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January 1978

## Liomys irroratus

Robert C. Dowler<br>Texas Tech University, Lubbock, TX<br>Hugh H. Genoways<br>University of Nebraska-Lincoln, h.h.genoways@gmail.com

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Dowler, Robert C. and Genoways, Hugh H., "Liomys irroratus" (1978). Mammalogy Papers: University of Nebraska State Museum. 84.
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# Liomys irroratus. By Robert C. Dowler and Hugh H. Genoways 

## Published 6 January 1978 by The American Society of Mammalogists

# 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 $\qquad$ 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).
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) <br> 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 Cañoas, 7000 ft ., Jalisco.
Liomys guerrerensis 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.


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. i. guerrerensis 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 (guerrerensis) 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; $2 N=$ $60, F N=62$; 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.

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, $\pm 2 \mathrm{SE}$, range, and number): total length, $238.0 \pm 5.18$ (216.0 to 262.0 ) 22 , $226.1 \pm 3.14$ (207.0 to 251.0 ) 34 ; length of tail, $120.1 \pm 3.31$ ( 106.0 to 138.0 ) 22 , $112.5 \pm 1.98$ ( 102.0 to 131.0 ) 34; length of hind foot, $29.2 \pm 0.49$ (26.0 to 31.0 ) $21,28.2 \pm 0.27$ (27.0 to 30.0 ) 36 ; greatest length of skull, $32.1 \pm 0.49$ ( 30.4 to 34.1 ) $21,31.4 \pm$ 0.21 ( 30.3 to 33.0 ) $33 ;$ zygomatic breadth, $15.6 \pm 0.29$ ( 14.8 to 16.6 ) $19,15.3 \pm 0.17$ ( 14.6 to 16.3) 27; interorbital constriction, $8.0 \pm$ 0.16 (7.2 to 8.7) 22, $7.7 \pm 0.09$ ( 7.2 to 8.3) 35; mastoid breadth, $14.5 \pm 0.18$ ( 13.8 to 15.4 ) $21,14.3 \pm 0.08$ ( 13.8 to 14.7 ) 33 ; length of nasals, $12.5 \pm 0.28$ ( 11.4 to 13.4 ) $22,12.2 \pm 0.20$ ( 11.0 to 13.5 ) 36 ; length of rostrum, $14.2 \pm 0.27$ ( 13.2 to 15.4) $22,13.8 \pm 0.13$ ( 13.0 to 14.9) 36 ; length of maxillary toothrow, $5.1 \pm 0.07$ ( 4.8 to 5.4$) 22,5.1 \pm 0.07$ (4.4 to 5.4) 36 ; depth of braincase, $8.7 \pm$ 0.12 ( 8.2 to 9.2 ) $20,8.6 \pm 0.06$ ( 8.2 to 9.0) 33 ; interparietal width $8.7 \pm 0.19$ (7.9 to 9.4 ) $21,8.5 \pm 0.13$ (7.8 to 9.5 ) 34 ; interparietal length, $3.6 \pm 0.11$ ( 3.0 to 4.1 ) $21,3.6 \pm 0.10$ ( 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 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 $1 \mu \mathrm{~m}$.

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,


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

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Figure 7. Karyotype of a male Liomys irroratus. The scale is $10 \mu \mathrm{~m}$.
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, 1935:198199). 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 onehalf 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 $\mathrm{m})$ 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 $28^{\circ} \mathrm{C}$ was recorded as ranging between 0.90 and $1.03 \mathrm{ng} / \mathrm{mm}^{3}$ of oxygen used. These values are comparable to those reported for other heteromyid rodents at comparable ambient temperatures. The average basal metabolic rate of oxygen consumption is $1120 \mathrm{~mm}^{3} / \mathrm{g} / \mathrm{hr}$ 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 $34^{\circ} \mathrm{C}$. The recorded mean body temperature of four Liomys irroratus (Hudson and Rummel, 1966) was $36.63 \pm 0.51^{\circ} \mathrm{C}$. The species was found to be slightly hypothermic below $12^{\circ} \mathrm{C}$ and hyperthermic at ambient temperatures exceeding $34^{\circ} \mathrm{C}$.

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. guerrerensis 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 northcentral 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 loomisi (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 Crbssley, 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 fahrenholzi (Eads et al., 1965:17); Hirstionyssus neotomae (Eads et al., 1965:17); Hirstionyssus n. sp. (Eads et al., 1965:17); Steptolaelaps liomydis (Grant, 1947:8; Furman, 1955:525; Eads et al., 1965:17); Ornithonyssus bacoti (Eads et al., 1965:17); Ornithonyssus sylvarium (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, jaliscensis, 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 MadroTertiary 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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Principal editor of this account was S. Anderson.
R. C. Dowler and H. H. Genoways, The Museum, Texas Tech University, LubBock, 79409 (PRESENT addresses: Museum of the High Plains, Ft. Hays Kansas State College, Hays, 67601, and Carnegie Museum of Natural History,


