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Liomys irroratus

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Liomys irroratus. By Robert C. Dowler and Hugh H. Genoways

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Liomys Merriam, 1902

Spiny Pocket Mice

Liomys Merriam, 1902:44. Type species *Heteromys alleni* Coues (= *Liomys irroratus alleni*).

CONTEXT AND CONTENT. Order Rodentia, Family Heteromyidae, Subfamily Heteromyinae. The genus *Liomys* contains five known species. The following key will aid in identification (measurements in millimeters):

- 1 Five plantar tubercles; pterygoid bones with broad wings; shaft of baculum oval to tip; glans penis long (more than 75%) in comparison with baculum; 60 chromosomes; no neck between head and midpiece of spermatozoon; upper parts grayish brown; lateral stripe pale pinkish to buffy; occurring on Mexican Plateau and in adjacent areas of northern and central México, south as far as south-central Oaxaca

Liomys irroratus

Usually six plantar tubercles; pterygoid bones with narrow wings; shaft of baculum either flattened dorsoventrally or flattened dorsoventrally and compressed laterally at some point; glans penis short (less than 75%) in comparison with baculum; 48 or 56 chromosomes; neck present between head and midpiece of spermatozoon; upper parts either reddish brown or chocolate brown, or somewhat paler, with either an ochraceous lateral stripe or lateral stripe absent; not occurring on the Mexican Plateau

- 2(1) Upper parts reddish brown with an ochraceous lateral stripe; interorbital region broad in comparison with greatest length of skull; distal end of the shaft of the baculum with a laterally compressed ventral keel and just posterior to this region, the shaft is flattened dorsoventrally; tip of glans penis long when compared with its total length; 48 chromosomes; head of spermatozoon long and with pointed apex; hairs on back not curled upward and not visible above spines; occurring along the Pacific slope of western México as far south as the vicinity of Tonalá, Chiapas, in the central valley of Chiapas, and in the southern half of Veracruz

Upper parts of chocolate brown to somewhat paler, lateral stripe absent; interorbital region narrow in comparison with greatest length of skull; shaft of baculum dorsoventrally flattened just posterior to slightly upturned tip, no laterally compressed ventral keel present; tip of glans penis short when compared with its total length; 56 chromosomes; head of spermatozoon short and with a bluntly rounded apex; hairs on back curled upward and visible above the spines; occurring in Central America and into México along the Pacific coast as far as the vicinity of Reforma, Oaxaca

- 3(2) In southeastern Jalisco, size small (greatest length of skull, 28.9 to 32.0, specimens approaching *L. spectabilis* in size do occur in Guerrero and Oaxaca but these are still slightly smaller and have a proportionally deeper braincase); in Jalisco hind foot rarely more than 30; laterally compressed ventral keel on baculum short, 0.85 to 1.25; fundamental number of chromosomes 66; head of spermatozoon similar to that of *L. spectabilis*, but significantly shorter and narrower; occurring along Pacific coast of western México, in the central valley of Chiapas, and in southern Veracruz

Liomys pictus

In southeastern Jalisco, size large (greatest length of skull, 33.0 to 35.3); hind foot rarely less than 30; laterally compressed ventral keel on baculum relatively long, 1.30; fundamental number of chromosomes 64; head of spermatozoon similar to that of *L. pictus*, but significantly longer and broader; occurring only in southeastern Jalisco

Liomys spectabilis

- 4(2) Size small (greatest length of skull averaging less than

33.5); fundamental number of chromosomes 86; morphology of head and neck of spermatozoon similar to that of *L. adspersus*, but head significantly broader and neck significantly shorter; occurring from southern Oaxaca to central Costa Rica

Liomys salvini

Size large (greatest length of skull averaging over 34.5); fundamental number of chromosomes 84 or less; morphology of head and neck of spermatozoon similar to that of *L. salvini*, but head significantly narrower and neck significantly longer; occurring only in central Panamá

Liomys adspersus

It is difficult to construct a useful key to members of the genus *Liomys* because some of the most easily observed characters, external and cranial measurements, exhibit a high degree of geographic variation within individual species. However, one fact that does help to simplify this problem is that zones of sympatry between species of the genus are restricted; therefore, chances are relatively low that more than one species will be collected at any one locality. Of the five recognized species, only in southeastern Jalisco is there a possibility of obtaining as many as three (*irroratus*, *pictus*, and *spectabilis*) together (all three have not yet been taken together there). *Liomys irroratus* and *Liomys pictus* occur sympatrically in a zone from central Jalisco southward through Michoacán, in the vicinity of the Balsas Basin and Sierra Madre del Sur of Guerrero, and along the Sierra Madre of Oaxaca. However, even within this area the two species many times are microallopatric with *irroratus* inhabiting the uplands and *pictus* the lower and generally more mesic situations. Specimens of *L. pictus* and

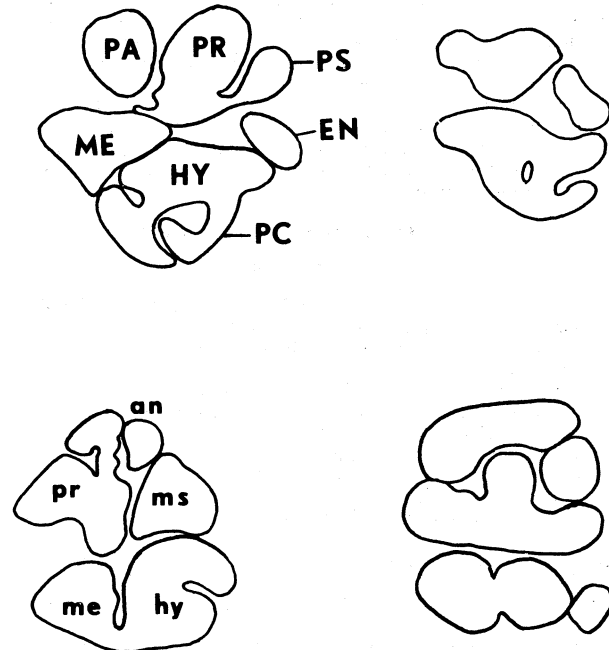


FIGURE 1. Crown patterns of the upper (at top) and lower (below) premolars of *Liomys irroratus* (upper, KU 31174; lower, KU 31129) on left and *Heteromys gaumeri* (upper, KU 92146) *Heteromys desmarestianus* (lower, KU 71255) on right. For all teeth, anterior is to the top; for the upper premolars, lingual is to the right and for the lower premolars it is to the left. Abbreviations for the upper premolars are: EN, entostyle; HY, hypocone; ME, metacone; PA, paracone; PC, posterior cingulum; PR, protocone; PS, protostyle. Abbreviations for the lower premolars are: an, anteroconid; hy, hypoconid; me, metaconid; ms, mesoconid; pr, protoconid.

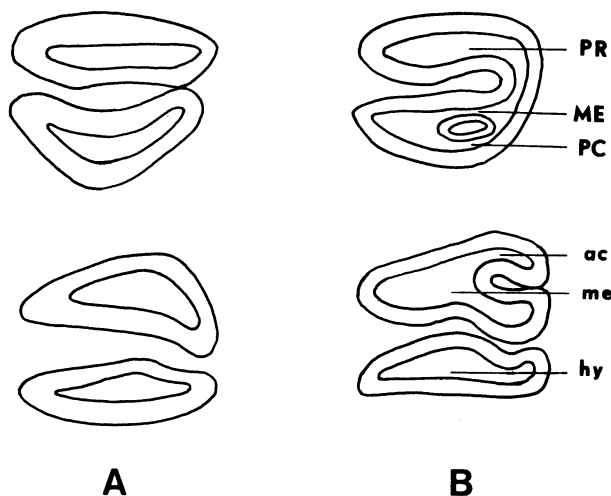


FIGURE 2. Crown patterns of the first upper (at top) and lower (below) molars of one species of *Liomys* and *Heteromys*. All teeth illustrated are from the right side. For all teeth, anterior is to the top; for the upper molar, lingual is to the right and for the lower it is to the left. Abbreviations used in the illustration are: ME, metaloph; PC, posterior cingulum; PR, protoloph; ac, anterior cingulum; hy, hypolophid; me, metalophid. The species are: A, *Liomys irroratus* (KU 97189); B, *Heteromys lepturus* (KU 99845).

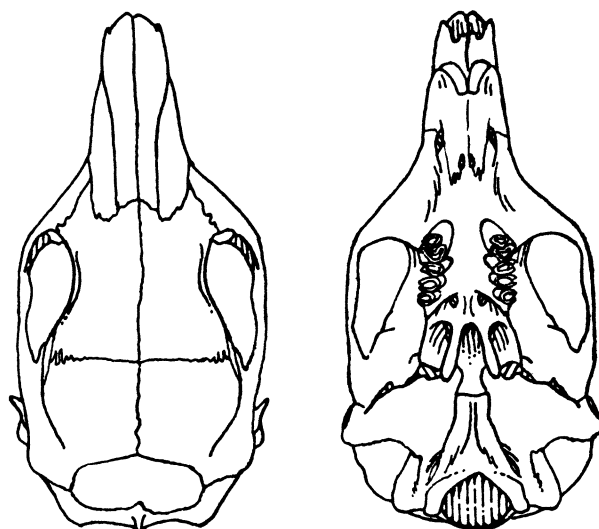


FIGURE 3. Dorsal, ventral, and lateral views of the cranium and lateral view of the lower jaw of *Liomys irroratus irroratus*. Specimen is a male from 3 mi. W Mitla, Oaxaca (KU 68855). The scale is 10 millimeters long.

L. salvini have been taken sympatrically from the vicinity of Reforma in southeastern Oaxaca to the vicinity of Tonalá in northwestern Chiapas.

DIAGNOSIS. Cheekteeth are medium crowned; upper incisors are asulcate; only two lophids on lower premolar (figure 1); accessory enamel island on molars persists only for short period (visible only in unworn molars, see figure 2); entostyle is closely united to hypocone so that Y-shape of median valley of upper premolar is poorly formed; auditory region is uninflated; pelage is hispid, consisting of stiff spines mingled with slender soft hairs; soles of hind feet are haired; interpterygoid fossa is U-shaped anteriorly; a specialized claw is present on hind foot; adapted for scampering.

The genus *Liomys* is most closely related to *Heteromys* from which it is distinguished mainly on dental characteristics. In *Heteromys*, the lower premolar consists of three or four lophids and the accessory enamel island on the molars persists in some taxa until adulthood.

Liomys irroratus (Gray, 1868)

Mexican Spiny Pocket Mouse

Heteromys irroratus Gray, 1868:205. Type locality restricted to Oaxaca, Oaxaca, by Genoways (1973:111).

Heteromys albolimbatus Gray, 1868:205. Type locality La Parada, Oaxaca.

Heteromys alleni Coues, in J. A. Allen, 1881:187. Type locality Hacienda Angostura, Río Verde, San Luis Potosí.

Heteromys bulleri Thomas, 1893:330. Type locality La Laguna, Sierra de Juanacatlán, Jalisco.

Liomys texensis Merriam, 1902:44. Type locality Brownsville, Cameron Co., Texas.

Liomys canus Merriam, 1902:44. Type locality near Parral, Chihuahua.

Liomys torridus Merriam, 1902:45. Type locality Cuicatlán, Oaxaca.

Heteromys exiguus Elliot, 1903:146. Type locality Puente de Ixtla, Morelos.

Heteromys jaliscensis J. A. Allen, 1906:251. Type locality Las Cañas, 7000 ft., Jalisco.

Liomys guerrensis Goldman, 1911:62. Type locality Omilteme, Guerrero.

CONTEXT AND CONTENT. Context is given in generic account above. The species contains seven subspecies (Genoways, 1973:99–123) as follows:

L. i. alleni (Coues, in J. A. Allen, 1881:187), see above (*canus* Merriam, *pullus* Hooper, and *acutus* Hall and Villa-R. are synonyms).

L. i. bulleri (Thomas, 1893:300), see above.

L. i. guerrensis Goldman (1911:62), see above.

L. i. irroratus (Gray, 1868:205), see above (*albolimbatus* Gray and *yautepecus* Goodwin are synonyms).

L. i. jaliscensis (J. A. Allen, 1906:251), see above.

L. i. texensis Merriam (1902:44), see above (*pretiosus* Goldman is synonym).

L. i. torridus Merriam (1902:45), see above (*minor* Merriam and *exiguus* Elliot are synonyms).

DIAGNOSIS. The size is generally medium for the genus in external and cranial measurements (figure 3) although some populations are relatively large (*guerrensis*) and others quite small (*torridus*); cranium is relatively broad in comparison with length; protoloph of upper permanent premolar composed of three discernable cusps; metaloph of upper premolar has three cusps (hypocone largest, metacone only slightly smaller than hypocone); entostyle is distinct but not widely separated from hypocone; re-entrant angle on labial side of lower premolar is not united with median valley; baculum is simple, with large rounded base, and slightly upturned tip (extreme tip of baculum may be slightly laterally compressed); structure of glans penis simple, with little sculpturing; urethral lappets trilobed; $2N = 60$, $FN = 62$; head of spermatozoon long and with relatively pointed apex; parasitized by the anopluran species, *Fahrenholzia ehrlichi* and *Fahrenholzia texana*; five plantar tubercles; upper incisors asulcate. See also the key to species.

GENERAL CHARACTERS. Pelage is hispid, consisting of stiff spines mingled with slender soft hairs; upper parts are grayish brown; lateral stripe, which is usually present, is generally pale pink to buff; underparts are white; hairs on back do not curl upward so are not conspicuous above spines. Juvenile pelage is grayish and consists primarily of soft slender hairs.

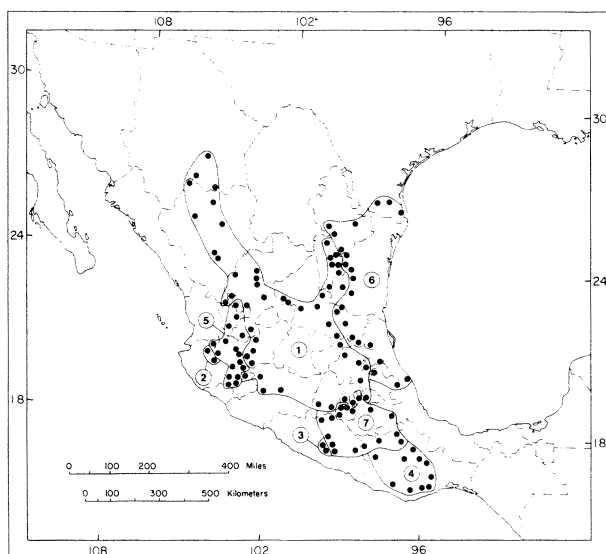


FIGURE 4. Geographic distribution of subspecies of *Liomys irroratus*: 1, *L. i. alleni*; 2, *L. i. bulleri*; 3, *L. i. guerrerensis*; 4, *L. i. irroratus*; 5, *L. i. jaliscensis*; 6, *L. i. texensis*; 7, *L. i. torridus*.

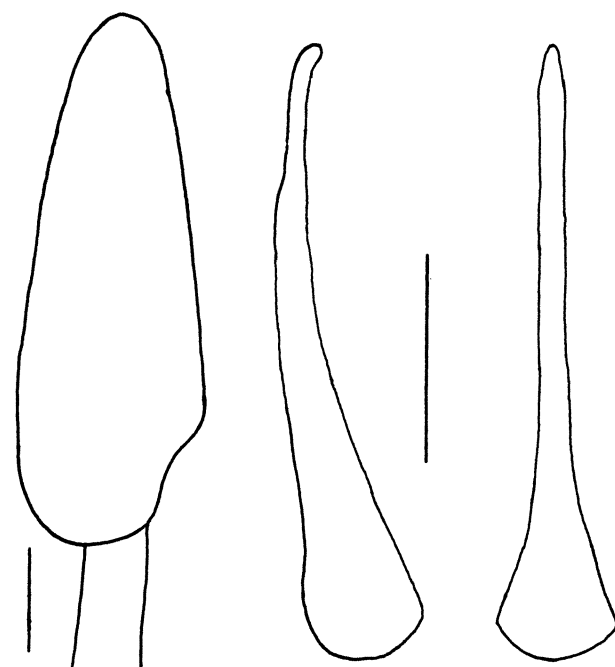
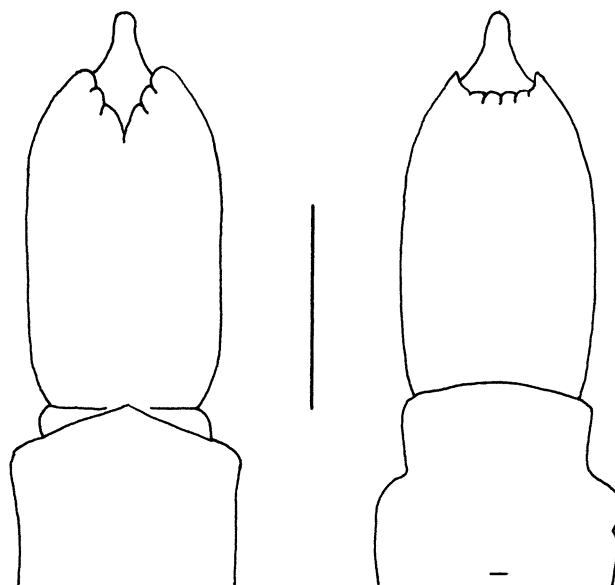


FIGURE 5. Glans penis (upper), baculum (lower right), and head and neck region of spermatozoon (lower left) of *Liomys irroratus*. The right drawings of the glans and baculum are dorsal views and the left are ventral and lateral views. A small horizontal line marks the posterior end of the baculum in the glans. Specimen used for glans is KU 67721, for baculum is KU 103781, and for sperm is TTU 9868. Scales for both glans and baculum is 3 mm and for sperm is 1 μ m.

Belt and southward into Puebla, Guerrero, and Oaxaca. The southernmost record for the species is Zapotitlán, Oaxaca (Genoways, 1973).

FOSSIL RECORD. The only fossil species that has been assigned to the genus *Liomys* is *Liomys centralis* described by Hibbard (1941a:349–350, 1941b:277) from the Rexroad Fauna of the upper Pliocene from southwestern Kansas. However, subsequent work by Hibbard (1972:88) showed that the species *Liomys centralis* is best assigned to the genus *Prodipodomys*.

Other fossil remains of *Liomys* have been reported from San Josecito Cave, near Aramberri, Nuevo León (Cushing, 1945; Jakway, 1958), a small cave 1 km S Aserradero del Paraiso,

Tests of secondary sexual variation (see Genoways, 1973) show males to be significantly larger than females in seven (total length, length of tail, length of hind foot, greatest length of skull, interorbital constriction, mastoid breadth and length of rostrum) of 13 external and cranial measurements. External and cranial measurements in millimeters for samples of males and females from central Jalisco are as follows (mean, ± 2 SE, range, and number): total length, 238.0 ± 5.18 (216.0 to 262.0) 22, 226.1 ± 3.14 (207.0 to 251.0) 34; length of tail, 120.1 ± 3.31 (106.0 to 138.0) 22, 112.5 ± 1.98 (102.0 to 131.0) 34; length of hind foot, 29.2 ± 0.49 (26.0 to 31.0) 21, 28.2 ± 0.27 (27.0 to 30.0) 36; greatest length of skull, 32.1 ± 0.49 (30.4 to 34.1) 21, 31.4 ± 0.21 (30.3 to 33.0) 33; zygomatic breadth, 15.6 ± 0.29 (14.8 to 16.6) 19, 15.3 ± 0.17 (14.6 to 16.3) 27; interorbital constriction, 8.0 ± 0.16 (7.2 to 8.7) 22, 7.7 ± 0.09 (7.2 to 8.3) 35; mastoid breadth, 14.5 ± 0.18 (13.8 to 15.4) 21, 14.3 ± 0.08 (13.8 to 14.7) 33; length of nasals, 12.5 ± 0.28 (11.4 to 13.4) 22, 12.2 ± 0.20 (11.0 to 13.5) 36; length of rostrum, 14.2 ± 0.27 (13.2 to 15.4) 22, 13.8 ± 0.13 (13.0 to 14.9) 36; length of maxillary toothrow, 5.1 ± 0.07 (4.8 to 5.4) 22, 5.1 ± 0.07 (4.4 to 5.4) 36; depth of braincase, 8.7 ± 0.12 (8.2 to 9.2) 20, 8.6 ± 0.06 (8.2 to 9.0) 33; interparietal width 8.7 ± 0.19 (7.9 to 9.4) 21, 8.5 ± 0.13 (7.8 to 9.5) 34; interparietal length, 3.6 ± 0.11 (3.0 to 4.1) 21, 3.6 ± 0.10 (2.9 to 4.1) 34.

The seven subspecies of *Liomys irroratus* fall into two major groups based on overall size (Genoways, 1973). Four of the subspecies are relatively large. The largest individuals of the species and probably the phenetically most distinct occur in the vicinity of Omilteme, Guerrero, and belong to the subspecies *Liomys irroratus guerrerensis*. Another highly distinctive subspecies, *Liomys irroratus bulleri* of west-central Jalisco is characterized by large size and a small interparietal bone. *Liomys irroratus irroratus* of central Oaxaca is large in size; a large percentage of individuals has the posterior margin of the nasals emarginate and a low percentage has nasals truncate. The remaining large subspecies, *Liomys irroratus alleni*, occurs on much of the Mexican Plateau and has few distinctive cranial characters with the possible exception of truncation of the posterior end of the nasals. The remaining three subspecies (*texensis*, *torridus*, and *jaliscensis*) are of small to medium size. Basically, these subspecies share many of the same cranial characteristics; however, they are recognized as separate populations because they are geographically isolated from each other.

Dental formula, as in all other heteromyids, is i 1/1, c 0/0, p 1/1, m 3/3, total of 20.

DISTRIBUTION. *Liomys irroratus* occurs on the Mexican Plateau and in adjacent areas (figure 4). In the northeastern part of its geographic range, this species extends into southern Texas and, in the northwest, specimens have been recorded from southern Chihuahua east of the Sierra Madre Occidental. From Chihuahua the species occurs southward to central Michoacan, generally to the east of the Sierra, and along the east coast it is known from as far south as central Veracruz. The species occurs in the vicinity of the Transverse Volcanic

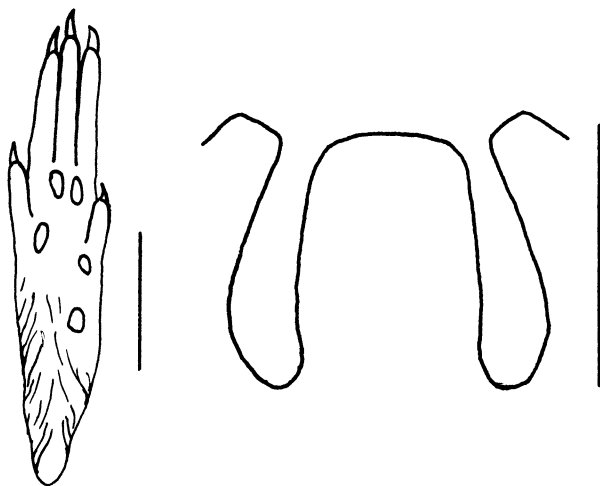


FIGURE 6. Semi-schematic drawings of the hind foot and pterygoid structure of *Liomys irroratus*. Scale for hind foot is 10 mm and for the pterygoids is 3 mm.

Tamaulipas (Koopman and Martin, 1959), and Cueva del Abra, Tamaulipas (Dalquest and Roth, 1970). All of this material is from late Pleistocene to sub-Recent deposits. Genoways (1973) compared six measurements of the San Josecito Cave material with *Liomys irroratus alleni* from the general area of the cave. The cave material was significantly larger than the specimens of *L. i. alleni* in two measurements but could be matched in these measurements by other Recent populations of *alleni* from Zacatecas, Durango, and Chihuahua. The San Josecito specimens were definitely representatives of *Liomys irroratus* and probably not much different from the Recent representatives of the species occurring in the area today. Genoways (1973) assigned the fossils from Tamaulipas to *L. i. texensis* although he did not have the opportunity to examine the material.

FORM AND FUNCTION. The glans of *Liomys irroratus* (figure 5) is nonspinous, cylindrical, and relatively long compared with the length of the baculum (78.5% the length of the baculum, see Genoways, 1973). The sides of the glans are nearly straight, the widest point being approximately at the mid-point of the glans. A large tip protrudes slightly from, and nearly fills, the terminal crater; the baculum extends to the end of the tip, with no cartilaginous elements present. The diameter of the glans of *Liomys irroratus* is relatively narrow compared with the length. The rim of the terminal crater of the glans is crenulate dorsally and ventrally; the lips are formed into a deep V-shape ventrally so that more of the tip is revealed ventrally than dorsally. The sculpturing on the glans is relatively weak so that the structure appears relatively simple and featureless. Located in the terminal crater ventral to the baculum is a pair of urethral lappets, which are relatively large and trilobed.

The baculum (figure 5) is of medium length for the genus. However, compared with overall body size the baculum is proportionately the shortest of any species of *Liomys*, but is not so short as that of *Heteromys desmarestianus* and *H. gaumeri*. The base of the baculum of *irroratus* is higher than wide as in all species of the genus. Both the width and height of the base of the baculum of *irroratus* average greater than in any other species of the genus. Bacular morphology of *L. irroratus* bears a striking resemblance to that in some species of *Heteromys* (Burt, 1960; Genoways, 1973). From the broad, high base, the shaft tapers rapidly for about the first one-third of its length, then gradually to the tip. The shaft is essentially oval in shape to its tip; this feature serves to distinguish *L. irroratus* from other species of *Liomys* and to ally it with *Heteromys*. The tip of the baculum is slightly upturned and simple in construction, although the extreme distal end may be laterally compressed. The extent of this flattened area is individually variable, but never was found to be extensive.

Studies of sperm morphology by Genoways (1973) show that the head of the sperm (figure 5) is long and has a rounded point at the apex. The base of the head is smoothly rounded with the exception of a notch on one side. The broadest part of the head is just anterior to the notch. No neck was observed between the head and midpiece in this species; this could be the result of preparation or staining techniques, but a distinct neck was observed in the four other species of *Liomys*. The



FIGURE 7. Karyotype of a male *Liomys irroratus*. The scale is 10 μ m.

head of the sperm of *irroratus* is significantly (Student's *t*-test, at 0.05) broader than in *L. pictus*. There was no significant difference in other measurements between *irroratus* and *pictus* or *spectabilis* (the two species with spermatozoa that most closely resemble those of *irroratus*).

In *Liomys irroratus* the protoloph of the upper premolar consists of three cusps arranged more or less in a straight line (figure 1). The cusps are more distinct in some individuals than in others, but were discernable in all specimens examined by Genoways (1973). The middle cusp, protocone, is the largest of the three and is located directly anterior to the hypocone of the metaloph. The labial cusp, paracone, is smaller than the protocone, but larger than the protostyle. As pointed out by Wood (1935:199), the cusp called the "paracone" may not represent that cone, but rather a labial style.

The metaloph also consists of three cusps (figure 1), but these are arranged in a crescent with the large middle cusp being the posteriormost. This middle cusp, which represents the hypocone, although largest of the three cusps of the metaloph, is not much larger than the labial metacone. The entostyle, which is noticeably smaller than the metacone and hypocone, is located anterior and slightly lingual to the hypocone. The entostyle is clearly distinct from the hypocone, but is not as widely separated from it as in *Liomys salvini* and *Heteromys*. The median valley separating the protoloph and metaloph is reminiscent of the Y-shape found in *L. salvini* and *Heteromys*, but the re-entrant angle between the hypocone and entostyle is not continuous with the lingual margin of the tooth. Thus, the median valley has a shape of a Y with one arm shorter than the other. As the premolar wears the hypocone and entostyle are quickly united. A well-developed posterior cingulum extends from about the middle of the metacone to the lingual edge of the hypocone. Between this cingulum and the hypocone is a deep pit of enamel, which persists for some time as an island of enamel surrounded by dentine as the tooth is worn.

The protolophid of the lower premolar of this species is generally composed of three cusps (figure 1). The two lateral cusps, protoconid (lingual) and mesoconid (labial), are large, but there is variability among individuals as to which is the largest. The anteriorly-placed anteroconid is smaller than the other two cusps and in many instances this cusp appears to be divided into at least two cusps (see also Wood, 1935:198-199). However, as wear progresses this division is quickly obliterated. The median valley separating the protolophid and metalophid is connected with a deep re-entrant angle that separates the protoconid and mesoconid at their posteriomedial borders. The enamel valley separating the mesoconid and protoconid extends anteriorly between the mesoconid and anteroconid and deeply separates these two cusps. A much shallower branch of this re-entrant angle separates the anteroconid and protoconid. These latter two cusps become joined relatively early in the wear of the tooth, whereas the mesoconid remains separated for a much longer time.

The metalophid is composed of two large cusps, which are situated side-by-side but separated by a shallow angle of enamel. The labial hypoconid is generally larger than the lingual metaconid. These two cusps quickly become united into a single loph as wear progresses.

Genoways (1973) observed no anterior cingulum in specimens of *Liomys irroratus*. The only possible remnant of a posterior cingulum is a re-entrant angle of enamel that extends to one-third to one-half the way across the hypoconid from its

labial side. This angle may persist for a short time as an island of enamel surrounded by dentine as wear progresses.

Within the genus, *Liomys irroratus* is unique in that all members of the species possess five rather than six plantar tubercles on the hind feet (figure 6), although a few individuals of *Liomys pictus* also possess five. The tubercle apparently absent in *irroratus* is the small tubercle slightly anterior and external to the large, posteriormost tubercle in other species. The soles of the hind feet of *irroratus* are haired as in all species of the genus.

The shape of the pterygoid bone of *Liomys irroratus* differs from that of all other members of the subfamily in that the bone extends laterally noticeably farther than in other species, giving it a teardrop shape when viewed ventrally (figure 6).

Genoways (1973) stated that all members of the genus *Liomys* follow a similar pattern of molt. Molt originates in a middorsal spot approximately one-third of the distance from the ears to the rump. The molt progresses anteriorly along the middorsal line to just posterior to the ears and posteriorly to one-half to two-thirds the distance to the rump; at the same time, molt lines spread slowly laterally. A second molt center originates on the top of the head and spreads to molt around the eyes and onto the rostrum. The two centers of molt are joined in the area between the ears. Molt on the back progresses to the lateral stripe first at a point lateral and just posterior to the ears; at the same time progressing posteriorly in the middorsal region. Molt is next completed on the cheeks and lateral to the ears; finally the rump will be molted. Genoways observed no line of molt that had progressed beyond the lateral stripe onto the venter. The greatest percent of specimens of *L. irroratus* undergoing molt have been taken in April and May, although molting individuals also were collected in February, March, June, August, and September. Genoways suggested that adult *Liomys* ordinarily undergo a single molt annually.

Four major patterns of locomotion—typical quadrupedal saltation, fore-alternating quadrupedal saltation, hind-alternating quadrupedal saltation, and within-pair alternating pattern—have been described for *Liomys irroratus* (Pinkham, 1973). The top speed for the species was reported as 60 inches (about 1.5 m) per second while utilizing quadrupedal saltation.

In laboratory studies by Hudson and Rummel (1966), *Liomys irroratus* was found to be unable to maintain body weight on a diet of wild bird seed unless free water was available. Weight was maintained, however, if the animals were permitted to burrow. Pulmocutaneous water loss for the species at an ambient temperature of 28°C was recorded as ranging between 0.90 and 1.03 ng/mm³ of oxygen used. These values are comparable to those reported for other heteromylid rodents at comparable ambient temperatures. The average basal metabolic rate of oxygen consumption is 1120 mm³/g/hr for an individual weighing 48.1 g. The thermal neutral zone or zone of minimum metabolism for the species is narrow, lying between ambient temperatures of 31 and 34°C. The recorded mean body temperature of four *Liomys irroratus* (Hudson and Rummel, 1966) was 36.63 ± 0.51°C. The species was found to be slightly hypothermic below 12°C and hyperthermic at ambient temperatures exceeding 34°C.

Quay (1965) reported the presence of small sebaceous glands in sections of the oral lips and angle of *Liomys irroratus*. Sudoriferous and mucous glands were not present.

REPRODUCTION. Genoways (1973) reported that of 281 adult females for which reproductive data were available, 52 were gravid and 12 were lactating. Pregnant females were recorded for all months except February, April, and June, and in one of these months, June, a lactating female was taken. Peak reproductive activity appears to be in the months of August to November when more than a third of the females examined from each month were pregnant. The mean number of embryos per female was 4.39 (mode, four) with a range of two to eight. Males with enlarged testes were collected in each of the eight months for which data were available (Genoways, 1973).

Some additional reproductive data were recorded by Dalquest (1953:122), Hall and Dalquest (1963:285), and Alvarez (1963:433). Davis (1944:389) recorded a female of *L. i. guerrensis* from 15 km SW Chilpancingo, Guerrero, that was found to be gravid on August 17 (no embryo count given), and Koestner (1941:12) obtained a female on an unspecified date at Ojo de Agua, Nuevo León, that carried five embryos. Fleming (1969) reported immature individuals of *Liomys irroratus* from all months except May; he believed that *irroratus* breeds throughout the year, but with a peak from November to February.

ECOLOGY. The Mexican spiny pocket mouse occupies an extensive geographic range from southern Texas to southern Oaxaca. The species occurs from sea level along the coasts of Tamaulipas and Veracruz to nearly 3050 m on Cerro San Felipe and Mount Zempoaltepec in Oaxaca. The species

usually is restricted to relatively dry situations and this is especially noticeable when contact is made with the geographic range of *Liomys pictus*. In such situations *pictus* occurs in lower more mesic areas, whereas *irroratus* is found in the drier upland areas. Although *irroratus* prefers relatively arid habitats, it does not appear to occur in those areas of the north-central Mexican Plateau that receive less than 500 mm of rainfall annually (see Vivo Escoto, 1964: fig. 10).

No comprehensive ecological study of *L. irroratus* has been undertaken, but ecological information about the species can be found in Alvarez (1963:432–434), Bailey (1905:127), Baker and Greer (1962:104), Baker *et al.* (1967:225–226), Dalquest (1953:122), Davis (1944:389; 1960:151), Davis and Russell (1954:73), Hall and Dalquest (1963:284–286), Hooper (1953:5), Koestner (1941:9, 12), and Villa-R. (1953:407–408).

Genoways (1973) described the local ecology of 10 areas where specimens of *Liomys irroratus* were obtained. Other species commonly taken with *L. irroratus* include the following: *Oryzomys melanotis*, *O. palustris*, *Peromyscus leucopus*, *P. boylii*, *P. truei*, *P. pectoralis*, *Reithrodontomys fulvescens*, *Onychomys leucogaster*, *Sigmodon hispidus*, *Baiomys taylori*, *B. musculus*, *Neotoma micropus*, and *N. mexicana*. The vegetation in the areas where *Liomys irroratus* occurs is mainly steppe, thicket, and scrub desert and montane formation series; the montane formation series contains xerophytic plants, mainly pine and oak. *Liomys irroratus* is sympatric only with *L. pictus*, although it approaches the range of *L. spectabilis*. Sympatry of *irroratus* and *pictus*, occurs in a band from central Jalisco to the mountains of the Sierra Madre del Sur of Oaxaca.

Twenty-five species of mites (18 trombiculids, four laelapids, two macronyssids, and one listrophorid), are known from *Liomys irroratus* as follows: *Ectonix fusicornis* (Brennan, 1960a:88); *Euschoengastia gagarini* (Brennan, 1962:618); *Euschoengastoides bigenuala* (Loomis and Crossley, 1963:379; Eads *et al.*, 1965:17); *Euschoengastoides lacerta* (Loomis and Crossley, 1963:380; Eads *et al.*, 1965:17); *Euschoengastoides loomisii* (Loomis and Crossley, 1963:380; Eads *et al.*, 1965:17); *Eutrombicula alfreddugesi* (Eads *et al.*, 1965:17); *Fonsecia (Parasecia) universitatis* (Hoffmann, 1963:108; Brennan, 1969:666); *Hexidionis allredi* (Eads *et al.*, 1965:83); *Hexidionis jessiemae* (Brennan, 1965:83); *Leptotrombidium panamense* (Loomis and Crossley, 1963:378; Eads *et al.*, 1965:17); *Odontacarus cayolargoensis* (Loomis and Crossley, 1963:381; Eads *et al.*, 1965:17); *Pseudoschoengastia audyi* (Brennan and Dalmat, 1960:191; Eads *et al.*, 1965:17); *Pseudoschoengastia farneri* (Loomis and Crossley, 1963:381; Eads *et al.*, 1965:17); *Pseudoschoengastia hoffmannae* (Genoways, 1973:355); *Pseudoschoengastia hungerfordi* (Genoways, 1973:355); *Trombicula bakeri* (Genoways, 1973:355); *Trombicula* n. sp. (Eads *et al.*, 1965:17); *Xenacarus plumosus* (Loomis and Crossley, 1963:382; Eads *et al.*, 1965:17); *Androlaelaps fahrenheitii* (Eads *et al.*, 1965:17); *Hirstionyssus neotomae* (Eads *et al.*, 1965:17); *Hirstionyssus* n. sp. (Eads *et al.*, 1965:17); *Steptolaeps liomydis* (Grant, 1947:8; Furman, 1955:525; Eads *et al.*, 1965:17); *Ornithonyssus bacoti* (Eads *et al.*, 1965:17); *Ornithonyssus sylvium* (Eads *et al.*, 1965:17); *Listrophorus* n. sp. (Eads *et al.*, 1965:17).

One argasid tick (*Ornithodoros talaje*) has been reported by Eads *et al.* (1965:17) and one ixodid tick (*Ixodes eadsi*) by Kohl and Clifford (1964:466) and Eads *et al.* (1965:17) for *L. irroratus*. Two species of lice—*Fahrenholzia ehrlichi* (Ferris, 1922:161; Johnson, 1962:417; Eads *et al.*, 1965:17; Emerson, 1971:374) and *Fahrenholzia texana* (Ferris, 1922:161; Stojanovich and Pratt, 1961:693; Johnson, 1962:426; Eads *et al.*, 1965:17)—are known from *irroratus*. Three species of fleas—*Hoplopsyllus (Euhoplopsyllus) galcialis* (Genoways, 1973:356), *Polygenis gwyni* (Eads and Menzies, 1949:37; Eads, 1950:62; Genoways, 1973:356), and *Polygenis martinezbaezi* (Genoways, 1973:356)—also have been reported.

Two species of coccidian endoparasites, *Eimeria liomysis* and *Eimeria picti*, have been described from *Liomys irroratus* from Jalisco (Levine *et al.*, 1958; Ivens *et al.*, 1959). These protozoan parasites were recovered from fecal samples of *irroratus*.

GENETICS. *Liomys irroratus* has a diploid number of 60 (figure 7), including one medium-sized pair of metacentrics, one pair of large submetacentrics, and 27 pairs of telocentrics. The X-chromosome is a large submetacentric and the Y-chromosome is a medium-sized subtelocentric. The fundamental number exclusive of the sex chromosomes is 62 (Genoways, 1973).

ETYMOLOGY. The generic name *Liomys* is a combination of two Greek words, *Lio* (plain) and *mys* (mouse), referring to the absence of the specialized characteristics of *Heteromys*. The specific name *irroratus* comes from the Latin *irror* meaning “sprinkled with dew,” probably referring to the dorsal coloration of the species. The subspecific name *alleni* is a patronym for

J. A. Allen, who sent the holotype to Coues for description; *bulleri* gives patronymic recognition to A. C. Buller, the collector of the holotype; *torridus* comes from the Latin *torrid*, meaning "dried up" or "parched," probably referring to the habitat in which the holotype was collected at Cuicatlan, Oaxaca; *guerrerensis*, *jalisensis*, and *texensis* refer to the geographic origin of the holotypes.

REMARKS. Genoways (1973) stated that the ancestor of the *Liomys* lineage probably most closely resembled the Recent species *Liomys irroratus*, but almost certainly differed from it in a number of ways. This basic stock underwent differentiation into three lines, giving rise to the precursors of *irroratus*, the *salvini-adspersus* group, and the *pictus-spectabilis* group. The ancestors of *Liomys irroratus* probably evolved in the Madro-Tertiary Geoflora on the southern Mexican Plateau in much the same area as the southern part of the geographic range of Recent *Liomys irroratus*.

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