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Zapus trinotatus.

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Zapus trinotatus Rhoads, 1894

Pacific Jumping Mouse

Zapus trinotatus Rhoads, 1894:421. Type locality "Lulu Island [mouth of Frazer River], British Columbia."
Zapus pacificus Merriam, 1897:104. Type locality "Prospect, Rogue River Valley, Oregon."
Zapus imperator Elliot, 1899:228. Type locality "Siegs Ranch, Elwah River, Clallam County, Washington."
Zapus orarius Preble, 1899:29. Type locality "Point Reyes, Calif."

CONTEXT AND CONTENT. Order Rodentia, Superfamily Dipodoidea, Family Dipodidae, Subfamily Zapodinae. The genus *Zapus* includes three extant species; *Z. trinotatus*, *Z. princeps*, and *Z. hudsonius*. Four subspecies of *Z. trinotatus* are recognized (Hall, 1981):

Z. t. eureka Howell, 1920:229. Type locality "Fair Oaks, Humboldt County, California."
Z. t. montanus Merriam, 1897:104. Type locality "Crater Lake, Mount Mazama, Klamath County, Oregon."
Z. t. orarius Preble, 1899:29, see above.
Z. t. trinotatus Rhoads, 1894:421, see above.

DIAGNOSIS. Pacific jumping mice can be distinguished from others of the genus by their slightly larger size and markedly distinct separation of colors between dorsum and ventrum (Fig. 1; Jones, 1981). Total length of this species range from 221 to 238 mm (Krutzsch, 1954). Other distinctive characteristics include: ears usually fringed with the same color as the dorsum or with light brown, unlike the fringe of white on *Zapus princeps* (Krutzsch, 1954); baculum 6.7 to 7.4 mm long and 0.7 to 0.9 mm wide at the base (Krutzsch, 1954), tip spade-shaped and wider than 0.43 mm (Hall, 1981; Fig. 2); skull broad; pterygoid fossae wide; mesopterygoid fossae narrow (Krutzsch, 1954); occlusal pattern of M1 and M2 with paracone isolated (free); first primary fold divides occlusal pattern of M1; ml lacks anteromedian fold in the anteroconid (Klingener, 1963; Jones, 1981); mandible with wide and inflected angle (Krutzsch, 1954); coronoid process long, slender, and divergent from condyloid process (Hall, 1981). *Z. trinotatus* most resembles *Z. princeps*, but exhibits morphologic and extensive allozymic differences that indicate it warrants specific designation (Petersen et al., in press).

FIG. 1. Adult male *Zapus trinotatus* from Jolly Giant Creek, Arcata, Humboldt Co., California (Humboldt State University 819).

GENERAL CHARACTERS. The pelage of *Z. trinotatus* is colorful, often strikingly so, with the colors brighter and more distinct than cogeners (Whitaker, 1972). It is strongly tricolored; the dorsum is dark brown to cinnamon-brown; the sides are dark orange-brown or ochraceous-buff, occasionally flecked with black; the ventrum is mostly white or diffused with dusky brown or with the same color as the sides (variable in some populations such as those of *Z. t. orarius*); the chest often has a patch of buff or buff wash that occasionally extends to the venter (Bailey, 1936; Hall, 1981; Jones, 1981; Krutzsch, 1954). In autumn, the pelage is paler with less contrast than during other seasons; however, a pronounced line of bright orange-buff separates the ventrum and dorsum (Cowan and Guiguet, 1965). The sparsely-haired tail is dark brown above and whitish below (Krutzsch, 1954). Guard hairs average 141 μm (range 133 to 154) in diameter (Krutzsch, 1954). The underfur has rectangular medullary patterns and small cuticular scales (Hausman, 1920; Short, 1978).

Pacific jumping mice are pentadactyl (although with reduced pollex) and have naked soles (Whitaker, 1972); the hind legs are much longer than forelegs (32 to 37% of the length of head and body); the tail is attenuate, 130 to 160% of the length of the head and body, and sometimes with a white distal tuft. The small head has a general murine appearance, but is slightly elongate (Lyon, 1901). The eyes are small and located midway between the nose and ears; the ears are short, but longer than the surrounding fur. *Z. trinotatus* has four pairs of mammae; one inguinal, one abdominal, and two pectoral (Bailey, 1936). Ranges in body measurements (in mm) for adult *Z. trinotatus* are: total length, 221 to 242; length of tail, 112 to 155; length of hind foot, 30 to 36; length of ear, 14 to 16 (Hall, 1981; Maser et al., 1981). Body mass averages 27.5 g (Krutzsch, 1954).

The skull (Fig. 3) is "broad and deep in proportion to length" (Hall, 1981:846). The coronoid process is long, wide across the base, and blunt; a few are notched at the tip. Relative to other *Zapus*, the pterygoid fossa and the nasofrontal juncture are broad, the zygomata are widely bowed, and the anterior ramus of the zygomatic process of the maxillary relatively narrow (Krutzsch, 1954). The dental formula is: i 1/1, c 0/0, p 1/0, m 3/3, total 18 (Hall, 1981). Ranges of means for cranial dimensions (in mm) of 66 males and females from eight localities are (sexes and localities pooled): mastoid width, 10.6 to 11.3; condylobasal length, 20.4 to 21.6; occipitonasal length, 22.6 to 24.8; interorbital breadth, 3.8 to 4.6; palatal length, 10.0 to 10.9; zygomatic breadth, 12.1 to 12.8; zygomatic length, 9.3 to 9.8; length of maxillary tooth row, 3.7 to 4.1; and braincase breadth, 9.9 to 10.6 (Krutzsch, 1954).

Krutzsch (1954) and Maser et al. (1981) suggested that *Z. trinotatus* has internal cheek pouches, though Klingener (1971) noted the belief that cheek pouches exist in these mice is based on

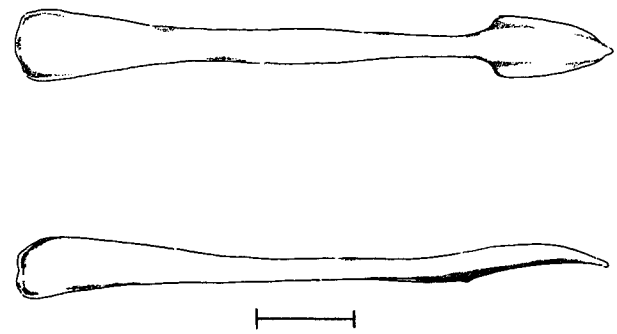

FIG. 2. Baculum of *Zapus trinotatus* (Museum of Southwestern Biology 40703; bar is 1 mm).

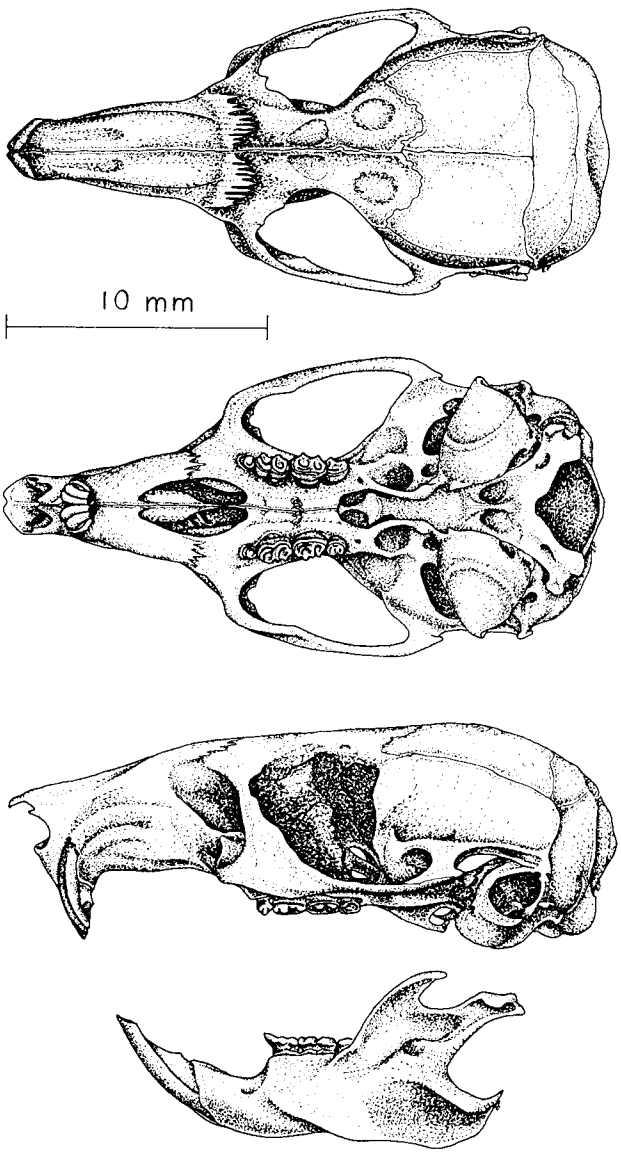

FIG. 3. Dorsal, ventral, and lateral view of the cranium and lateral view of the lower jaw of *Zapus trinotatus* Big Lagoon State Park, Humboldt Co., California (HSU 204).

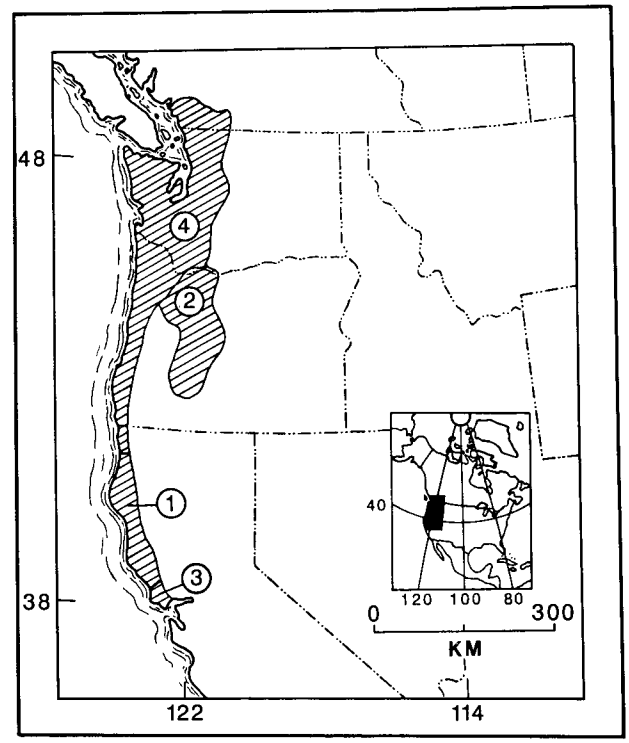

FIG. 4. Distribution of *Zapus trinotatus* and its subspecies (modified from Hall, 1981): 1, *Z. t. eureka*; 2, *Z. t. montanus*; 3, *Z. t. orarius*; and 4, *Z. t. trinotatus*.

one, century-old, and erroneous observation. Dalquest (1948) wrote that these mice have small, naked ears, when actually the ears are well haired (Krutzsch, 1954).

DISTRIBUTION. This species occupies a range (Fig. 4) that generally extends from southwestern British Columbia (Cowan and Guiguet, 1965) southward through western Washington and Oregon along the humid coastal strip mostly west of the crest of the Cascade-Sierra Nevada mountain chain through California (Hall, 1981) to Point Reyes (Grinnel, 1933) and Elk Valley, Marin Co., California, on the northern shores of San Francisco Bay (Hooper, 1944). San Francisco Bay may be a barrier blocking further southern expansion of the range of *Z. trinotatus*. Populations of *Z. t. orarius* in west-central California may be isolated from other populations of *Z. trinotatus* (*Z. t. eureka*) in northern California by a zone of dry habitat called the Sonoma-Marin gap (Hooper, 1944). Initially, the formation of the Cascade-Sierra Nevada mountain ranges isolated populations of *Zapus* causing a speciation event from which *Z. trinotatus* and *Z. princeps* arose. Further isolation by Pleistocene glaciation maintained separation and caused further divergence between the two species (Krutzsch, 1954). No fossils of *Z. trinotatus* are known.

FORM AND FUNCTION. Specializations for locomotion include especially well-developed hind legs, lengthening of the distal elements of the hind limbs and digits, general shortening of the body, and lengthening of the tail (Dagg, 1973; Howell, 1944; Lyon, 1901). The Pacific jumping mouse is a bounding rodent that pushes-off with the hind feet and lands on both forefeet together (Dagg, 1973). The tail may be an organ of balance (Preble, 1899; Seton, 1909). One jumping mouse whose tail was severed, jumped 35 cm high, travelled 1 m, and could not land properly, but instead turned somersaults and landed on its back with each jump. *Z. trinotatus* is a mouse of the meadowland, hence is adapted for escape by a few erratic hops amid dense cover (Svihla and Svihla, 1933). However, jumping mice do not possess extensive adaptations that other saltatorial rodents have (for example, *Dipodomys*), such as greatly tufted tails, fused cervical vertebrae and metatarsals, reduced number of toes, and digital brushes and combs (Howell, 1944). However, they do have some specializations for leaping that include shortening of the neck (although the cervical vertebrae are unfused) with increased cervical flexure, a posterior shift of the center of gravity, a modification of the vertebral column to 39 vertebra, and a lengthened pseudosacrum (Hatt, 1932; Lyon, 1901).

Annual molt proceeds with new hair simultaneously appearing on the anterior-dorsal surface of the nose and on the middorsal surface between the scapulae. The molt progresses from the scapulae over the head, anteriorly to the nose and posteriorally towards the tail and down the sides to the mid-ventral line. The molt is complete when the last new hairs appear on the rump (Krutzsch, 1954).

Anomalies include extra cusplets on teeth of two specimens from Oregon (Jones and Walley, 1976). One had an extra cusplet on the internal side of the M1; the other had an extra cusplet on the labial side of the m2. Two specimens had unossified holes in the basioccipital, another had one unossified hole in the center of the basiosphenoid, and one had an unossified hole in the right zygomatic plate (Jones, 1981).

ONTOGENY AND REPRODUCTION. Males become sexually active in May or June and may remain so as late as September (Johnstone, 1979; Maser et al., 1981; Svihla and Svihla, 1933). Females become receptive in May and June and usually give birth in July or August (Maser et al., 1981). One annual litter of from four to eight young are born (Bailey, 1936). Gestation is estimated to be 18 to 23 days (Maser et al., 1981).

The altricial newborn are pink and hairless, with eyes shut, ears folded, head short and stubby, facial vibrisse not visable, and

a mass from 0.7 to 0.9 g (Svihla and Svihla, 1933). The young become independent in about 1 month and are sexually mature the next year (Maser et al., 1981). Measurements (in mm) of five 12 to 15 day-old mice were: total length, 78 to 80; length of tail, 44 to 45; length of hind foot, 10 to 11; and length from tip of ear to notch, 1 (Johnstone, 1979).

ECOLOGY. In general, *Z. trinotatus* inhabits alder-salmonberry (*Alnus-Rubus spectabilis*), riparian alder (*Alnus*), and skunk cabbage (*Veratrum*) marsh ecosystems found among coastal redwood (*Sequoia sempervirens*) and Douglas fir (*Pseudotsuga menziesii*) forests. To a lesser extent, these mice are found in lodgepole pine-rhododendron (*Pinus contorta-Rhododendron macrophyllum*), lodgepole pine-salal (*P. contorta-Gaultheria shallon*), Sitka spruce-salal (*Picea sitchensis-G. shallon*), headland prairie and headland scrub communities, and edges of other habitats (Maser et al., 1981). *Z. trinotatus* become more numerous with increasing percipitation with populations concentrated in less mesic and more riparian habitats; they may be restricted to areas that receive more than 30 cm of precipitation annually. Furthermore, *Z. trinotatus* is isolated from *Z. princeps* through most of Oregon and parts of Washington by an inhospitable south-to-north physiographic strip of low annual precipitation (<30 cm; Jones, 1981).

In the northern part of its range, *Z. trinotatus* occurs in dense forests, alpine meadows, and wet-grassy areas of the Olympic Peninsula and Cascade Mountains of Washington, and in moist meadows, marshy thickets, and woodland edges with ferns and weedy understory (Svihla and Svihla, 1933). A dense population of *Z. trinotatus* was found at Lake Cushman, Mason Co., Washington, that inhabited deciduous forests, marshes, open grasslands, sphagnum bogs, alder (*Alnus*) and willow forests (*Salix*), and high alpine meadows on Mt. Steele (Dice, 1932).

In Oregon, the central part of its range, the Pacific jumping mouse has been found in riparian-deciduous woodlands, wet meadows where the ground is peaty, and brushy successional stages of redwood (*Sequoia sempervirens*), Douglas fir (*Pseudotsuga menziesii*), and mixed-evergreen forests (Hooper, 1944; Maser et al., 1981). Moreover, *Z. trinotatus* was exclusively found in low-elevation meadows near the Columbia River, Oregon, during the early summer months (Hedlund and Rickard, 1976).

In the southern part of its range, *Z. trinotatus* was reported in the looser, humus-filled dark soils along the humid Pacific coast from central California typified by redwood forest (*S. sempervirens*; Hooper, 1944). Characteristic plants of this habitat near Inverness, California, include: rushes (*Juncus*), sedges (*Carex*), bracken fern (*Pteris aquilinia*), swordfern (*Polystichum munitum*), Johnsongrass (*Holcus halepensis*), poison hemlock (*Conium maculatum*), and monkey flower (*Mimulus*; Hooper, 1944).

Remains of *Z. trinotatus* had an average frequency of occurrence of 3.1% in pellets of the barn owl (*Tyto alba*) in southwestern British Columbia and was estimated to constitute 0.4% of the total biomass of prey species (Dawe et al., 1978). These mice composed 0.16% of the diet of the barn owl and 0.21% of the diet of the great horned owl (*Bubo virginianus*) in western Oregon (Maser and Brodie, 1966); they constituted nearly 2% of the diet of long-earred owls (*Asio otus*) in the same region (Reynolds, 1970). Four jumping mice were discovered among remains of 338 vertebrates found at barn owl nests in the San Francisco Bay area, California (Smith and Hopkins, 1937).

Felis rufus and *F. catus* catch and consume Pacific jumping mice (Jones, 1981; Nussbaum and Maser, 1975). Some "snakes, martens, mink, weasel, spotted skunks, fox, coyotes, other owls, and hawks undoubtedly catch them when the opportunity exists" (Maser et al., 1981:235).

Bailey (1936) wrote that Pacific jumping mice are generally not numerous enough to cause damage to fields or crops; however, he did note that where they are unusually numerous, meadows can be damaged from the amount of grass that they cut to get at seed heads. It is doubtful that these mice are sufficiently numerous to be considered economically detrimental (Maser et al., 1981). *Z. trinotatus* were 6% of the small mammal fauna in Lane Co., Oregon (Hooven, 1976). Density of populations of *Z. trinotatus* undergoes periodic fluctuations; at times, they occur in pockets of unusual abundance (Howell, 1923). Jumping mice were described as "fairly swarming" in the Cascade Mountains of Washington, whereas they were found relatively scarce only a year before (Howell, 1923:153). *Z. t. trinotatus* was numerous in dense forests bordering the Straits of Juan de Fuca at Bowman's Creek, at the mouth of the Sekiu River, and in alpine meadows near timberline at Boulder Lake in western Washington (Svihla and Svihla, 1933), but were scarce near Cave Junction, Oregon (Roest, 1951). Aerial application of herbicides (2,4-D in combination with atrazine, delapon, and silvex) reduced abundance of Pacific jumping mice in western Oregon through restructuring of habitat (Borrecco et al., 1979).

Although fruits, insects, fungi, and even mollusks and fish (Svihla and Svihla, 1933) are consumed by *Z. trinotatus*, they are considered granivorous (Whitaker, 1972) with seeds composing at least 50% of the diet (Jones et al., 1978). Seeds consumed include those of *Holcus lanatus*, *Rumex*, and *Lysichitum americanum* (Dalquest, 1948; Jones et al., 1978; Maser and Franklin, 1974). To secure seeds, these mice cut plant stems into sections until the seed head is reached, leaving the stem cuttings in a neat pile (Bailey, 1936). *Z. trinotatus* are adept at selecting and consuming hypogeous Phycomycetes that constitute nearly 10% of their diet; of this, the genus *Glomus* occurs in 75%, the genus *Sclerocystis* in 17%, and *Endogone* in 8% of the digestive tracts collected (Jones et al., 1978; Maser et al., 1978; Whitaker, 1962). However, jumping mice mostly forage at ground level, and eat berries of *Rubus parviflorus*, *R. spectabilis*, *R. procerus*, *Ribes bracteosum*, *Vaccinium ovatum*, *V. deliciosum*, and *V. parvifolium* that fall within their grasp (Franklin et al., 1972). Coleopteran and dipteran insects compose 3.5 to 6.3% of the total food consumed (Jones et al., 1978). Lepidopteran larvae have been found to account for as much as 13.4% of the total amount of food consumed (Jones, 1981).

Generally, *Z. trinotatus* is associated with microtine and soricid species that occur in its habitat. Most frequently, the Pacific jumping mouse is associated with *Microtus oregoni*, *Sorex vagrans*, *S. trowbridgii*, *Peromyscus maniculatus*, *Aplodontia rufa*, and *Neurotrichus gibbsii* (Borrecco et al., 1979; Dalquest, 1941; Gashwiler, 1970; Hooven, 1976; Jones, 1981). *Z. trinotatus* occasionally may be associated with *Clethrionomys occidentalis*, *Sorex pacificus*, *S. benderii*, and *Arborimus albipes* (Jones, 1981). The Pacific jumping mouse has been trapped in runways of *N. gibbsii* (Dalquest and Orcutt, 1942) and *Aplodontia rufa* (Pfeiffer, 1953; Svihla and Svihla, 1933); it is not known to make its own runways (Bailey, 1936).

Museum special traps are an effective method of capturing Pacific jumping mice (Jones, 1981). However, conventional Sherman live traps or conical pitfall traps also are successful (Nellis et al., 1974). Additionally, these mice have been collected with spring-floor and snap traps baited with fish (Svihla and Svihla, 1933).

Feces collected from *Z. t. eureka* from Humboldt Co., California, contain coccidian oocysts (*Eimeria zapi*; Duszynski et al., 1982). Other parasites of Pacific jumping mice include (unless otherwise indicated, from Jones, 1981, and Whitaker, 1979): Protozoa, *Trypanosoma lewisi*-like (Davis, 1952); Siphonaptera, *Megabothris abantis* (Holland, 1949; Hubbard, 1941) and *M. quirini* (Hubbard, 1947); Acarina (mites), Trombiculinae, *Neotrombicula harperi*, *N. zapi*, *N. microti*, *N. cavicola*, *Euschoengastia*, *Shunsennia ochotona*; Mycoptidae, *Gliricoptes zapi* (Fain and Whitaker, 1974); Glycyphagidae, *Dermacarus newyorkensis*, *D. hypudaei*; Laelapidae, *Haemogamasus ambulans*, *H. reidi*, *Androlaelaps fahrenholzi*, *Hirstionyssus isabellinus*, *Hypoapsis*; Myobiidae, *Radfordia ewingi*; Macrochelidae, *Macrocheles*; Acarina (ticks), *Ixodes angustus* (Cooley and Kohls, 1945). The mycoptid mite, *Gliricoptes zapi*, collected from *Z. trinotatus* was reported as a new species by Fain and Whitaker (1974).

BEHAVIOR. Pacific jumping mice do not make satisfactory laboratory animals nor friendly pets because of their nervous and high-strung dispositions (Harthill, 1935; Svihla and Svihla, 1933). These mice also can become aggressive when trapped and bite the handler (Jones, 1981).

Zapus trinotatus produce a squeaking noise when fighting and vibrate their tail rapidly against a substrate to produce a drumming noise (Svihla and Svihla, 1933). Infant Pacific jumping mice were located in their nest by tracing their high-pitched squeals (Johnstone, 1979). Noises made by sucking air through the lips irritated a captive *Z. trinotatus* to the extent that the mouse "would jump wildly from side to side" (Harthill, 1935:19).

Zapus trinotatus primarily is nocturnal, but also crepuscular (Allen, 1899; Harthill, 1935; Maser et al., 1981). A captive Pacific jumping mouse ate bread, popcorn, raisins, celery, lettuce, cabbage, parsnips, and carrots; it seized foot items in its forepaws, sat back on its haunches, and nibbled on the food (Harthill, 1935).

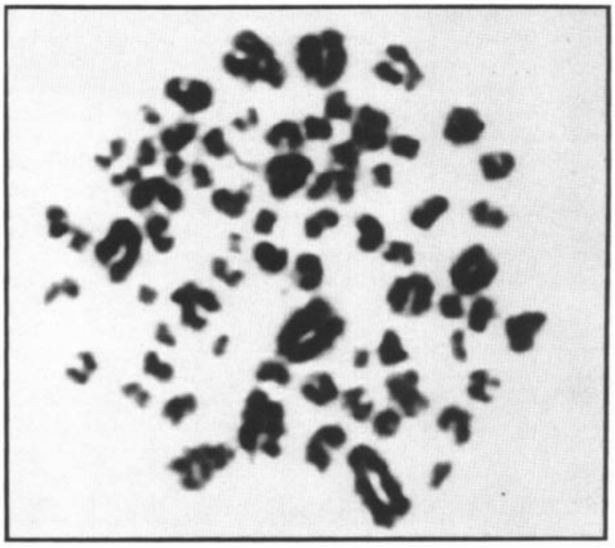

FIG. 5. Karyotype of *Zapus trinotatus* (MSB 40702) from Arcata, Humboldt Co., California.

When escaping a predator, Pacific jumping mice leap upward 90 to 180 cm, turn the head downward, arch the back, and dive to the ground like a frog into water. The forefeet strike first then the hind feet are quickly pulled underneath as the animal prepares to jump again (Taylor and Shaw, 1927). Alternately, these mice remain motionless when a predator is detected, apparently relying on their pelage as camouflage, then move on to cover after danger has passed. However, if noticed by a predator while still, jumping mice quickly escape by bounding to safety (Wrigley, 1975). When bounding away from a predator jumping mice usually head for dense cover (Hatt, 1932).

A dark-eyed junco (*Junco hyemalis*) nest that contained four eggs, was usurped by a Pacific jumping mouse near Randle, Washington. The mouse appropriated the cup-shaped nest as its own and consumed four junco eggs. The egg shells were used to line the nest entrance; the only record of a jumping mouse implicated as a predator of ground-nesting birds. The mouse then modified the junco nest by installing a dome over it that consisted of dried grasses and elk hair (*Cervus elaphus*; Smith, 1984). In laboratory feeding trials, captive *Z. trinotatus* broke open the shells and consumed junco eggs (Smith, 1984).

One grass-lined nest containing five altricial young was found 1.4 m above the ground in the crook of a coast redwood. The nest was 14.5 cm in diameter and weighed 28.3 g (Johnstone, 1979). Another nest was constructed of shredded newspaper in the basement of a home (Flahaut, 1939), and another, made of straw, was found nearly 75 cm below ground (Harthill, 1935). During summer, Pacific jumping mice construct well-hidden, fragile, dome-shaped nests with a single entrance most often on the ground (Maser et al., 1981). The nest material is loosely interwoven, coarse or broad-leaved grasses, sedges, or sphagnum moss (Maser et al., 1981).

During fall, *Z. trinotatus* find vacant burrows or make their own nests with an entrance tunnel forming a gooseneck to the main chamber. Chambers may be 13 cm in diameter with an entrance hole of 4 cm (Flahaut, 1939). One nest found 30 cm below ground, contained a hibernating jumping mouse. Nests have been found as far as 76 cm below ground and as close as 10 cm to the next nest. Separate nests have been found with connecting tunnels indicating that Pacific jumping mice may hibernate in pairs (Flahaut, 1939; Jones, 1981; Preble, 1899).

Pacific jumping mice gain weight and accumulate fat under the skin, over the muscles of the body, and around the viscera and reproductive organs (Maser et al., 1981). They nearly double their mass to survive hibernation (Bailey, 1936). As cold weather approaches, jumping mice retreat to their burrows and hibernate (Flahaut, 1939). They become drowsy and sluggish then go into torpor, but can be aroused from torpor if their environment warms (Harthill, 1935; Svihla and Svihla, 1933). During hibernation, the mice attain a curled position with their head tucked ventrally and the tail wrapped over the head and back then around the body (Flahaut, 1939; Svihla and Svihla, 1933). Jumping mice remain torpid and hibernate until mid-April when ambient temperatures rise to −6°C or more (Edson, 1932).

GENETICS. The karyotype for coastal populations of Pacific jumping mice was reported as 2n = 72 and 76 and fn = 80 to 90 (Jones, 1981). A karyotype for *Z. trinotatus* from Arcata, Humboldt Co., California, exhibited a diploid number of 68 (Fig. 5).

REMARKS. Klingener (1984) placed jumping mice in the family Dipodidae based on morphology of the hind limb. Jones (1981) considered *Z. trinotatus* and *Z. princeps* conspecific. Carl et al. (1952), Cowan and Guiguet (1965), and Krutzsch (1954) reported there was no indication of hybridization in areas where *Z. trinotatus* was sympatric with *Z. princeps* or *Z. hudsonius*.

Krutzsch (1954) cited eastern North America as the region of origin and center of dispersal for the genus *Zapus*. He suggested that *Z. trinotatus* is geographically the most distant from the region of origin and displays means for characters that deviate most from the means of characters of the other species. However, on the basis of parasite similarities, Whitaker (1979) postulated that progenitors of the genus originated in Eurasia and moved across the Bering Straits area into northwestern North America. Examination of the dental evolution of the genus by Klingener (1963) and the morphometric analyses of the group by Jones (1981), support the postulation that progenitors of jumping mice invaded North America by crossing in the vicinity of the Bering Strait.

Vernacular names include Pacific jumping mouse, Point Reyes jumping mouse, kangaroo mouse, and Coast jumping mouse (Maser et al., 1981). The generic name *Zapus* is derived from the Greek words *za* (very) and *podos* (foot). The specific name *trinotatus* is from the Latin word *trinus* (triple) and the Greek word *notos* (the back) in combination with the Latin suffix *atus* (provided with; Maser et al., 1981).

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