnetic bead isolations in these types of samples. Statistical analyses revealed that extraction method only explained 5% of the observed variation, and that specimen age explained variation (29%). Our initial extraction of the *P. longimembris* sample of dried tissue adhering to the skull, which had been removed and cleaned sometime between 1889 and 1900, was highly contaminated with bacterial sequences. It is likely the contamination was introduced from the specimen itself, as other samples in the same extraction batch and library preparation did not contain high amounts of bacteria, and negative controls were clean. As a result, we performed a second extraction, with tissue removed from the fluid-preserved remains of the specimen that contained adherent muscle pieces cut from inside the skin, specifically from the cavity where the skull had been extracted. However, after following repeated protocols with this second sample, no improvement resulted with respect to bacterial contaminants. Thus, we have no molecular data from Coues's holotype to compare to its morphological placement.

We recovered a partial mitogenome from the holotype of *inornatus* Merriam, an alcohol-preserved specimen with skull subsequently removed, and with a much higher percentage of endogenous reads. These reads match data from population samples identified as *P. inornatus*.

RESULTS

UNIVARIATE CHARACTERS DIFFERENTIATING *P. inornatus* AND *P. longimembris*: Osgood (1918: 96) contrasted the large and small species in the following statement: "As compared with the larger species of the San Joaquin Valley (*inornatus*) they [the smaller species, *longimembris*] are characterized by smaller size, smaller mastoid bullae, narrower brain-

TABLE 1. Hypotheses of cranial character differences identified by Osgood (1918: 65) to distinguish between *P. inornatus* and *P. longimembris*.

Osgood characterization	Measured variable	Prediction (H_o): *P. longimembris* vs *P. ornatus*	*P. longimembris* value[a]	*P. inornatus* value[a]	Probability of H_o acceptance[b]
Size	ONL	smaller : larger	20.85 ± 0.59	22.20 ± 1.05	$P = 0.0038$
			20.11 ± 0.46	22.58 ± 0.95	$P < 0.0001$
Mastoid bullae size	ratio BullaW / BullaL × 100	smaller : larger	28.89 ± 1.42	31.12 ± 2.71	$P = 0.0277$
			30.79 ± 1.79	31.62 ± 2.60	$P = 0.0497$
Braincase width	BullarW	narrower : broader	11.44 ± 0.28	12.37 ± 0.53	$P < 0.0001$
			11.85 ± 0.31	12.50 ± 0.48	$P < 0.0001$
Mastoid width	BullaW	narrower : broader	2.15 ± 0.18	2.45 ± 0.27	$P = 0.0138$
			2.39 ± 0.19	2.50 ± 0.25	$P = 0.0205$
Nasal length	NL	shorter : longer	7.33 ± 0.29	7.80 ± 0.07	$P = 0.0491$
			7.60 ± 0.27	8.01 ± 0.58	$P < 0.0001$
Parietal-frontal suture width	antParietalW	narrower : broader	7.11 ± 0.36	7.10 ± 0.04	$P = 0.9269$
			7.11 ± 0.26	7.16 ± 0.35	$P = 0.2998$
Interorbital breadth	IOC	broader : narrower	5.13 ± 0.18	4.69 ± 0.03	$P < 0.0001$
			5.11 ± 0.19	4.88 ± 0.29	$P < 0.0001$
Relative interorbital width	ratio IOC / ONL × 100	larger : smaller	24.58 ± 0.62	21.17 ± 1.03	$P < 0.0001$
			24.20 ± 0.95	21.62 ± 1.00	$P < 0.0001$

[a] The mean plus or minus one standard deviation for the Osgood Sample of 43 *P. inornatus* and 6 *P. longimembris* skulls (above) and the Osgood Expanded Sample of 96 *P. inornatus* 47 and *P. longimembris* skulls (below).

[b] Probabilities are one-way ANOVA, with $DF_{1,48}$ and $DF_{1,142}$ for the two analyses, respectively.

case, less mastoid width, slightly shorter nasals, less width across parietal-frontal suture, and always greater relative and usually greater actual width across the interorbital space." He gave no measurements, nor did he define each character. We were able to replicate some of his variables (e.g., nasal length), but how he took others is less clear (e.g., less mastoid width). We used our best estimate for each variable, which we measured as described above. We used ratios to compare variables that were not linear, but proportional, such as mastoid bulla size (ratio BW/BL × 100) or relative width of the interorbital region (ratio IOC/ONL × 100). We provide the results of these pairwise comparisons for both datasets in table 1, which includes character means, one standard deviation, and one-way ANOVA *P*-values for sample comparisons. We provide means, standard deviations, ranges, and sample sizes for the variables in table 1 for each a priori group of the Osgood Expanded Sample in appendix 2.

Osgood (1918) was correct that the "large" *P. inornatus* and "small" *P. longimembris* are well differentiated in all but one of the variables he referenced (width across the parietal-frontal suture; table 1). He was also correct that samples of *P. inornatus* included a wide range of specimen sizes, with some just as small as those of the *P. longimembris* sample he had available, although most were much larger. The average coefficient of variation for the individual variables listed in table 1 is twice that for *P. inornatus* (4.861) than for *P. longimembris* (2.439). We return to the significance of this finding below, but here compare size distribu-

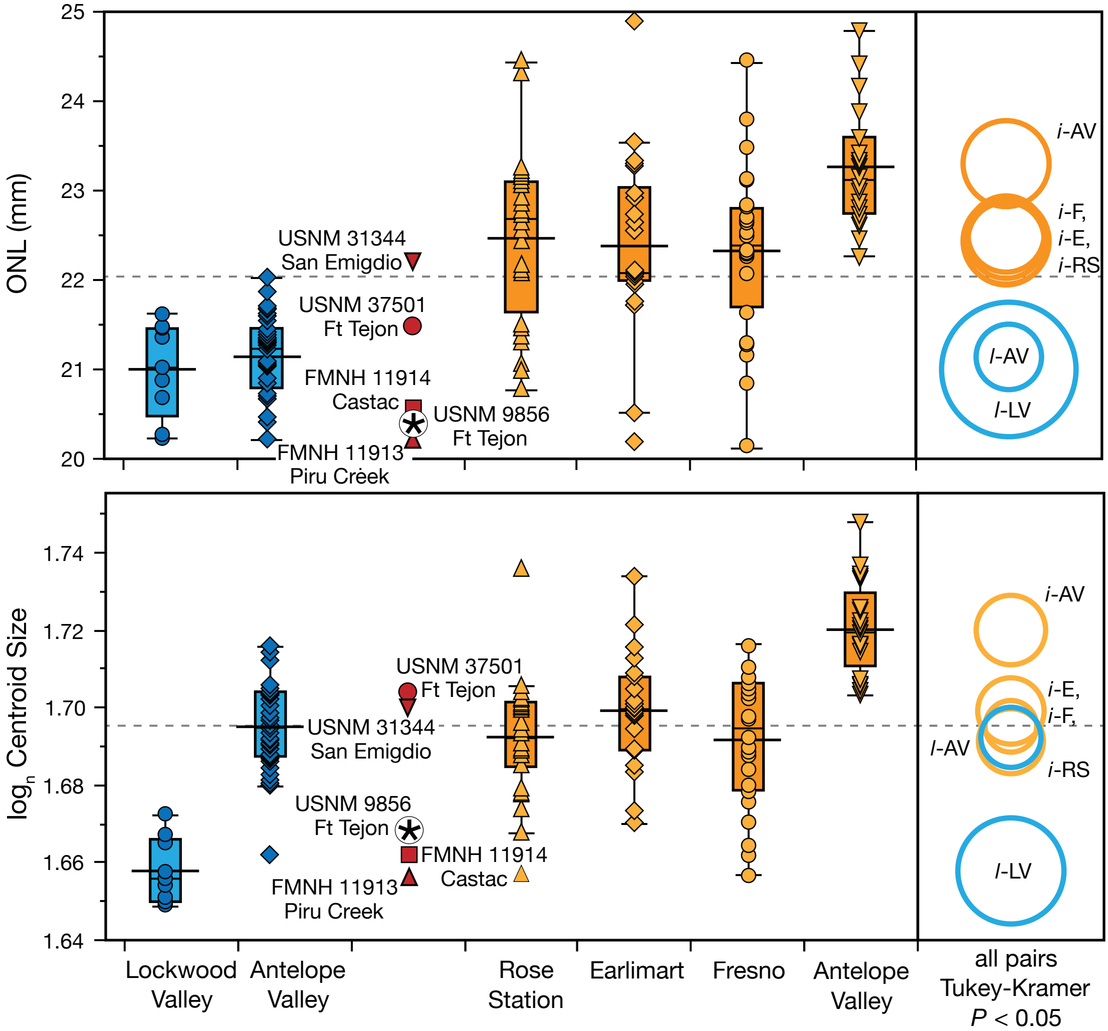

FIG. 4. Box plots of occipito-nasal length (ONL; above) and $\log_n$ centroid size (logCS; below) for the Osgood Expanded Samples (*longimembris* samples in blue; *inornatus* samples in orange), including sample means and the value placements for each of the five specimens from Fort Tejon and vicinity (white circle with star, USNM 9856/37356, the holotype of *longimembris* Coues; red circle, topotype USNM 37501; red square, Castac Lake, FMNH 11914; red triangle, Piru Creek, FMNH 11913; and inverted red triangle, San Emigdio, USNM 31344/43209; see maps, fig. 3). The right-hand box contains significant sample subsets (non-overlapping circles) derived from a post-hoc Tukey-Kramer test following the ANOVA comparing all samples (from left to right: *i*-AV = *inornatus* Antelope Valley; *i*-F = Fresno; *i*-E = Earlimart; *i*-RS = Rose Station; *l*-AV = *longimembris* Antelope Valley; *l*-LV = Lockwood Valley).

tions for samples of both species using the univariate occipito-nasal length (a measure of linear size) and centroid size (the measure of geometric scale) obtained from the landmark shape data, with pairwise comparisons derived from one-way ANOVAs followed by Tukey-Kramer post-hoc significance tests of pairwise sample means. We illustrate these distributions for the Osgood Expanded Sample of six groups in figure 4. For comparative purposes, each distribution also places the value for the five unknown specimens from the vicinity of Fort Tejon (the holotype and topotype of *longimembris* Coues and those from San Emigdio, Castac, and Piru Creek).

The shorter occipital-nasal length in the Lockwood Valley and Antelope Valley samples of *P. longimembris* compared with all samples of *P. inornatus* is consistent with Osgood's size differential hypothesis (fig. 4: box plots for ONL). However, note that for geometric size, the Antelope Valley sample of *P. longimembris* overlaps with the three San Joaquin Valley samples of *P. inornatus*, although significantly different from the *P. inornatus* Antelope Valley sample (i.e., the two have nonoverlapping confidence limits shown in the right panel). Further note that for each of the five single specimens, their values fall within and between the distributions of the original set of four Osgood Samples (those excluding the two Antelope Valley samples). The combined evidence illustrated in figure 4, while consistent with Osgood's first hypothesis, remains ambiguous for a clearly definitive decision regarding name application. The ONL of the *longimembris* holotype (USNM 9856/37356) falls within the Lockwood Valley sample and below that from Rose Valley, but the topotype (USNM 37501) is intermediate between the two sample groups. In centroid size, the holotype overlaps both distributions, but the topotype falls well within the Rose Valley sample. The three other specimens (FMNH 11913 from Piru Creek and FMNH 11914 from Castac, both localities south of Fort Tejon, and USNM 31344/43209 from San Emigdio on the floor of the San Joaquin Valley) are positioned similarly for both their ONL and centroid size values.

Note that both holotype and topotype have the narrowed interorbital region that Osgood (1900: 34) characterized as "peculiar to the San Joaquin Valley form [*P. inornatus*]." Respective measurements for the two specimens are 4.72 and 4.80 mm, both within one standard deviation of the mean for the Rose Station sample of *P. inornatus* and outside one standard deviation of the means of both the Lockwood Valley and Antelope Valley samples of *P. longimembris* (table 1, appendix 2). In a pooled *t*-test comparing each specimen to the geographically closest sample groups, the holotype is indistinguishable from the Rose Station sample ($P = 0.1979$), but significantly different from the Lockwood Valley sample ($P = 0.0431$). The topotype does not differ from either the Rose Station sample ($P = 0.0861$) or Lockwood Valley sample ($P = 0.3065$), although its IOC value falls below one standard deviation from the mean of the latter (5.07 ± 0.170 mm; appendix 2).

Multivariate Discrimination of *P. inornatus* and *P. longimembris*: We employed canonical variate analyses (CVA) on both the 18 linear measurement and landmark shape datasets. The former used $\log_{10}$ values for each variable and the latter used scores of the first 16 or 18 of the 94 PC axes generated by the analysis, which combined to explain 95.83% and 95.37% of the total variation respectively for the Osgood Expanded and Osgood samples. These PC axes were derived from the projection of Procrustes residuals in principal component space using the covariance matrix in MorphoJ. We ran analyses on both the Osgood Sample and Expanded Sample sets and illustrate the dispersion of *a priori* sample groups as well as positions of the five specimens from the vicinity of Fort Tejon (see appendix 1 and above) in biplots of CV1 and CV2 scores in figure 5 (linear variables) and figure 6 (PC shape scores). These separate pairs of analyses combine to

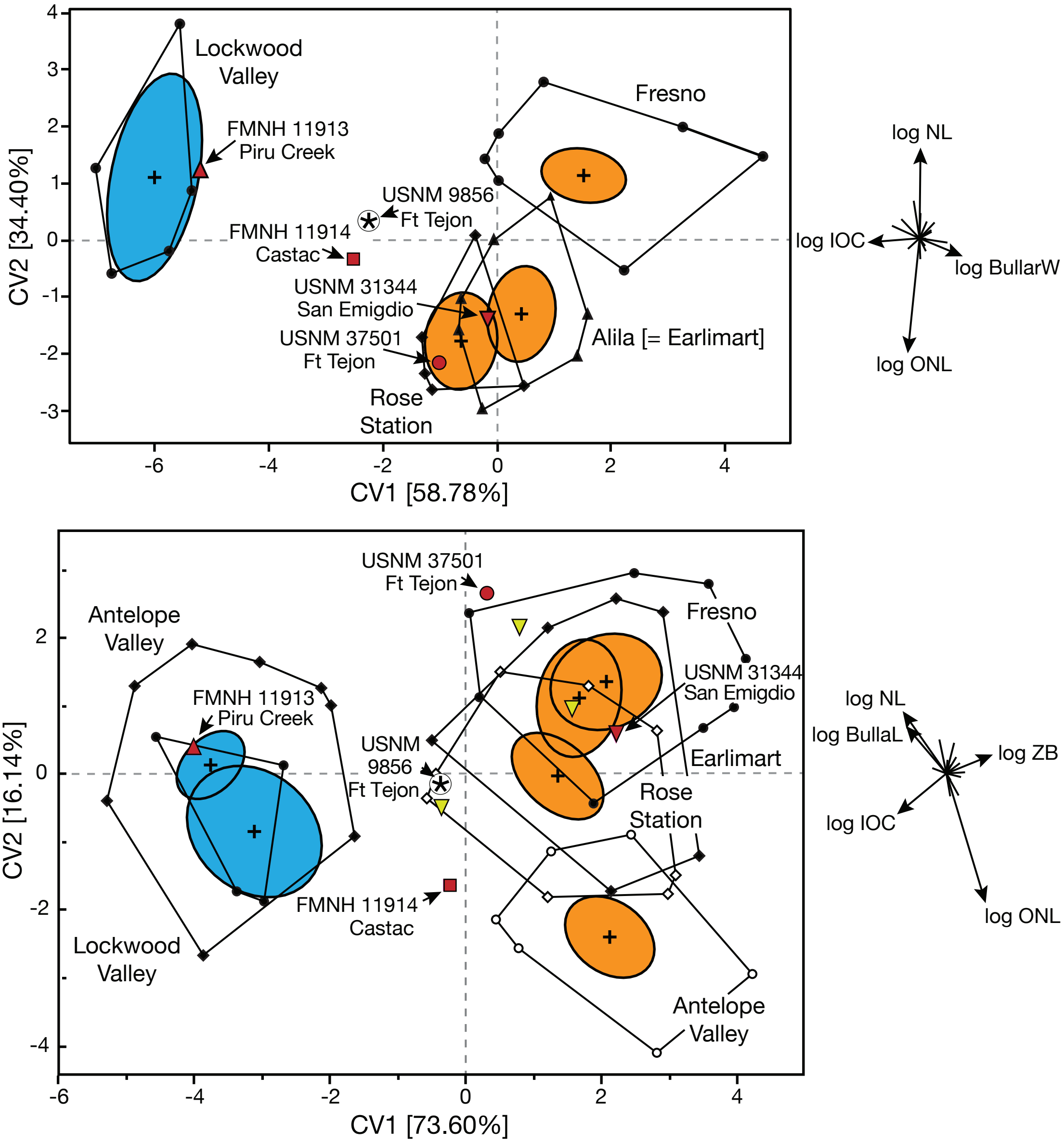

FIG. 5. Bivariate plots of sample scores on CV1 and CV2 axes derived from analyses of 18 linear measurements for the Osgood Sample (above) and Osgood Expanded Sample (below). Data are depicted as polygons connecting marginal specimen scores and 95% confidence limits around each mean (+). Panels of variable vectors that load most highly on each axis are shown to the right. The position of each of the five specimens from the vicinity of Fort Tejon mentioned by Osgood (1918) is indicated by separate symbols and museum voucher number. Inverted yellow triangles in the lower diagram are three specimens from San Emigdio trapped subsequent to Osgood's studies.

TABLE 2. Canonical analysis standardized scoring coefficients for 18 dorsal linear variables.

	Osgood Sample		Osgood Expanded Sample	
variable	CV1	CV2	CV1	CV2
$\log_{10}$ ONL	-0.7818	-2.3800	0.7708	-2.5457
$\log_{10}$ NL	0.4926	2.6941	-0.8581	1.2245
$\log_{10}$ FL	0.0281	0.8777	-0.1376	0.6671
$\log_{10}$ PL	0.2318	0.5537	0.1525	0.6013
$\log_{10}$ IPL	0.1215	-0.3204	0.2660	0.2029
$\log_{10}$ preMaxtipL	0.3259	0.1590	0.0930	0.1723
$\log_{10}$ RL	0.5408	0.7481	0.2879	-0.0715
$\log_{10}$ MaxW	0.3664	0.2012	0.2406	-0.4325
$\log_{10}$ premaxtipW	0.0934	-0.1052	0.0842	-0.1338
$\log_{10}$ IOC	-1.2698	-0.0517	-0.9694	-0.8035
$\log_{10}$ ZB	0.7674	-0.4737	0.9136	0.3711
$\log_{10}$ antParietalW	-0.0543	-0.7451	0.0223	0.2675
$\log_{10}$ IPW-ant	-0.6641	0.1103	-0.2768	0.1053
$\log_{10}$ IPW-post	0.3685	0.4099	0.0756	-0.4483
$\log_{10}$ ExOccW	0.3083	0.4262	0.1937	0.3219
$\log_{10}$ BullarW	1.0852	-0.6021	0.3672	0.0231
$\log_{10}$ BullaL	-0.8756	-0.1328	-0.7938	0.9342
$\log_{10}$ BullaW	-0.4434	-0.2916	-0.0471	0.0768
Eigenvalue	5.323	3.115	6.832	1.499
% contribution	58.782	34.401	73.597	16.143
Cumulative %	58.782	93.183	73.597	89.740

explain 93.18% or 89.74% and 86.96% or 83.60%, respectively, of the variation in the linear and shape datasets for both the Osgood Sample and Osgood Expanded Sample. We provide standardized scoring coefficients for the CVA on the linear variables and geometric shape principal components for both sample sets in tables 2 and 3, respectively.

Analyses of both datasets gave commensurate results with respect to the a priori sample groups relative to differences between both species and similarities within each. Samples of the two species are markedly disparate in multivariate space (figs. 5, 6), especially the sympatric samples from Antelope Valley. Relative to the five specimens identified by Osgood (1918) from the vicinity of Fort Tejon, three are assigned with very high posterior probabilities to one or the other of the *P. inornatus* samples, a fourth with somewhat lower posterior probabilities to *P. inornatus*, and one with very high probabilities to *P. longimembris*. For clarity, we provide mean probability assignments of these five specimens for comparison to pooled samples of both species in table 4. Of significance, the holotype of *longimembris* Coues is assigned to *P. inornatus* with posterior probabilities from 0.6439 and 0.9161 (linear variables for both Osgood sample datasets, respectively) to 1.0000 (for

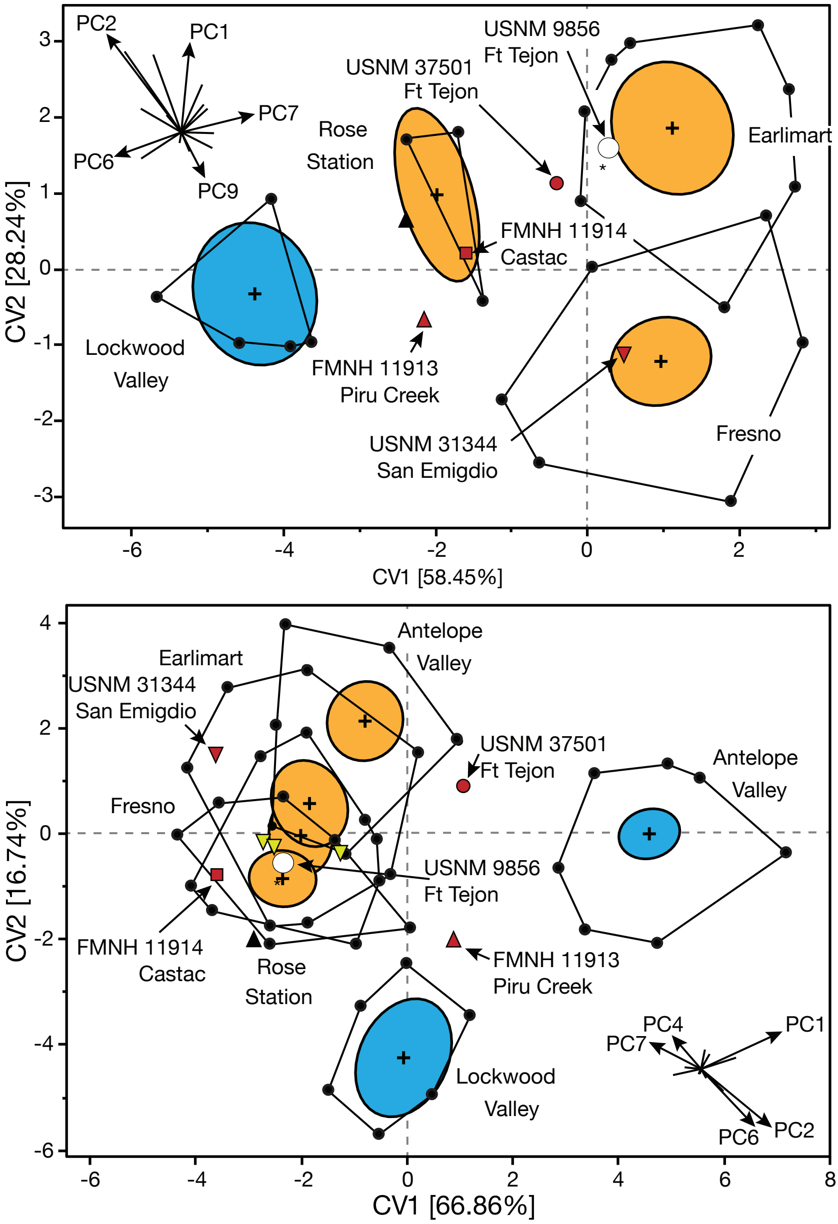

FIG. 6. Bivariate plots of sample scores on CV1 and CV2 axes derived from analyses of 25 principal component scores for the Osgood sample (above) and expanded Osgood sample (below). Sample data are depicted as polygons connecting marginal specimen scores and 95% confidence limit ellipses around each mean (+). Vectors of PC scores that influence sample positions in multivariate space are illustrated for each analysis. The position of each of the five specimens from the vicinity of Fort Tejon mentioned by Osgood (1918) is indicated by separate symbols and museum voucher number; position of the holotype of *P. longimembris* Coues (USNM 9856/37356) is indicated by the white circle with asterisk; the black triangle places the specimen from "Fort Tejon, near Rose's Station" (USNM 31388/43203). Inverted yellow triangles in the lower diagram are three specimens from San Emigdio collected subsequent to Osgood's studies.

TABLE 3. Canonical analysis standardized scoring coefficients for geometric shape principal component variables.

	Osgood Sample		Osgood Expanded Sample	
variable	CV1	CV2	CV1	CV2
PC1	0.0849	0.8821	1.0287	0.4748
PC2	-0.7303	0.9631	0.8971	-0.7437
PC3	-0.2732	0.7577	-0.0227	-0.0478
PC4	0.3025	-0.1542	-0.3700	0.4286
PC5	-0.1441	0.1677	0.4423	0.1425
PC6	-0.6575	-0.2386	0.7672	-0.6421
PC7	0.7182	0.1782	-0.6598	0.3424
PC8	-0.5519	0.7882	0.2833	-0.2803
PC9	0.2329	-0.4488	0.0491	0.2456
PC10	0.0801	-0.1871	-0.0307	-0.0662
PC11	0.2562	0.2306	0.1081	0.1886
PC12	0.3183	-0.0088	-0.3528	-0.0776
PC13	-0.0170	-0.1048	0.2169	-0.1986
PC14	-0.3906	-0.2564	0.0657	-0.1167
PC15	-0.3945	0.2300	-0.2068	0.0209
PC16	0.2190	0.2710	-0.0142	-0.0631
PC17	-0.4120	0.5433	—	—
PC18	0.2040	0.4655	—	—
eigenvalue	4.072	1.967	8.338	2.088
% contribution	58.452	28.240	66.860	16.743
cumulative %	58.452	86.963	66.860	83.602

both Osgood sample shape datasets). Moreover, the topotype (USNM 37501) is also assigned to *P. inornatus* with similar posterior probabilities (from 1.0000 or 0.9995 and 1.0000 or 0.9831 for the Osgood Sample and Expanded Sample linear and shape variables, respectively). Similar probability assignments to *P. inornatus* were obtained for the Castac Lake (from 0.8369 to 1.0000 for both datasets) and San Emigdio specimens (uniformly 1.0000 for USNM 31344/43209, between 0.9592 and 1.0000 for three additional specimens). The placement of the Piru Creek specimen is also unambiguous, with high probability (0.9558 to 1.0000) to *P. longimembris* in all four datasets. These results generally mirror the placement of each specimen in the CV biplots (figs. 4, 5).

Overall, the assignments for four of these key specimens are contrary to Osgood's view of their species membership (note: he did not explicitly mention the Piru Creek specimen although it would have been available to him among the other FMNH specimens he did examine and mention). These assignment probabilities to one or the other species are fully supported by those derived from our analysis of our larger specimen dataset (see total available sample, table 4).

TABLE 4. Posterior probability assignment of six unknown specimens to pooled species reference groups derived from canonical variates analyses of the Osgood Sample and Osgood Expanded Sample for dorsal skull linear and shape variables.

Analysis[a]	Holotype USNM 9856/37356	Topotype USNM 37501	Castac Lake FMNH 11914	Piru Creek FMNH 11913	San Emigdio USNM 31344/43209	Rose Station USNM 31338/43203[b]
Dorsal skull linear variables						
Osgood Sample N = 54	0.6439 to *P. inornatus*	1.0000 to *P. inornatus*	0.8369 to *P. inornatus*	1.0000 to *P. longimembris*	1.0000 to *P. inornatus*	1.0000 to *P. inornatus*
Osgood Expanded Sample N = 151	0.9161 to *P. inornatus*	0.9995 to *P. inornatus*	0.8445 to *P. inornatus*	1.0000 to *P. longimembris*	1.0000 to *P. inornatus*	1.0000 to *P. inornatus*
Total available sample[c] N = 561	0.9954 to *P. inornatus*	0.9904 to *P. inornatus*	0.9481 to *P. inornatus*	1.0000 to *P. longimembris*	1.0000 to *P. inornatus*	1.0000 to *P. inornatus*
Dorsal skull shape variables						
Osgood Sample N = 54	1.0000 to *P. inornatus*	0.9986 to *P. inornatus*	1.0000 to *P. inornatus*	0.6077 to *P. longimembris*	1.0000 to *P. inornatus*	0.9931 to *P. inornatus*
Osgood Expanded Sample N = 151	1.0000 to *P. inornatus*	0.7852 to *P. inornatus*	1.0000 to *P. inornatus*	0.9920 to *P. longimembris*	1.0000 to *P. inornatus*	1.0000 to *P. inornatus*
Total available sample[d] N = 563	0.9999 to *P. inornatus*	0.7141 to *P. inornatus*	0.9998 to *P. inornatus*	0.8301 to *P. longimembris*	0.9999 to *P. inornatus*	0.9891 to *P. inornatus*

[a] See text and appendix 1 for list of localities and museum voucher numbers for specimens included in both the Osgood Sample and Osgood Expanded Sample.

[b] Posterior probability when this specimen was treated as unknown rather than part of the remaining a priori *P. inornatus* sample Rose Station.

[c] The total available sample for linear variables includes 255 specimens of *P. inornatus* from 75 localities within the San Joaquin Valley and adjacent areas and 306 *P. longimembris* from 57 localities in the western Mojave Desert (data to be published elsewhere).

[d] The total available sample for shape variables includes 271 specimens of *P. inornatus* from 88 localities within the San Joaquin Valley and adjacent areas and 292 *P. longimembris* from 51 localities in the western Mojave Desert (data to be published elsewhere).

DISCUSSION

We return to the two questions stemming from Osgood's 1918 paper: (1) is the holotype of Coues's *longimembris* correctly assigned to the southern "small" species he identified and subsequently has been applied to the very widespread species universally bearing the name *P. longimembris* since 1918? and (2) do both "small" and "large" species cooccur at localities in the San Joaquin Valley, the larger of the two being *P. inornatus* Merriam?

Osgood's 1918 suggestion that *P. inornatus* and *P. longimembris* cooccurred in the southern Central Valley of California was followed by similar assertions by Grinnell (1933) and Hall (1981), among others. Williams et al. (1993) were the first, to our knowledge, to argue that only a single species, *P. inornatus*, was present throughout this region, and that *P. longimembris* was restricted to the more arid coastal and interior basins of southern California and Baja California, western Sonoran Desert in southeastern California, southwestern Arizona, and coastal Sonora, Mexico, and throughout the Mojave and Great Basin deserts of the interior western

United States. Osgood's interpretation has been followed by virtually all subsequent authors including the most recent taxonomic assessments (e.g., Patton, 2005, Hafner, 2016).

Our review of character diversity in both univariate and multivariate comparisons reveals substantial variation among those samples of *P. inornatus* available to Osgood, as well as additional specimens not available to him. However, while Osgood was correct in that his samples from the San Joaquin Valley included both small and large individuals, we believe he was mistaken in his interpretation of what that size spread actually meant. A single sample containing a mixture of two species, one small and the other large, should exhibit a bimodal distribution for differentiating individual variables, but this is not what we found. Our statistical comparisons of value distributions under normal unimodal versus bimodal models reject Osgood's two species hypothesis in every case, whether San Joaquin samples are treated separately or pooled. The Akaike information criterion (AICc, an estimator of prediction error, or the relative quality of a statistical model) weights for a unimodal distribution average 0.899 (on a scale from 0 to 1) for the set of univariate characters Osgood used to distinguish the two species (table 1). This result contrasts with a similar model comparison for the Antelope Valley where both occur (fig. 3A). Here, the bimodal distribution model has an average AICc weight of 0.999 compared to a unimodal one. There are small and large individuals in samples of *P. inornatus* from most localities where the species has been collected, but these are only at the extreme ends of a continuous, unimodal distribution. Interestingly, while young individuals are included in each *P. inornatus* sample, age as defined by toothwear classes is not a significant contributor to the sample variance. In least squares analyses with age a covariate, only four of the 48 variable-by-sample combinations were significant by ANOVA tests, each of which disappeared with application of the Bonferroni correction for multiple comparisons. Osgood's hypothesis that two species occur throughout the San Joaquin Valley is unsupported by current evidence.

The question of Osgood's assessment that Coues' holotype represents the smaller species is a more difficult one, in part because the answer may have considerable taxonomic implications. The results of canonical variate analytical assignments, both the pictorial placement of the unknown specimens in figures 5 and 6 and their posterior probabilities of assignment (table 4) indicate that Osgood erred in 1918 by changing his earlier (1900) assignment of names. The holotype of *longimembris* Coues is positioned within, or closer, to samples of *P. inornatus* examined by Osgood from the southern and eastern San Joaquin Valley, and it is consistently assigned to those samples by their posterior probabilities, but not to the sample he treated as *P. longimembris*. Although we were unable to confirm this morphological assignment by molecular evidence, our morphological analyses strongly support Osgood's original (1900) name assignments.

Reversing Osgood's 1918 application of both *longimembris* Coues and *inornatus* Merriam to his earlier 1900 position requires overturning uncontested usage of these names over the past century. Doing so would clearly threaten nomenclatural stability and universality, core principals underlying the International Code of Zoological Nomenclature. Therefore, pursuant to Article 75.6 of the Code (ICZN, 1999), the specific goal of which is to conserve prevailing usage by designating a neotype to replace the original type, we hereby propose to designate MVZ 232023, a postreproductive adult female (age class 3) *Perognathus longimem-*

FIG. 7. Neotype MVZ 232023: At left, dorsal (above) and ventral (below) views of the skull with scale bar = 1 cm; at right, dorsal view of study skin.

bris, collected at 7.4 mi N Willow Springs, Kern County, California (34.98466N, 118.30149W [WGS84 datum], 3179 ft elevation) by James L. Patton (original number 26354) on 9 April 2015. This locality is within the Antelope Valley, that part of the distribution of *P. longimembris* currently recognized as closest geographically to Fort Tejon, the locality assigned to Coues's holotype. The neotype we propose is a museum study skin and cleaned cranium, mandibles, and postcranial skeleton in excellent condition (dorsal and ventral views of the skull and dorsal view of the skin in fig. 7), and liver tissue preserved and maintained in liquid nitrogen. We have requested the International Commission on Zoological Nomenclature to use its plenary power to accept the neotype proposed herein to replace USNM 9856/37356 as the name bearing type of *longimembris* Coues, 1875 (Patton and Gardner, in review).

RESULTING SIMPLE SYNONYMY

Perognathus inornatus Merriam, 1889

Perognathus inornatus Merriam, 1889: 15; type locality "Fresno, [Fresno County,] California."

Perognathus longimembris neglectus Taylor, 1912: 155; type locality "McKittrick, Kern County, California, altitude 1111 feet."

Perognathus inornatus neglectus: Osgood, 1918: 96; first use of current name combination.

Perognathus longimembris psammophilus von Bloeker, 1937: 153; type locality "west side of Arroyo Seco Wash, 150 feet altitude, four miles south of Soledad, Monterey County, California."

Perognathus inornatus psammophilus: Williams, Genoways, and Braun, 1993: 177; first use of current name combination.

Perognathus inornatus sillimani von Bloeker, 1937: 154; type locality "west side of Arroyo Seco Wash, 150 feet altitude, four miles south of Soledad, Monterey County, California"; synonym of *P. i. psammophilus* (Williams et al., 1993).

Perognathus longimembris (Coues, 1875)

O[*tognosis*]. *longimembris* Coues, 1875: 305; type locality "Fort Tejon, [Kern County,] Cal[iforni]a.;" neotype MVZ 232023 proposed herein from "7.4 mi N Willow Springs, Kern Co., California, 3170 feet" (pending Commission ruling).

Perognathus nevadensis Merriam, 1894: 264; type locality "Halleck, East Humboldt Valley, [Elko County,] Nevada."

Perognathus longimembris panamintinus Merriam, 1894: 265; type locality "Perognathus Flat, Panamint Mts., California" (further refined by Grinnell [1933: 148] to "Perognathus Flat, altitude 5200 feet, near Emigrant Gap [= near B.M. 4899, 2 miles northwest of Harrisburg, on U.S.G.S. Ballarat Quadrangle, edition of March 1913] Panamint Mountains, Inyo County, California"); now Harrisburg Flat, Death Valley National Park.

Perognathus pacificus Mearns, 1898: 299; type locality "from the edge of the Pacific Ocean, at the last Mexican boundary monument (No. 258) [San Diego County, California)."

Perognathus longimembris bangsi Mearns, 1898: 300; type locality "Palm Springs, Colorado Desert, [Riverside County,] southern California."

Perognathus panamintinus arenicola Stephens, 1900: 153; type locality "San Felipe Narrows, San Diego Co[unty]., California."

Perognathus panamintinus brevinasus Osgood, 1900: 30; type locality "San Bernardino, [San Bernardino County,] Cal[ifornia]."

Perognathus elibatus Elliot, 1904: 252; type locality "Mount Pinos, Los Angeles County, California, altitude 5,000 feet" (further refined by Grinnell [1933: 147] to "Lockwood Valley, 5500 feet altitude, near Mount Pinos, Ventura County, California)."

Perognathus pericalles Elliot, 1904: 252; type locality "Keeler, Owens Lake, Inyo County, California."

Perognathus bombycinus Osgood, 1907: 19; type locality "Yuma, [Yuma County,] Arizona."

Perognathus longimembris arenicola: Osgood, 1918: 96; first use of current name combination.

Perognathus longimembris brevinasus: Osgood, 1918: 96; first use of current name combination.

*Perognathus longimembris aestivu*s Huey, 1928: 87; type locality "Sangre de Cristo in Valley San Rafael on the western base of the Sierra Juarez, Lower [Baja] California, Mexico (upper Sonoran zone), lat. 31°52′ north, long. 116° 06′ west.

Perognathus longimembris venustus Huey, 1930: 233; type locality "San Agustín, Lower [Baja] California, Mexico, lat. 30° north, long. 115° west."

Perognathus longimembris arizonensis Goldman, 1931: 134; type locality "10 miles south of Jacobs Pools, Houserock Valley, north side of Marble Canyon of Colorado River, Arizona (altitude 4000 feet)."

Perognathus longimembris cantwelli von Bloeker, 1932: 128; type locality "Hyperion, Los Angeles County, California."

Perognathus longimembris elibatus: Grinnell, 1933: 147; as synonym of *P. l. longimembris* (Coues).

Perognathus longimembris pericalles: Grinnell, 1933: 147; as synonym of *P. l. longimembris* (Coues).

Perognathus longimembris nevadensis: Grinnell, 1933: 147; first use of current name combination.

Perognathus longimembris bombycinus: Grinnell, 1933: 147; first use of current name combination.

Perognathus longimembris pacificus: Grinnell, 1933: 149; first use of current name combination.

Perognathus longimembris kinoensis Huey, 1935: 73; type locality "Bahia Kino, Sonora, Mexico (more precisely – from the northern end of the sand dune peninsula that borders the bay and forms the northern arm of the estuary)."

Perognathus longimembris arcus Benson, 1935: 451; type locality "Rainbow Bridge, San Juan County, Utah."

Perognathus longimembris pimensis Huey, 1937: 355; type locality "11 miles west of Casa Grande, Pinal County, Arizona."

Perognathus longimembris tularensis Richardson, 1937: 510; type locality "one mile west of Kennedy Meadows, 6000 feet, South Fork Kern River, Tulare County, California."

Perognathus longimembris salinensis Bole, 1937: 3; type locality "1 Mi. N. of Salt Camp, elev. 1060 feet, on the west edge of the salt lake, Saline Valley, Inyo County, California."

Perognathus longimembris internationalis Huey, 1939a: 47; type locality "Lower California side of the International Boundary at Jacumba, San Diego County, California."

Perognathus longimembris virginis Huey, 1939b: 55; type locality "Saint George, Washington County, Utah, altitude 2950 feet."

Perognathus longimembris gulosus Hall, 1941: 55; type locality "near [1/4 mi. S.] Smith Creek Cave, 5800 feet, Mount Moriah, White Pine County, Nevada."

ACKNOWLEDGMENTS

This work could not have been done without the hospitality of curators and collection managers of the museums who allowed us to examine specimens under their care, notably Darrin Lunde (National Museum of Natural History), Lawrence Heaney (Field Museum of Natural History), Joseph Cook and Jon Dunnum (Museum of Southwestern Biology, University of New Mexico), Eric Rickart (Utah Museum of Natural History), Jim Dines, Shannen Robson, and Kacey Bell (Natural History Museum of Los Angeles County), Duke S. Rogers (Monte L. Bean Natural History Museum, Brigham Young University), Philip Unitt and Scott Tremor (San Diego Museum of Natural History), Philip Myers and Cody Thompson (University of Michigan Museum of Zoology), Mark Omura (Museum of Comparative Zoology, Harvard University), and Krista Fahey (Santa Barbara Museum of Natural History). We thank Lawrence Heaney, Robert Voss, and an anonymous reviewer for comments that greatly improved the final manuscript. J.L.P. is especially grateful to David Laabs and Mark Allaback, Biosearch Environmental Consulting, for securing most of the specimens of *P. inornatus* from the Antelope Valley.

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APPENDIX 1

Specimens Examined

Locality, sample size, and voucher specimen numbers organized by sample groups (see fig. 3A, B) used in all morphometric analyses. The Osgood Sample included only specimens from the USNM and FMNH; the Osgood Expanded Sample included all specimens listed. Specimens listed as unknowns are those treated as such in canonical variates analyses.

Perognathus inornatus

Fresno (N = 24)

CALIFORNIA. —FRESNO CO.; Fresno (N = 23, MVZ 19068; USNM 22737, 13394/23790 [holotype of *inornatus* Merriam], 43812–43813, 43815–43816, 47678, 54717, 54719–54724, 54782, 54784–54785, 93722–93727); ca. 2 mi W Lanes Bridge, 10 mi N Fresno (N = 1, MVZ 14488).

Earlimart (N = 22)

CALIFORNIA. —KERN CO.; Delano (N = 4, USNM 41787, 41789, 115896, 116112). TULARE CO.; Alila (=Earlimart) (N = 9, USNM 43204–43205, 126384, 126397, 127164, 127166, 127557, 149799–149800); Earlimart (N = 4, MVZ 14500-14502, 14504); 1 mi N Earlimart (MVZ 28362); 2.7 mi SW Earlimart (N = 1, MVZ 182257); Pixley National Wildlife Refuge (N = 2, MVZ 182713–182714); Tipton (N = 2, MVZ 14494, 14499).

Rose Station (N = 28)

CALIFORNIA. —KERN CO.; Fort Tejon, near Rose's Station (N = 1, USNM 31338/43203); Ft Tejon, Rose Station (N = 7, FMNH 11951, 11955–11956, 11958, 11960, 11962-11963); Rose Station (N = 19, MVZ 44290–44294, 44296–44299, 44301–44304, 44307–44309, 47391, 47393); 1.5 mi SSW Rose Station (N = 1, MVZ 200076).

Antelope Valley (N = 22)

CALIFORNIA. —KERN CO.; 5 mi E California City (N = 1, MVZ 158772); Mojave (N = 1, LACM 3136); 0.7 mi E Monolith, Tehachapi Mts. (N = 3, MVZ 231955–231957); 1 mi E Monolith, Tehachapi Mts. (N = 8, MVZ 231958, 231960, 231963–231964, 231967, 231969, 231973, 231979); 2 mi SW Monolith (N = 1, LACM 48809); 4 mi SW Monolith (N = 1, LACM 48810); 7 mi N and 9 mi E Rosamond (N = 2, MVZ 184638–184639); 11 mi E Rosamond (N = 1, MVZ 182539); 5.5 mi E & 6 mi W Randsburg (N = 3, MVZ 182540–182541, 184643). LOS ANGELES CO.; 1 mi S Peck's Butte (N = 1, MVZ 44317).

Perognathus longimembris:

Lockwood Valley (N = 9)

CALIFORNIA. —VENTURA CO.; Lockwood Valley (N = 3, MVZ 239563–239565); Mt. Pinos, Lockwood Valley (N = 6, FMNH 11971 [holotype of *elibatus* Elliot], 11973–11975, 11977, 11979).

Antelope Valley (N = 39)

CALIFORNIA. —KERN CO.; 5 mi E California City (N = 5, MVZ 158769, 158771, 158774, 158776, 158779); Mojave (N = 1, LACM 3144); 3 mi N Mojave (N = 6, MVZ 185799, 158803–158805, 158807, 158811); 7.4 mi N Willow Springs (N = 2, MVZ 232023-232024). LOS ANGELES CO.; 2 mi NW Palmdale (N = 3, MVZ 42177, 42179–42180); 18 mi E Palmdale [Lovejoy Butte] (N = 3, MVZ 125712, 125713, 125714); 1 mi S Peck's Butte, Mohave Desert (N = 3, MVZ 44318–44319, 44324); 3 mi S Peck's Butte, Mohave Desert (N = 15, MVZ 42147–42149, 42151–42152, 42154, 42160–42161, 42163–42165, 42169, 42172, 42174–42175); 4.5 mi NE Shoemaker (N = 1, MVZ 42175).

Unknowns (N = 8)

CALIFORNIA. —KERN CO.; Castac Lake, Ft Tejon (N = 1, FMNH 11914); Fort Tejon (N = 1, USNM 37501); Fort Tejon, Canyon de las Uvas [=Grapevine Canyon], Tehachapi Mts (N = 1, USNM 9856/37356 [holotype of *longimembris* Coues]); San Emigdio (N = 1, USNM 31344/43209); San Emigdio Canyon bajada (N = 2, MVZ 231985–231986); San Emigdio Creek (N = 1, MVZ 28354); LOS ANGELES CO.; Piru Creek, Bailey's Ranch (N = 1, FMNH 11913).

APPENDIX 2

Cranial Measurements (mm) for Six a Priori Groups in the Osgood Expanded Sample[a]

Variable[b]	*P. longimembris* Lockwood Valley[c] N = 9	*P. longimembris* Antelope Valley[c] N = 38	*P. inornatus* Fresno[c] N = 24	*P. inornatus* Earlimart[c] N = 22	*P. inornatus* Rose Station[c] N = 28	*P. inornatus* Antelope Valley[c] N = 22
ONL	20.99 ± 0.523 20.23–21.62	21.14 ± 0.444 15.30–16.26	22.34 ± 0.965 20.13–24.45	22.36 ± 1.003 20.16–24.86	22.44 ± 0.924 20.75–24.42	23.23 ± 0.636 22.25–24.77
NL	7.51 ± 0.357 6.93–7.93	7.62 ± 0.241 7.15–8.02	8.00 ± 0.528 6.84–9.09	7.83 ± 0.656 6.55–9.67	7.88 ± 0.559 6.88–8.63	8.35 ± 0.466 7.73–9.55
IOC	5.07 ± 0.170 4.83–5.33	5.12 ± 0.199 4.60–5.55	4.65 ± 0.234 4.39–5.34	4.79 ± 0.235 4.32–5.28	4.92 ± 0.220 4.57–5.42	5.17 ± 0.203 4.90–5.46
antPrietalW	7.09 ± 0.299 6.73–7.73	7.11 ± 249 6.40–7.68	7.04 ± 0.459 6.34–8.80	7.15 ± 0.324 6.54–7.94	7.21 ± 0.316 6.67–8.31	7.26 ± 0.229 6.86–7.76
BullarW	11.59 ± 0.335 11.17–12.06	11.91 ± 0.280 11.30–12.37	12.37 ± 0.553 11.44–14.25	12.53 ± 0.487 11.68–13.42	12.45 ± 0.509 11.65–13.74	12.64 ± 0.268 12.15–13.19
BullaW	2.18 ± 0.160 1.92–2.43	2.45 ± 0.160 2.12–2.95	2.35 ± 0.219 1.83–2.71	2.59 ± 0.297 1.90–3.33	2.56 ± 0.208 2.19–3.03	2.48 ± 0.242 1.97–2.83
Ratio BullaW / BullaL × 100	29.11 ± 1.250 27.13–31.23	31.19 ± 1.669 28.23–34.87	30.06 ± 2.255 25.53–33.72	32.26 ± 2.778 26.01–39.15	32.52 ± 2.477 28.46–36.98	31.54 ± 2.247 26.25–34.20
Ratio IOC / ONL × 100	24.14 ± 0.737 22.88–24.83	24.22 ± 1.004 22.23–26.83	20.84 ± 0.917 19.14–22.38	21.45 ± 1.046 19.90–24.09	21.91 ± 0.729 20.20–23.50	22.26 ± 0.719 21.25–23.92

[a] See appendix 1 for sample provenance data and voucher specimen catalog numbers.

[b] Those variables identified by Osgood (1918) that distinguish the skulls of *P. longimembris* from *P. inornatus* (see table 1 and text).

[c] Sample name and sample size (N); values for each variable are the mean plus or minus one standard deviation with range below.