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Liomys salvini.

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Liomys salvini (Thomas, 1893)

Salvin's Spiny Pocket Mouse

Heteromys salvini Thomas, 1893:331. Type locality Dueñas, Guatemala.
Liomys crispus Merriam, 1902:49. Type locality Tonalá, Chiapas.
Liomys heterothrix Merriam, 1902:50. Type locality San Pedro Sula, Honduras.
Heteromys vulcani J. A. Allen, 1908:652. Type locality Volcán de Chinandega, about 4000 ft., Nicaragua.
Liomys anthonyi Goodwin, 1932:2. Type locality Sacapulas, 4500 ft., Guatemala.

CONTEXT AND CONTENT. Order Rodentia, Family Heteromyidae, Subfamily Heteromyinae. The species contains three subspecies (Genoways, 1973:231–244) as follows:

L. s. crispus Merriam (1902:49), as above (*setosus* Merriam is a synonym).
L. s. salvini (Thomas, 1893:331), as above (*nigrescens* Thomas, *heterothrix* Merriam, *anthonyi* Goodwin, and *aterrimus* Goodwin are synonyms).
L. s. vulcani (J. A. Allen, 1908:652), as above.

DIAGNOSIS. External and cranial measurements (figure 1) are small for the genus, the tail being especially short; protoloph of permanent upper premolar appears to be composed of one cusp, metaloph composed of three and sometimes four cusps, metacone of metaloph sometimes larger than hypocone, entostyle distinctly separated from other cusps of metaloph; reentrant angle on labial margin of lower premolar connects with median valley; baculum has large rounded base, shaft oval to point just posterior to the slightly upturned tip where it is dorsoventrally flattened; glans penis is medium-sized in comparison with length of baculum, tip of glans short; glans is highly sculptured, ventral folds deeply incised; urethral lappets are bilobed; $2N = 56$; $FN = 86$; head of spermatozoon is short, having a bluntly rounded apex and distinct neck between head and midpiece; wings of pterygoids are narrow; six plantar tubercles are present; upper incisors are asulcate.

GENERAL CHARACTERS. Pelage is hispid, consisting of stiff spines mingled with slender soft hairs; slender hairs on back curl upward, conspicuous above spines; upper parts are grayish brown to deep chocolate brown; there is no lateral stripe; underparts are white. Juvenile pelage is grayish and consists primarily of soft slender hairs.

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

Males were significantly larger than females in six (total length, length of hind foot, greatest length of skull, zygomatic breadth, interorbital breadth, and length of rostrum) of the 13 external and cranial measurements tested. Males had the larger mean in five measurements (length of tail, mastoid breadth, length of nasals, depth of braincase, and interparietal length) in which the means were not significantly different. In two measurements (length of maxillary toothrow and interparietal length), females had the larger mean (Genoways, 1973).

External and cranial measurements in millimeters (mean, ± 2 SE, range, and number) of northern populations from southeastern Chiapas and southwestern Guatemala are as follows (males followed by females): total length, 209.8 ± 4.65 (196.0 to 235.0) 18, 199.8 ± 5.82 (185.0 to 225.0) 13; length of tail, 100.1 ± 3.16 (88.0 to 110.0) 18, 93.2 ± 4.19 (81.0 to 110.0) 13; length of hind foot, 26.9 ± 0.52 (25.0 to 30.0) 22, 26.3 ± 0.60 (24.0 to 29.0) 15; greatest length of skull, 32.1 ± 0.32 (30.4 to 33.7) 24, 30.8 ± 0.46 (29.0 to 32.3) 17; zygomatic breadth, 14.9 ± 0.25 (14.2 to 16.0) 18, 14.7 ± 0.38 (13.8 to 15.9) 13; interorbital constriction, 6.5 ± 0.09 (5.9 to 7.0) 30, 6.5 ± 0.08 (6.1 to 6.8) 20; mastoid breadth, 13.8 ± 0.15 (13.2 to 15.0) 29, 13.7 ± 0.18 (13.1 to 14.5) 20; length of nasals, 12.1 ± 0.24 (10.8 to 12.8) 25, 11.6 ± 0.33 (10.2 to 12.8) 18; length of rostrum, 13.5 ± 0.20 (12.2 to 14.4) 24, 12.9 ± 0.31 (11.8 to 14.0) 14; length of maxillary toothrow, 4.8 ± 0.08 (4.3 to 5.2) 28, 4.8 ± 0.11 (4.4 to 5.2) 15; depth of braincase, 8.7 ± 0.11 (8.0 to 9.4) 27, 8.4 ± 0.09 (8.0 to 8.8) 17; interparietal width, 8.6 ± 0.17 (7.9 to 10.0) 28, 8.8 ± 0.22 (8.0 to 10.0) 19; interparietal length, 3.8 ± 0.13 (3.1 to 4.4) 29, 3.8 ± 0.14 (3.2 to 4.5) 19. External and cranial measurements (statistics in the same order as above) of southern populations from central Nicaragua are as follows (males followed by females): total length, 229.2 ± 4.31 (213.0 to 253.0) 26, 218.7 ± 5.54 (196.0 to 248.0) 27; length of tail, 116.8 ± 4.02 (94.0 to 151.0) 26, 111.6 ± 3.06 (100.0 to 128.0) 27; length of hind foot, 27.6 ± 0.52 (25.0 to 30.0) 31, 26.7 ± 0.47 (24.0 to 29.0) 34; greatest length of skull, 31.8 ± 0.40 (29.3 to 33.8) 32, 31.1 ± 0.47 (28.7 to 33.8) 32; zygomatic breadth, 14.5 ± 0.25 (13.5 to 15.7) 22, 14.3 ± 0.25 (13.0 to 15.3) 25; interorbital constriction, 6.8 ± 0.09 (6.2 to 7.4) 36, 6.6 ± 0.08 (6.1 to 7.3) 37; mastoid breadth, 13.7 ± 0.14 (12.9 to 14.7) 34, 13.6 ± 0.17 (12.7 to 14.9) 37; length of nasals, 12.2 ± 0.24 (11.0 to 13.9) 37, 11.8 ± 0.22 (10.4 to 13.3) 35; length of rostrum, 13.7 ± 0.20 (12.4 to 14.6) 36, 13.2 ± 0.26 (11.9 to 14.7) 30; length of maxillary toothrow, 4.7 ± 0.09 (4.2 to 5.5) 36, 4.7 ± 0.08 (4.2 to 5.2) 39; depth of braincase, 8.4 ± 0.12 (7.6 to 9.0) 31, 8.2 ± 0.13 (7.5 to 9.2) 34; interparietal width, 8.7 ± 0.23 (7.2 to 10.5) 34, 8.6 ± 0.18 (7.5 to 9.8) 35; interparietal length, 4.1 ± 0.11 (3.6 to 4.8) 34, 4.0 ± 0.11 (3.4 to 4.7) 35.

Three subspecies are recognized. In coastal areas of south-

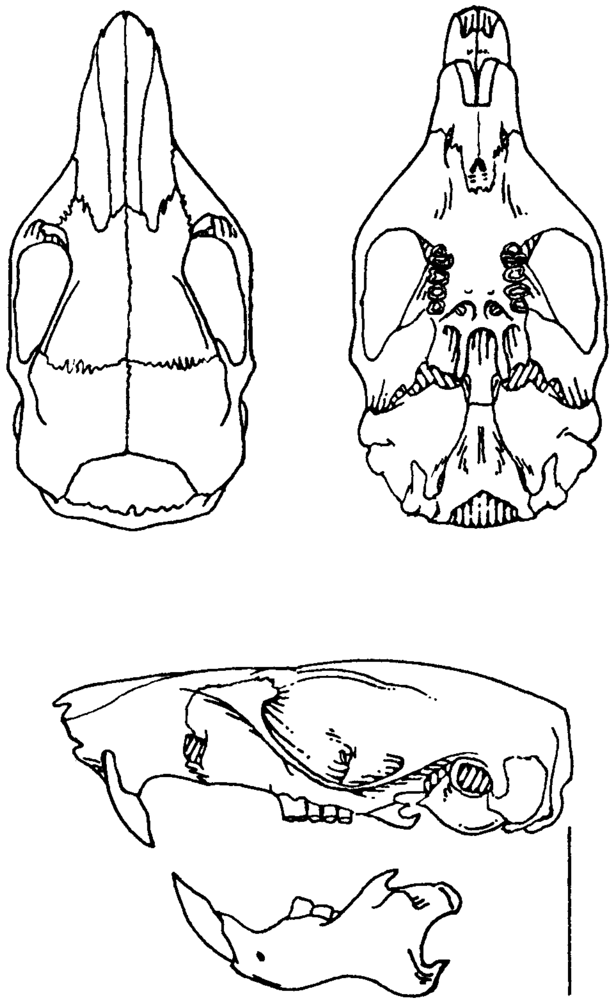

FIGURE 1. Dorsal, ventral, and lateral views of the cranium and lateral view of lower jaw of *Liomys salvini salvini*. The specimen figured is a male from 2 3/10 mi. W, 1/4 mi. N Istapa, Escuintla, Guatemala. The scale is 10 mm.

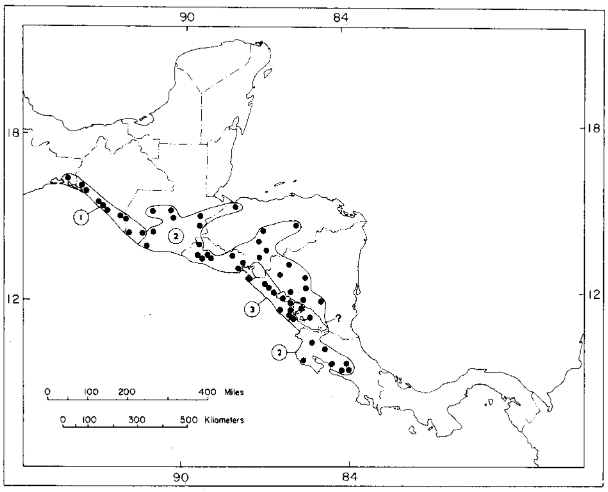

FIGURE 2. Geographic distribution of subspecies of *Liomys salvini*: 1, *L. s. crispus*; 2, *L. s. salvini*; 3, *L. s. vulcani*. The occurrence of *L. s. salvini* to the east of Lake Nicaragua is questionable at present.

eastern Oaxaca, Chiapas, and southwestern Guatemala, *Liomys salvini crispus* is distinguished by medium size, short body and tail, no individuals with a divided interparietal bone, and a high percentage (more than 64%) of individuals with the posterior margin of the interparietal bone deeply notched. *Liomys salvini vulcani* from western Nicaragua is distinguished by its consistently smaller size in both external and cranial measurements. The remainder of the geographic range of the species is occupied by *Liomys salvini salvini* distinguished by its large external and cranial measurements, the presence of at least some individuals in all populations with divided interparietal bones, and a low percentage of individuals (usually less than 50%) with the posterior margin of the interparietal bone deeply notched (see Genoways, 1973, for additional information).

DISTRIBUTION. *Liomys salvini* is the only species of the genus that occurs throughout much of the Pacific coast and slopes of the adjacent mountains of Central America (figure 2). The northernmost record is Reforma, Oaxaca. From there, the species occurs southward through Chiapas, Guatemala, El Salvador, Honduras, Nicaragua, to central Costa Rica. Although *L. salvini* is mainly confined to the Pacific drainage, it does occur in the dry valleys of the Caribbean drainage of central and eastern Guatemala; evidently the species occurs along the dry valley of the Río Motagua and its tributaries as far as San Pedro Sula in northern Honduras. The southernmost record for the species is from Monte Rey, 22 km S San José, Costa Rica (Genoways, 1973).

FORM AND FUNCTION. The glans penis of *Liomys salvini* is cylindrical in the basal two-thirds and flared outward in the distal third, being broadest in this region (figure 3), although most of this terminal flaring may be attributed to swelling during preparation. In actual length the glans of this species is the shortest of any species of *Liomys*; however, compared with length of baculum, the glans of *L. salvini* is proportionally longer than the glans of *pictus*, *spectabilis*, and *adspersus*, but is shorter than in *L. irroratus* and *Heteromys lepturus*. The diameter of glans studied was large compared with the length, possibly resulting from swelling of the diameter in preparation. The tip protrudes only a short distance beyond the rim of the terminal crater. The baculum extends to the end of the tip and no cartilaginous structures are present (as in all other species of *Liomys* studied). Dorsally, the rim of the terminal crater is notched into a fairly deep V-shape, whereas no such notch was evident below, although this may have been partly due to swelling in this area. In any event, more of the tip is evident dorsally in this species than ventrally. The rim of the crater is crenate ventrally, with the incisions being deeper than in any other species save *L. adspersus*. The urethral lappets are bilobed (Genoways, 1973).

The average length of the baculum of this species is the shortest of any species of *Liomys*, although compared with overall body size, it is in the middle of the range of variation within the genus. The average height of the base (1.53 mm) and the average width (1.36) also are in the middle of the range of variation of species studied. From the base, the shaft tapers steeply at first and then more gradually (figure 3). The slope near the base is not as steep as seen in the baculum of *L. irroratus*. Near the upturned tip of the baculum of *salvini*, the shaft is dorsoventrally flattened. At this point the shaft is somewhat expanded laterally, giving the bone the appearance of an arrowhead in dorsal view. The dorsoventral flattening and lateral expansion of the baculum near its tip serve to distinguish *salvini* from all other species of *Liomys* except *adspersus* (Burt, 1960; Genoways, 1973).

The head of the sperm of this species is short, being broadest in the basal region and bluntly rounded at the apex (figure 3). The base is relatively smooth, showing some minor irregularities that are individually variable. No notch is evident on a side of the base. A neck is present between the head and midpiece (Genoways, 1973).

In *Liomys salvini* the protoloph of the upper premolar appears to be composed of a single cusp, the protocone, because the two lateral cusps are so compressed against it that they are indistinguishable (Wood, 1935:198) (figure 4). The crescent-shaped metaloph is always composed of at least three cusps and many times four. The metacone is as large, and in some

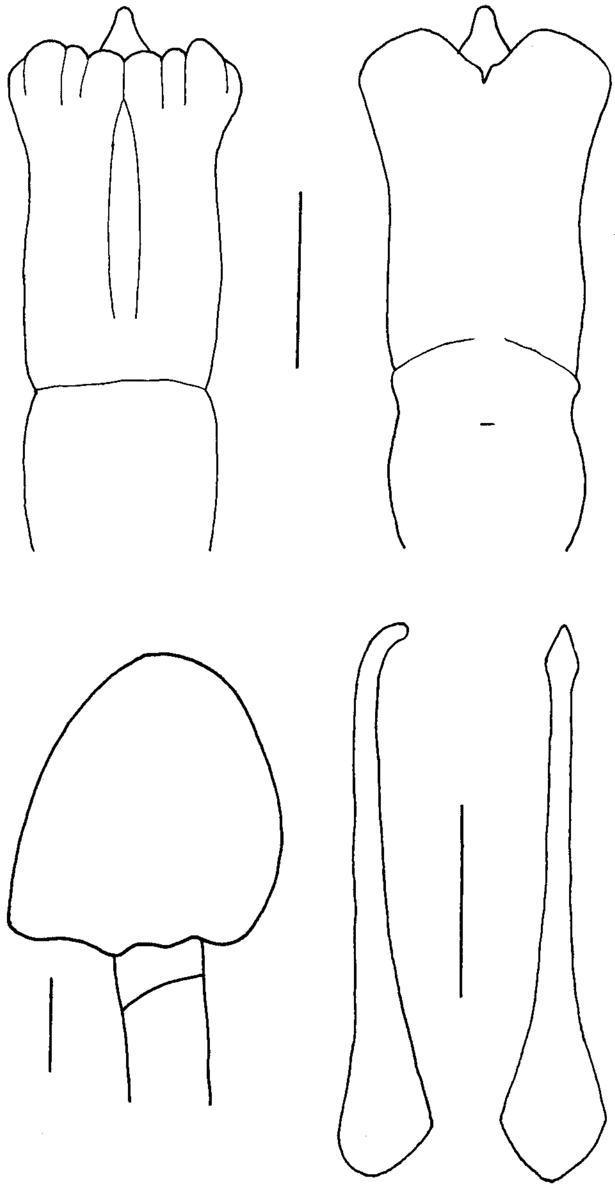

FIGURE 3. Glans penis (upper), baculum (lower right), and head and neck region of spermatozoan (lower left) of *Liomys salvini*. The right drawings of the glans and baculum are dorsal views and the left drawings are ventral and lateral views. A small horizontal line marks the posterior end of the baculum in the glans. Specimen used for glans is KU 120600, for baculum is KU 71164, and sperm is KU 120597. Scale for both glans and baculum is 3 mm and for sperm is 1 μm.

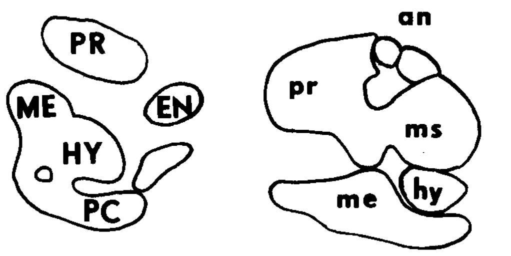

FIGURE 4. Crown patterns of the upper (left) and lower (right) premolars of *Liomys salvini* (upper, KU 71118; lower, KU 83963). Anterior is to the top; for the upper premolar, lingual is to the right and for the lower premolar it is left. Abbreviations for the upper premolar are: EN, entostyle; HY, hypocone; ME, metacone; PC, posterior cingulum; PR, protocone. Abbreviations for the lower premolar are: an, anteroconid; hy, hypoconid; me, metaconid; ms, mesoconid; pr, protoconid.

cases larger, than the hypocone. The extra cusp seen on the premolars of many specimens appears to be the result of a deep re-entrant angle of enamel that divides a loph, extending from the hypocone toward the entostyle. This cusp quickly becomes joined with the hypocone as wear on the tooth begins, although the re-entrant angle of enamel is evident for some time (first as an angle of enamel extending from the lingual edge of the tooth into the lake of dentine formed by wear and then as an island of enamel surrounded by dentine). The entostyle is placed anterior and lingual to the hypocone and is separated from the other cusps of the metaloph by a re-entrant angle of the median valley. The median valley has a Y-shape much as in *Heteromys*, but as the tooth begins to wear the entostyle does become connected with the hypocone, thus giving the median valley a shape as in the other species of *Liomys*. A well-developed posterior cingulum is present on P4 of *L. salvini*. The cingulum extends from the metacone to the lingual side of the hypocone and is separated from the hypocone by a re-entrant angle of enamel, which eventually forms an island before disappearing.

In *Liomys salvini* the protolophid of the lower premolar is composed of three cusps (figure 4). However, the cusps are rather weakly defined in *salvini* because the enamel angles separating them are shallow. The mesoconid and protoconid are about equal in size and only slightly separated, if at all, at their posteromedial borders. The anteroconid appears to be composed of two cusps, which are weakly separated from the protoconid and mesoconid. There is a deep pit of enamel near the center of this loph where all of the re-entrant angles coalesce between the cusps. All cusps appear to become united almost simultaneously early in the wear of the tooth leaving an island of enamel near the center of the loph. No anterior cingulum was observed on specimens examined.

The configuration of the metalophid of the lower premolar is somewhat different than in *L. irroratus* and *L. pictus*. The re-entrant angle of enamel seen in those species extends to, and is united with, the deep median valley of enamel separating protolophid and metalophid; thus, a large cusp (hypoconid) is isolated on the labial margin of the tooth. The area posterior to this angle of enamel is probably a posterior cingulum. In none of the specimens is a break evident between the metaconid and the posterior cingulum. The separation of the hypoconid remains longer than the separation of cusps of the protolophid, but eventually the hypoconid and metaconid unite to form a single straight loph (for additional information on dentition in *Liomys*, see Genoways, 1973).

Genoways (1973) described molt in *Liomys salvini* as originating in a middorsal spot approximately one-third of the distance from the ears to the rump. From this point 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 top of the head and spreads to molt around the eyes and onto the rostrum. 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. Genoways found that most annual molting occurs in May, but some individuals were noted as molting in March, June, July, and August.

Liomys salvini is characterized by possession of six plantar tubercles and hairy soles of the hind feet (figure 5). In *salvini* the pterygoid bones extend ventrally and then turn laterally (figure 5). The interpterygoid fossa is somewhat U-shaped anteriorly (Genoways, 1973).

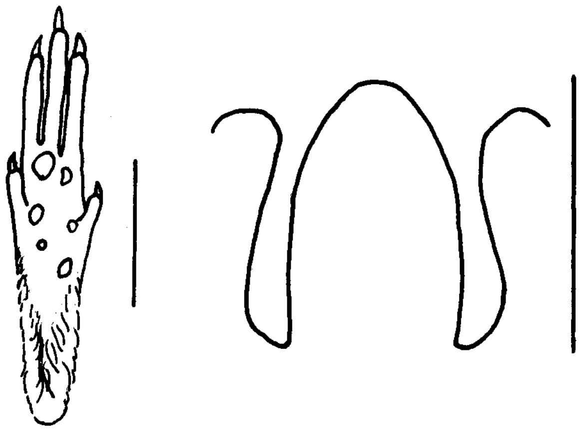

FIGURE 5. Semi-schematic drawings of the hind foot and pterygoid structure of *Liomys salvini*. Scale for hind foot is 10 mm and for the pterygoids is 3 mm.

Hudson and Rummel (1966) found that *Liomys salvini* is able to maintain its body weight under laboratory conditions without free water when given a diet of wild bird seed. The pulmocutaneous water loss ranged between 0.90 and 1.03 ng/mm^3 of oxygen consumed at an ambient temperature of 28°C, values comparable to those reported for other heteromyids at comparable ambient temperatures. Hudson and Rummel also found that *salvini* illustrates the characteristic heteromyid feature of poor tolerance to ambient temperatures above 34°C, although *salvini* is better able to resist lethal body temperatures when hyperthermic. *L. salvini* can tolerate ambient temperatures of 0°C for at least one hour. It maintains a relatively constant body temperature at ambient temperatures between 12 and 34°C. The mean body temperature of *L. salvini* is 37.09 ± 0.44°C. It is unaffected by ambient temperature as low as 10°C. Its basal metabolic rate was found to be 15% below predicted, which is probably characteristic of heteromyids. The average basal metabolic rate of oxygen consumption is 1070 $mm^3/hr/g$ of body weight for *L. salvini* weighing 43.8 g.

REPRODUCTION. Females carrying embryos have been taken in eight different months (those available from April and June were nonpregnant and no data are available from September or October, according to Genoways, 1973). Females with embryos formed the largest percentage of those taken in November, December, and February, although the total sample from the first two months was small. The mean number of embryos per female for this species is 3.55 (mode, three) with a range of two to six. Adult males with enlarged testes have been taken in the months of January through April and in July and August (Genoways, 1973).

Goodwin (1946:375) reported that *L. salvini* in Costa Rica bred at all seasons of the year and the usual number in the litter was four. In El Salvador, Burt and Stirton (1961:54) recorded single females taken on 8 and 9 January that each carried three embryos; Felten (1957:154) reported a female taken in February with two embryos and one taken in March with three.

Fleming (1974*a*) found that reproduction is highly seasonal in Costa Rica. Breeding season in this population was approximately six months long with an average of 1.8 litters per female being produced during this time. The average litter size was 3.8 giving an annual productivity of 6.8 offspring per female per year (Fleming, 1974*a*:508). Adults increase markedly in weight during the breeding season.

ECOLOGY. The major part of the geographic range of *salvini* is in the dry tropical lowland forests of the Pacific coast of Oaxaca, Chiapas, and Central America. The species also occurs rather extensively along the Pacific slopes of the mountains of Central America, reaching an altitude of about 1500 m around Guatemala City and 1220 m in the vicinity of San José, Costa Rica. The only region in the Caribbean drainage in which *salvini* is common is in the dry habitat along the Río Motagua and Río Negro in Guatemala and extreme northwestern Honduras. Some field observations on *salvini* can be found in Goodwin's reports on the mammals of Guatemala (1934:32–35) and Costa Rica (1946:375) and in Villa-R's account of the mammals of the department of Soconusco, Chiapas (1949).

Genoways (1973) described the local ecology of 10 areas where specimens of *Liomys salvini* were obtained. In these areas it was found to occur sympatrically with *Oryzomys fulvescens*,

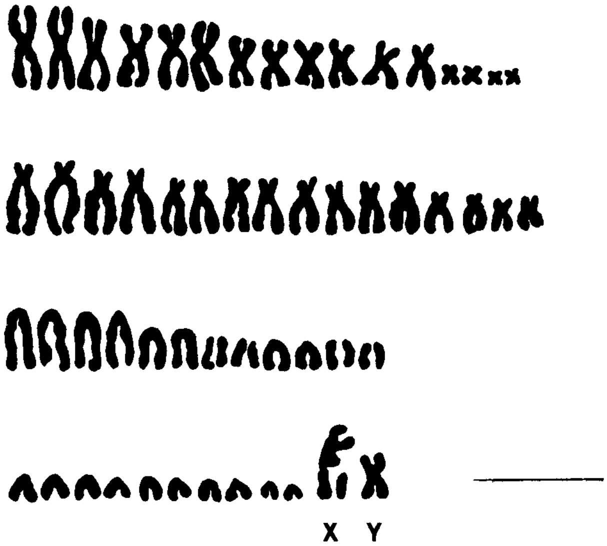

FIGURE 6. Karyotype of a male *Liomys salvini*. The scale is 10 μm.

O. palustrus, *Peromyscus gymnotis*, *P. mexicanus*, *Baiomys musculus*, *Sigmodon hispidus*, *Reithrodontomys gracilis*, *R. fulvescens*, and *Ototylomys phyllotis*. Basically the vegetation of these areas is generally lowland dry forest and lower montane dry forest, which is largely pine-oak. This species is known to occur sympatrically with *L. pictus*, the area of sympatry being in southeastern Oaxaca and northwestern Chiapas.

Fleming (1974*a*) studied the demographic characteristics of a population of *L. salvini* inhabiting the deciduous (seasonal) tropical forests of western Costa Rica. Cheek pouch contents included the following items: many *Cochlospermum vitafolium* seeds; a few *Enterolobium cyclocarpum* seeds (which are poisonous); several unidentified seeds and nuts; two beetle pupae. The changes in age composition and density of the population reflected the seasonal pattern of reproduction, which generally extended from January to about mid-June. The population density ranged from near four per ha in March to more than eight per ha in June. The overall sex ratio did not differ significantly from 1:1. Fleming calculated that for both sexes of *salvini* the minimum annual probability of survival was about 18%. The average distance between successive capture sites for males ranged from 35.2 m to 47.1 m during the year, whereas females ranged from 28.1 m to 32.8 m. The longest distance between two capture sites was found to average 71.3 m in postbreeding males and 49.5 m in breeding females. The average home range size for males ranged from 1600 m^2 to 2566.7 m^2 depending upon the season of the year, whereas the range for females was from 1311.1 m^2 to 1800 m^2 (Fleming, 1974*a*).

Twenty species of mites (14 trombiculids and six laelapids) are presently known from this Middle American species of *Liomys* as follows: *Anahaucia* sp. (Genoways, 1973:357); *Ascoschoengastia dyscrita* (Genoways, 1973:357); *Cordiseta mexicana* (Genoways, 1973:357); *Euschoengastia* sp. (Genoways, 1973:357); *Eutrombicula alfredduges* (Genoways, 1973:357); *Fonsecia* (*Parasecia*) sp. (Genoways, 1973:357); *Leptotrombidium panamense panamense* (Genoways, 1973:357); *Leptotrombidium panamense potosinum* (Genoways, 1973:357); *Microtrombicula perplexa* (Webb and Loomis, 1973:5); *Pseudoschoengastia costaricensis* (Geest and Loomis, 1968:38,40); *Pseudoschoengastia guanacastensis* (Geest and Loomis, 1968:36,38); *Pseudoschoengastia hoguei* (Geest and Loomis, 1968:25,28); *Pseudoschoengastia* sp. (Genoways, 1973:358); *Trombicula dunni* (Genoways, 1973:358); *Androlaelaps fenilis* (Genoways, 1973:358); *Eubrachylaelaps* (?) *circularis* (Genoways, 1973:358); *Hirstionyssus galindoi* (Genoways, 1973:358); *Hypoaspis lubrica* (Genoways, 1973:358); *Hypoaspis* sp. (Genoways, 1973:358); *Steptolaelaps heteromys* (Genoways, 1973:358). A listrophorid mite, *Listrophorus* sp. (Genoways, 1973:358), and a cheyletid mite, *Eucheylitia* sp. (Genoways, 1973:358), also are known from this species. Three species of ticks—*Amblyomma* sp. (Genoways, 1973:358), *Ixodes eadsi* (Genoways, 1973:358), and *Ixodes sinaloa* (Keirans and Jones, 1972:474)—and one flea (*Polygenis vulcanius*, Genoways, 1973:358) are known from this species. The one species of louse, *Fahrenholzia fairchildi*, known from *L. salvini* also has been reported from *L. adspersus* and *Heteromys desmarestianus*.

The following endoparasites were described in *Liomys salvini*. Esquivel *et al.* (1967:954) described *Trypanosoma zaledoni* based on blood smears prepared from specimens of *Liomys salvini* from Costa Rica. Caballero y Caballero (1959) reported specimens of two species of nematodes, *Trichuris* sp. and *Longistriata vexillata*, from specimens of *Liomys salvini* taken in the vicinity of Mapastepec, Chiapas. No bacterial or viral diseases have been reported from species of either *Liomys* or *Heteromys*, although 51 specimens of *Liomys salvini* were examined during a leptospirosis survey in Nicaragua (Clark *et al.*, 1966).

GENETICS. In *Liomys salvini* the diploid number is 56 including eight pairs of metacentrics, eight pairs of submetacentric-subtelocentrics, and 11 pairs of telocentrics (Genoways, 1973). The X-chromosome is a large submetacentric and the Y-chromosome is a medium-sized metacentric. The fundamental number is 86 (figure 6).

BEHAVIOR. Fleming and Brown (1975) studied the seed hoarding and burrowing behavior of *L. salvini* and concluded that this species is a strong seed hoarder and usually places its nest in a burrow system. These are characteristics shared with most other heteromyid rodents. Fleming (1974*b*) found in both laboratory and field observations that individuals of *salvini* were less tolerant of conspecifics than were individuals of *Heteromys desmarestianus*. This conclusion stems from the fact that dominant-subordinant relationships are more often formed, retaliatory behavior is more frequent, submissive behavior is less frequent, and home ranges are less likely to be clumped in *L. salvini* than in *H. desmarestianus*. Fleming believed that this might support the hypothesis that populations of *Liomys* are "closed-dispersed." In laboratory encounters size was found to be a good predictor of dominance in *Liomys salvini*.

ETYMOLOGY. The specific name *salvini* gives patronymic recognition to Osbert Salvin who collected the holotype on 31 July 1873 at Dueñas, Guatemala. The subspecific name *crispus* is Latin meaning curled, probably referring to the curled hairs on the back of this species. The subspecific name *vulcani* refers to the place of capture of the holotype of this subspecies, at Volcán de Chinandega, Nicaragua.

REMARKS. Genoways (1973) placed *Liomys salvini* in a group with *Liomys adspersus* within the genus. He believed that these two species had diverged in relatively late Wisconsin time. The ancestral stock for these species was probably isolated along the west coast of Central America south of the Isthmus of Tehuantepec.

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