

Perognathus inornatus. By Troy L. Best

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Perognathus inornatus Merriam, 1889

San Joaquin Pocket Mouse

Perognathus inornatus Merriam, 1889:15. Type locality "Fresno [Fresno Co.—Miller, 1912:264], California."

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciurognathi, Superfamily Geomyoidea, Family Heteromyidae, Subfamily Perognathinae, Genus *Perognathus*. There are nine species of *Perognathus*. Three subspecies of *P. inornatus* are recognized (Williams et al., 1993):

P. i. inornatus Merriam, 1889:15, see above.

P. i. neglectus Taylor, 1912:155. Type locality "McKittrick, Kern County, California, altitude 1111 feet."

P. i. psammophilus Von Bloeker, 1937:153. Type locality "west side of Arroyo Seco Wash, 150 feet altitude, four miles south of Soledad, Monterey County, California" (*sillimani* Von Bloeker is a synonym). Originally, *psammophilus* was described as a subspecies of *P. longimembris* (Von Bloeker, 1937), but Williams et al. (1993) referred *psammophilus* to *P. inornatus* and synonymized *sillimani* with *psammophilus*.

DIAGNOSIS. *Perognathus inornatus* (Fig. 1) is similar phenetically to *P. amplus* (Best, 1993). No single character of skin or skull is known that can distinguish all individuals of *P. inornatus* from *P. amplus*. However, *P. amplus* averages larger than *P. inornatus* in most dimensions, has a relatively longer and more penciled tail, and an interorbital breadth >5.1 mm (average, 5.3–5.6 mm), whereas interorbital breadth in *P. inornatus* averages 4.8–4.9 mm, and rarely exceeds 5.1 mm (Williams et al., 1993). These two species are allopatric (Hall, 1981).

Distinguishing between *P. inornatus* and *P. longimembris* requires examination of fully adult specimens, because these species are so similar (Hall, 1981; Osgood, 1918). *P. inornatus* is distinguished from *P. longimembris* by larger size (Merriam, 1889) and relatively shorter and less-penciled tail. The interorbital region of *P. inornatus* is relatively narrower, but there is broad overlap in absolute measurements. *P. inornatus* may be sympatric with *P. alticolus* and *P. parvus*. From these two species, *P. inornatus* differs in having a less-penciled tail, smaller average size (length of hind foot usually is <21 mm compared with ≥ 21 mm), relatively larger mastoid bullae, greater mastoid breadth, and relatively narrower interparietals. From the allopatric species *P. fasciatus*, *P. flavescens*, *P. flavus*, and *P. merriami*, *P. inornatus* differs in having a slightly penciled tail averaging longer than head and body, whereas the tails of the other species lack pencils and average shorter than head and body (Williams et al., 1993).

GENERAL CHARACTERS. *Perognathus inornatus* is a medium-sized *Perognathus*, with a slightly penciled tail that averages longer than length of head and body (Williams et al., 1993). The ear is small with no antitragal lobe. The posterior one-third of the sole of the hind foot is haired, the pelage is soft, and the vibrissae are rather short (Merriam, 1889). The upperparts are ochraceous buff to pinkish overlaid with blackish hairs; the extent of overlay determines the overall tone in the various subspecies. The lateral line is moderately well marked, underparts are white, and the tail is faintly bicolored (Hall, 1981).

The skull (Fig. 2) is flattened and the interorbital region is narrow. The mastoids are greatly swollen and project considerably behind the plane of the occiput (mastoid breadth is 55.6% of occipitonasal length). The auditory bullae meet anteriorly in symphysis. The interparietal is small and squarish-pentagonal in shape with sharp angles (length of interparietal is 84.8% of breadth). The nasals fall considerably short of the nasal branch of the premaxillaries. The mastoid border of the parietal is longest. The coronoid process of the mandible

is relatively large. The lower premolar is about the size of the last molar, its crown is squarish, and it is narrower externally than internally (Merriam, 1889). The dorsal profile of the skull is relatively flat (Williams et al., 1993).

Length of head and body averages 70–75 mm, ratio of length of tail to head and body averages 1.0–1.1, interorbital breadth ranges from 4.8 to 5.7 mm and averages 4.9–5.1, and width of interparietal ranges from 3.3 to 4.7 mm, averaging 3.6–3.9 (Williams et al., 1993). Average measurements (in mm) of 20 adult males and 20 adult females, respectively, from throughout the range of the species are: total length, 148.8, 146.6; length of body, 72.6, 72.1; length of tail, 76.2, 74.5; length of hind foot, 19.6, 19.4; length of ear, 7.8, 7.4; basal length of cranium, 14.5, 14.2; greatest length of cranium, 23.6, 23.0; spread of maxillary arch, 11.7, 11.3; interorbital width, 5.2, 5.2; nasal length, 8.9, 8.5; intermaxillary width, 4.2, 4.2; alveolar length, 3.4, 3.4; lacrimal length, 1.7, 1.4; width of maxillary arch, 1.1, 1.1; basioccipital length, 3.8, 3.7; greatest depth of cranium, 7.7, 7.8; greatest width of cranium, 13.1, 13.0; zygomatic width, 12.1, 11.8; nasal width, 2.4, 2.4 (Best, 1993). Mass has been reported as 7.0–12.0 (Kooos, 1979) and 7.6–8.0 g (Warner, 1976); in captivity, mass by reach 13.0–17.4 g (average, 14.6—Chew et al., 1965). Males are significantly larger than females in spread of maxillary arch, nasal length, and lacrimal length (Best, 1993).

Subspecies of *P. inornatus* differ in size of body, relative length of tail, coloration, and in characters of the cranium (Von Bloeker, 1937). In addition, *P. i. inornatus* from the eastern side and floor of the San Joaquin Valley in Fresno, Kern, Kings, Madera, and Stanislaus counties has 50 chromosomes and differs structurally from San Joaquin pocket mice from the western side of the San Joaquin Valley and areas to the west in Alameda, Fresno, Kern, Merced, San Benito, San Luis Obispo, and San Joaquin counties. Individuals of the western population (*P. i. neglectus*) have 56 chromosomes and generally are larger, with relatively longer tails. One *P. inornatus* from Lake Co. in the Sacramento Valley region had 60 chromosomes, but no other population from that region has been examined cytologically (Williams et al., 1993).

DISTRIBUTION. The San Joaquin pocket mouse occupies westcentral California, ranging from the upper Sacramento Valley, Tehama Co., southward through the San Joaquin and Salinas valleys and contiguous areas to the Mojave Desert in Los Angeles, Kern, and extreme western San Bernardino counties. It also occupies the Tehachapi Mountains and the foothills of the western Sierra Nevada below ca. 600 m (Fig. 3; Williams et al., 1993).

FOSSIL RECORD. The genus *Perognathus* is known from the



FIG. 1. A male *Perognathus i. inornatus* from Bakersfield, Kern Co., California. Photograph courtesy of D. F. Williams.

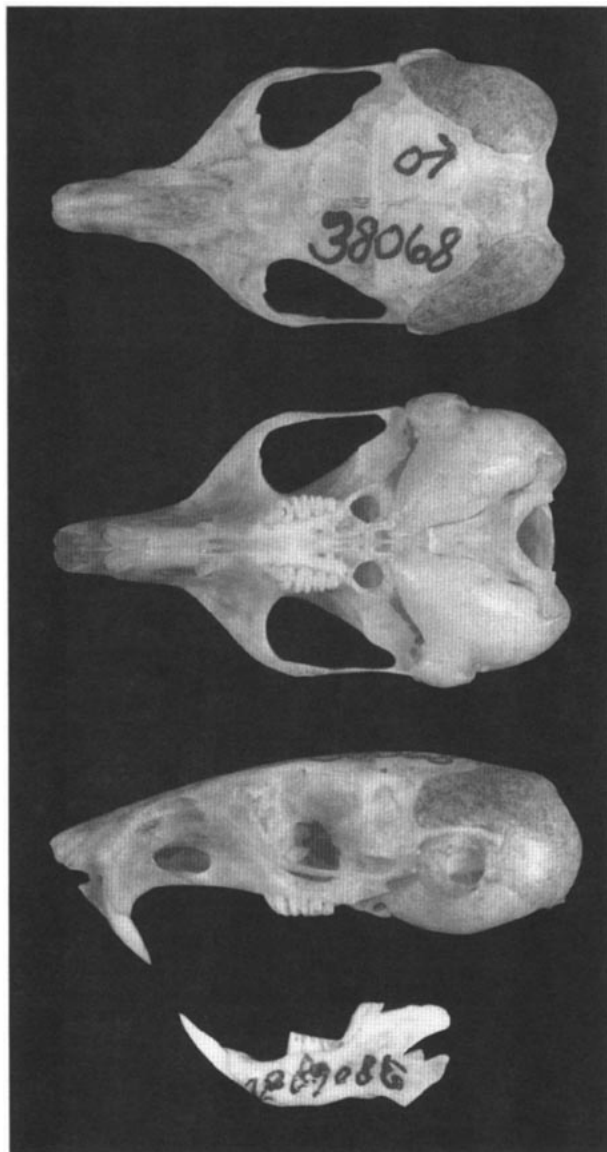


FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Perognathus i. inornatus* from near La Grange, 150 m, Stanislaus Co., California (male, University of New Mexico Museum of Southwestern Biology 38068). Greatest length of cranium is 24.1 mm. Photographs by T. H. Henry.

Miocene (Wood, 1935). However, the only fossils that may be referable to *P. inornatus* are from a Pleistocene deposit at McKittrick, Kern Co., California (Schultz, 1938).

FORM AND FUNCTION. As in all *Perognathus*, the dental formula is $i\ 1/1, c\ 0/0, p\ 1/1, m\ 3/3$, total 20 (Ingles, 1965). *P. inornatus* has external fur-lined cheekpouches on each side of the mouth. The forefeet are used to hold food materials and to thrust these into the cheekpouches. When the cheekpouches are filled with food, *P. inornatus* deposits the food in its burrow for use in times when the weather is too cold or rainy to venture forth (Grinnell and Storer, 1924). Locomotion involves all four feet (Hatt, 1932).

The pelage has no bristles or spines (Ingles, 1965). The pale region of dorsal guard hairs is ≥ 3 mm in length. Shafts of these hairs are up to 45–47 μm in width (Mayer, 1952).

The San Joaquin pocket mouse has a diel metabolic rhythm (Lindberg and Chew, 1964). Even under conditions of 10°C, dry air, continuous darkness, and no food, it showed circadian metabolic rhythms. At 10°C without food, frequency and extent of hypometabolism varied inversely with body mass. When kept without food at 10°C, in continuous darkness, and in air saturated with water vapor there was a rhythm with 21–25-h intervals (average, 23.2

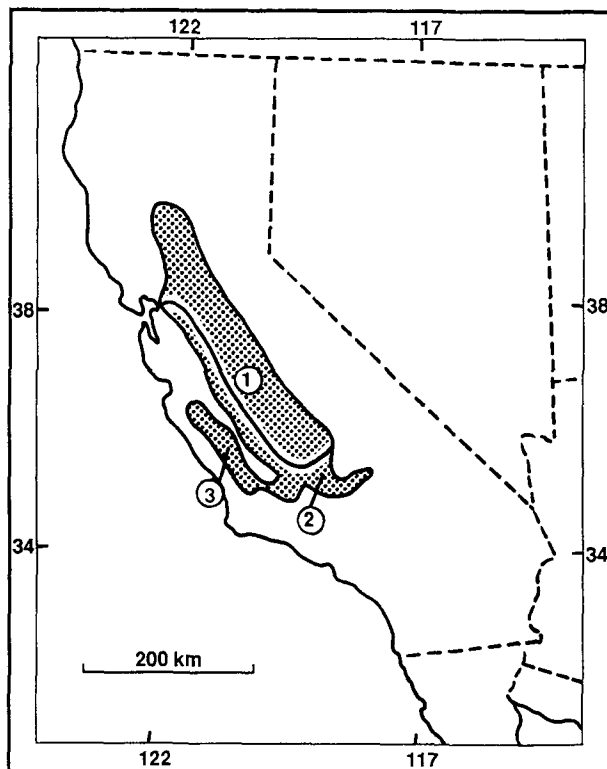


FIG. 3. Distribution of *Perognathus inornatus* in California: 1, *P. i. inornatus*; 2, *P. i. neglectus*; 3, *P. i. psammophilus* (Williams et al., 1993).

h). After the 3rd day, a lessening of the synchronization of animals disrupted the clear-cut rhythm. There was a 100% incidence of deep hypometabolism and a progressive decline in the metabolic peak each day as a result of failure of some animals to arouse daily (Chew et al., 1965).

When field-caught and caged in a laboratory for many months, San Joaquin pocket mice may not survive freezing temperatures without nesting material, unless they are first acclimatized to low temperatures. When the temperature suddenly is lowered ca. 30°C and to below freezing, they are likely to die with little loss of mass. *P. inornatus* died during the 1st night when temperature was reduced to -7°C (Howard, 1951).

The parenchymal cells of the pancreatic islets contain alpha and beta types; there are no other chromophilic cells. Beta granules are moderate in abundance and there are central and partly scattered cords of alpha cells among the beta cells. Of 1,000 chromophil cells, 25% were of the alpha type. In samples of tissue from retro-splenic and juxta-intestinal sites of the pancreas, the retro-splenic pancreas had a higher alpha-cell ratio (32 compared with 18%, respectively). Since these differences were found in only one animal, their significance is unknown. Mitoses were observed in two areas of the islets, most commonly along the periphery, and sometimes in the boundary between alpha and beta cellular zones. None of the mitotic cells contained beta granules, and it was uncertain whether a few of them contained alpha granules (Quay, 1960).

The shaft of the baculum tapers from the enlarged base to a pointed upturned tip. Average and range of bacular measurements (in mm) are: length, 6.4 (6.0–6.6); height of base, 0.8 (0.6–1.2—Burt, 1960).

ONTOGENY AND REPRODUCTION. The San Joaquin pocket mouse breeds from March to July. At least two litters of four to six young are produced each year (Jameson and Peeters, 1988). The estrus cycle is 5–6 days in length (Eisenberg, 1967b). At Snelling, Merced Co., two females had two and six embryos, respectively, on 26 May. On 29 May at the same locality, a nearly full-grown young-of-the-year in immature, bluish-tinged, and soft pelage was observed (Grinnell and Storer, 1924).

ECOLOGY. *Perognathus inornatus* inhabits arid, annual grassland, savanna, and desert-shrub associations (Williams et al., 1993), with sandy washes (Von Bloeker, 1937), fine-textured soils, grassy or weedy ground (Grinnell, 1933), and sites with sagebrush (*Artemisia*), sage (*Salvia*), filaree (*Erodium*), oats (*Avena*), and brome grass (*Bromus*—Eisenberg, 1963). At the northern extreme of its range in Lake Co., it occurs on a rocky south-facing slope in chamise (*Adenostoma fasciculatum*) and buck brush (*Ceanothus cuneatus*) chaparral at an elevation of 420 m (Slayden, 1985). In San Benito Co., it occurs in hilly areas with various amounts of plant cover, density of Mormon tea (*Ephedra*) reaching 5.6–9.2 plants/ha, a number of rock outcrops, and narrow watercourses (Hawbecker, 1951). On the Carrizo Plain, *P. inornatus* occurs in habitats where soils primarily are sandy loam. Summer high temperatures there often reach 40°C and winter lows rarely are less than –10°C. Rainfall averages <15 cm/year. The plain is dominated by annual herbs such as red-stemmed filaree (*Erodium cicutarium*), fiddleneck (*Amisackia intermedia*), locoweed (*Astragalus oxyphysus*), and species of grasses in the genus *Bromus*. Nearby hillsides support scattered shrubs, including saltbush (*Atriplex*) and Mormon tea. Green herbage is available for only a few weeks in winter and early spring; dry brome grass is present for the remainder of the year (Braun, 1985).

At the San Joaquin Experimental Range, Madera Co., density was 0.40/ha (Horn and Fitch, 1942). The number of *P. inornatus* may be lower on areas grazed by cattle (Howard, 1953), but in Fresno Co., density on a site grazed by cattle was 7.3/ha and 5.0/ha on ungrazed sites. In this alkali-sink community, its average home range on sites grazed by cattle was 148 m² (range, 0–333 m²) and 258 m² (range, 0–385 m²) on ungrazed sites; home ranges on ungrazed sites were significantly larger. Sex ratio varied from 2.5 males:1 female on sites grazed by cattle to 3.0:1 on ungrazed sites (Warner, 1976).

The burrows are conspicuous in the low grass (Eisenberg, 1963). As in other pocket mice, its small burrows are 2–3 cm in diameter, usually in sandy soil near bases of bushes. Occupied burrows are plugged with earth during the daytime (Grinnell and Storer, 1924). It routinely builds a nest (Eisenberg, 1963) and will inhabit burrows of *Dipodomys heermanni* (Tappe, 1941). In the laboratory, it can be kept individually in 3.8-l jars, with a substrate of sand or granulated absorbent clay (Chew et al., 1965).

Perognathus inornatus is a granivore that mainly subsists on minute seeds of grasses, shrubs (e.g., *Artemisia* and *Atriplex*), and forbs. Insects do not form a major part of the diet, but it will eat soft-bodied insects such as cutworms (Horn and Fitch, 1942; Jameson and Peeters, 1988; Koos, 1979; Morton, 1979). In captivity, it will eat a mixture of parakeet seeds, rolled oats, sunflower seeds, and small amounts of vegetable greens (Chew et al., 1965).

In Fresno Co., *Peromyscus maniculatus* and *P. inornatus* showed a temporal separation during the year, but during periods of environmental stress *P. maniculatus* seemed to replace *P. inornatus*. During summer months, *P. inornatus* was most active and populations of *P. maniculatus* decreased. However, with the onset of drought conditions, populations of *P. maniculatus* nearly doubled whereas populations of *P. inornatus* declined (Koos, 1979).

Associated reptiles include *Gambelia silus*, *Uta stansburiana*, *Phrynosoma coronatum*, *Crotalus viridis*, *Cnemidophorus tigris* (Koos, 1979), *Sceloporus occidentalis*, *S. graciosus*, and *Xantusia vigilis* (Warner, 1976). Associated mammals include *Lepus californicus*, *Sylvilagus audubonii*, *Spermophilus beecheyi*, *Peromyscus maniculatus*, *Vulpes macrotis*, *Canis latrans*, *Dipodomys heermanni*, *D. nitratoides* (Warner, 1976), *D. ingens*, *Onychomys torridus*, *Ammospermophilus nelsoni* (Braun, 1983), *Taxidea taxus* (Koos, 1979), *Thomomys bottae*, *Neotoma*, and *Reithrodontomys megalotis* (Schwarz and Bleich, 1985). Predators include the barn owl (*Tyto alba*—Hawbecker, 1945; Schwarz and Bleich, 1985), the coyote (*Canis latrans*—Fitch, 1948), and potentially the burrowing owl (*Speotyto cucularia*—Warner, 1976).

The San Joaquin pocket mouse did not have Buttonwillow virus or hemagglutination-inhibiting antibodies for this virus (Hardy et al., 1970), nor did it test positive for western equine encephalomyelitis, St. Louis encephalitis, Powassan, or Modoc viruses (Hardy et al., 1974). However, the bacterium *Haemobartonella* was recovered from samples of blood (Wood, 1952); the only ectoparasite known is the mite *Ischyropoda armatus* (Keegan, 1951; Whitaker and Wilson, 1974). No fleas, ticks (Hardy et al., 1974), coccidians (Ford et al., 1990), or other parasites are known (Whitaker et al., 1993).

Perognathus inornatus has been captured in Sherman and Havahart live traps baited with seeds and oats (Warner, 1976), and in live traps set for pocket gophers (*Thomomys*—Howard and Childs, 1959). It is susceptible to poisoning with 1080 (sodium monofluoroacetate—Hegdal et al., 1986). *P. i. inornatus* and *P. i. psammophilus* were proposed for listing as a threatened or endangered species by the United States Fish and Wildlife Service (Dodd et al., 1985), but *P. i. inornatus* later was removed from the list of candidates (Drewry, 1991).

BEHAVIOR. The San Joaquin pocket mouse is nocturnal and spends the day below ground in a simple burrow, and forages at night on the surface of the ground (Grinnell and Storer, 1924). It is not skilled at climbing in vegetation (Eisenberg, 1963).

Inability to locate *P. inornatus* in October, January, and March, indicates that it hibernates (Schwartz and Bleich, 1985). The seasons of hibernation can be divided into autumn, winter, and spring phases based on changes in duration of torpor. Torpors are shorter than in species that store fat (e.g., *Spermophilus*), but the intervening episodes of euthermia are 2–3 times longer in the spring compared with the winter phase of hibernation. Presumably, seasonal changes in duration of episodes of euthermia and torpor are endogenous; animals were given food caches at the start of the experiment and then kept under constant environmental conditions with minimal disturbances until their energy supplies were nearly exhausted. *P. inornatus* has open-ended hibernation seasons. One remained in the experiment long enough to begin a second seasonal cycle, but at no time did any animal cease hibernation altogether. Unlike *Spermophilus*, the amount of time a pocket mouse spends in torpor is influenced by its initial supply of energy. Pocket mice given 400 g of seeds at the start of dormancy had episodes of torpor, both in the winter and spring phases of hibernation, that averaged <50% as long as those of individuals that started with 200 g of seeds or less. Average duration of episodes of torpor and euthermia, respectively, during winter were 111.8 and 5.3 h when 100–200 g of seeds were provided at the start of dormancy. When 400 g of seeds were provided, duration of torpor was 49.1 h and euthermia 7.1 h in winter. During the spring phase, torpor lasted 46.6 h and euthermia 14.1 h when 100–200 g of seeds were provided and 16.1 and 15.7 h for torpor and euthermia, respectively, when 400 g of seeds was provided (French, 1989).

When sandbathing, *P. inornatus* has a tendency to alternate side-rubs. It may rub the same side, opposite side, or belly following a side rub in a sandbathing sequence. Sandbathing consists of several well-integrated movements. Initially, it digs rapidly with its forepaws in the substrate. It then lowers its cheek to the sand and extends its body while sliding forward on its side. Alternate extension and flexion of the body results in a series of side rubs. The extension and flexion may be performed with the ventrum pressed against the sand; in this instance, the movement is a ventral rub. Generally, it will perform isolated side rubs or ventral rubs, but an extended sequence of sandbathing usually includes both acts. Stretching involves extension of the body and limbs followed by flexion. Its perineal drag (scent marking) consists of depressing the anal-genital area against the substrate and walking forward. Stretching and dragging also are seen in a modified form during sandbathing. While rubbing the ventrum, the perineal region is pressed against the substrate and the extension and flexion of the body is comparable to the movements in stretching. The pocket mouse tends to concentrate its sandbathing at one locus, and the sandbathing spots of one animal affect the behavior of others. Sandbathing may have originated from a movement pattern for spreading scent. Sandbathing also serves as a means of dressing the pelage (Eisenberg, 1964).

During estrus, females are involved in rushing, chasing, fighting, sandbathing, marking, digging, kicking back, naso-anal contacting, grooming, mounting, and escape leaping. Interactions between sexes change cyclically as the female passes through estrus (Eisenberg, 1963). Generally, there is one bout of mounting with ejaculation on the terminal mount. At the time of ejaculation, the female usually twists over on her side, often throwing the male over (Eisenberg, 1967a).

Vocalizations include growl, squal, and low grunt. Tooth-chattering and foot-drumming are used in nonvocal auditory communication. However, drumming is rare and the sound is barely audible to the human ear. Tooth-chattering is by rapidly bringing the incisors together. This often occurs in situations where aggressive behavior occurs; either during encounters or by females when defending the

nest. *P. inornatus* is less aggressive than *Liomys pictus* and *Chaetodipus californicus*, but more aggressive than *Dipodomys panamintinus*, *Microdipodops pallidus*, and *Heteromys anomalous* (Eisenberg, 1963). In addition, it is less aggressive than *Chaetodipus penicillatus* and *Perognathus flavus* (Eisenberg, 1967b).

GENETICS. The diploid number of chromosomes of *P. i. neglectus* is 56 and the fundamental number is 86–88. There are 16–17 biarmed chromosomes and 10–11 acrocentric autosomes. The X chromosome probably is a submetacentric and the Y probably is a metacentric. For *P. i. inornatus*, the diploid number of chromosomes is 50, the fundamental number is 88, there are 20 biarmed pairs and 4 pairs of small acrocentric autosomes, the X chromosome is large and submetacentric, and the Y is a small metacentric (Williams, 1978). One *P. inornatus* from Lake Co. had 60 chromosomes (Williams et al., 1993).

REMARKS. The literature on *P. inornatus* shows great confusion about the taxonomy of *P. inornatus* and *P. longimembris* and the systematic relationships among populations of these two species (e.g., Osgood, 1918; Williams et al., 1993). However, *P. longimembris* does not occur in central California. Pocket mice from within the San Joaquin, Sacramento, and Salinas valleys, identified as *P. longimembris*, are *P. inornatus*. On the bases of different karyotypes (50 compared with 56 chromosomes) and body proportions, *P. i. neglectus* and *P. i. inornatus* probably are different species (D. F. Williams, in litt.). *P. i. neglectus* and *P. i. psammophilus* may belong to the same taxon (Williams et al., 1993).

Perognathus is from the Greek *pera* meaning pouch and *gnathos* meaning jaw. The specific epithet *inornatus* is from the Latin *inornatus* meaning undecorated (Jaeger, 1955).

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