January 1978

Liomys irroratus

Robert C. Dowler
Texas Tech University, Lubbock, TX

Hugh H. Genoways
University of Nebraska-Lincoln, h.h.genoways@gmail.com

Follow this and additional works at: http://digitalcommons.unl.edu/museummammalogy

Part of the Zoology Commons


This Article is brought to you for free and open access by the Museum, University of Nebraska State at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Mammalogy Papers: University of Nebraska State Museum by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.
**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 spermatogonium; upper parts grayish brown; lateral stripe pale pinkish to buffy; occurring on Mexican Plateau and in adjacent areas of northern and central Mexico, south as far as south-central Oaxaca

2(1) Upper parts reddish brown with an ochreous 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; upper parts either reddish brown or chocolate brown; or somewhat paler, with either an ochreous lateral stripe or lateral stripe absent; not occurring on the Mexican Plateau

3(2) In southeastern Jalisco, size small (greatest length of skull, 23.0 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 only in southeastern Jalisco

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 Panama

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 upper; and neck significantly longer; occurring only in southeastern Jalisco

**Liomys spectabilis**
L. salini 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, Mexico, by Genoways (1973:111).

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


Heteromys balleri 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 tortidus Merriam, 1902:45. Type locality Cuicatlan, Oaxaca.

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

Heteromys jaliscensis J. A. Allen, 1906:251. Type locality Las Cañitas, 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. allenii (Coues, in J. A. Allen, 1881:187), see above (canus Merriam, pullus Hooper, and acutus Hall and Villa-R. are synonyms).

L. i. balleri (Thomas, 1893:300), see above.
Liomys irroratus guerrerensis. Another highly distinctive subspecies of central Oaxaca is large in size; a large females from central Jalisco are as follows (mean, 29.2 0.21 (30.3 to 33.0) 33; zygomatic breadth, 15.6 0.12 (13.8 to 15.4) 33; percentage of individuals has the posterior margin of the 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 (4.8 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 irroratus. Another highly distinctive subspecies, Liomys irroratus alleni, occurs on 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. 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 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 Paraíso, and for sperm is TTU 9068. Scales for both glans and baculum is 3 mm and for sperm is 1 μm.

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 ± 0.09 (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 (4.8 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.

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 9068. Scales for both glans and baculum is 3 mm and for sperm is 1 μm.
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 specimens of Heteromys texensis with material of *Liomys irroratus* allenii from the general area of the cave. The cave material was significantly larger than the specimens of *L. i. allenii* in two measurements but could be matched in these measurements by other Recent populations of *allenii* 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 3) is nonspinous, cylindrical, and relatively long compared with the length of the baculum (78.3% 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. The base of the baculum of *Liomys* is relatively narrow compared with the length. The protolophid of the lower premolar of this species 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 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). These cusps are more distinct individually 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 metapodium 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 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 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 metapodium 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 knob as wear proceeds towards the base of the tooth.

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 hypocone from its 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*).
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 more than six pairs of 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 exterior to each of the outer digits.

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 other members of the genus. Whereas the bases of the horizontal laminae in other characters, the head of the bone is almost square. In several others, in that region. The soles of the hind feet of irroratus are powdered with microsporous glands.
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 *torridus*, meaning "dried up" or "parched," probably referring to the habitat in which the holotype was collected at Cuicatlan, Oaxaca; *guerrerensis, jalsacensis, and mexensis* 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 *L. 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 *salvani*-*adipurus* group, and the *pictus*-*spectabilis* group. The ancestors of *Liomys irroratus* probably evolved in the Madre- Tertiary Geoflora on the southern Mexican Plateau in much the same area as the southern part of the geographic range of Recent *Liomys irroratus*.

**LITERATURE CITED**


Eads, R. B., and G. C. Menzies. 1949. A preliminary list of ancestors of *Liomys irroratus* probably evolved in the Tertiary Geoflora on the southern Mexican Plateau in much the same area as the southern part of the geographic range of Recent *Liomys irroratus*.


Goldman, E. A. 1911. Revision of the spiny pocket mouse (gena *Heteromys* and *Liomys*). N. Amer. Fauna 34:1-70.


Principal editor of this account was S. Anderson.