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Heteromys gaumeri.

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Heteromys Desmarest, 1817

Heteromys Desmarest, 1817:181. Type species *Mus anomalus* Thompson, 1815.

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciurognathi (Carleton, 1984), Infraorder Myomorpha, Superfamily Geomyoidea, Family Heteromyidae, Subfamily Heteromyinae.

The genus *Heteromys* includes seven to ten species, depending on authority consulted, arranged in two subgenera. The subgenus *Heteromys* includes *H. anomalus*, *H. australis*, *H. desmarestianus*, *H. gaumeri*, and *H. goldmani*; the subgenus *Xylomys* includes *H. nelsoni* and *H. oresterus*. A key to species follows (modified from Goldman, 1911; Hall, 1981):

1 Adult pelage composed of soft bristles, resembling juvenile pelage of other members of the subfamily 2
Adult pelage composed of stiff bristles or spines 3

2(1) Ears edged with white, posterior ends of premaxillae extending beyond posterior margins of nasals, posterior molars narrower than premolars ..... *H. oresterus*
Ears without white edges, posterior ends of premaxillae flush with posterior margins of nasals, posterior molars equal to or broader than premolars ..... *H. nelsoni*

3(1) Soles of hind feet haired posterior to last tubercle, broad, bright orange-buff lateral line present ..... *H. gaumeri*
Soles of hind feet naked, orange-buff lateral line narrow or absent 4

4(3) Inner side of forearm dusky 5
Inner side of forearm white 6

5(4) Length of tail usually less than 145 mm in adults and about equal to length of head and body, underhairs on dorsum grayish ..... *H. australis*
Length of tail usually greater than 145 mm in adults and greater than length of head and body, underhairs on dorsum dull orange-buff ..... *H. anomalus*

6(4) Length of head and body usually greater than 140 mm and length of tail greater than 170 mm in adults, underhairs on dorsum grayish, lateral line absent ..... *H. goldmani*
Length of head and body usually less than 140 mm and length of tail less than 170 mm in adults, underhairs on dorsum orange-buff, narrow lateral line present ..... *H. desmarestianus*

Heteromys gaumeri Allen and Chapman, 1897

Gaumer's Spiny Pocket Mouse

Heteromys gaumeri Allen and Chapman, 1897:9. Type locality "Chichen-Itza, Yucatan, Mexico."

CONTEXT AND CONTENT. Context as noted above for genus. Subgenus *Heteromys*, *desmarestianus* species group. *H. gaumeri* is monotypic (Engstrom et al., 1987; Goldman, 1911).

DIAGNOSIS. *Heteromys gaumeri* differs from other *Heteromys* by the presence of hair on the posterior portion of the sole of the hind foot, which is naked in all other species in the genus (Genoways, 1973; Goldman, 1911). *H. gaumeri* is geographically isolated from all other heteromyines except *H. desmarestianus*, with which it might overlap on the southern portion of the Yucatán Peninsula (Engstrom et al., 1987; Jones et al., 1974). Morphologically, *H. gaumeri* is distinguished from *H. desmarestianus* by averaging smaller in most external and cranial measurements; having relatively large auditory bullae; having a broad, bright ochraceous (orange buff) lateral line extending onto cheeks and ankles (a narrow pale-ochraceous lateral line often is present in *H. desmarestianus*, but seldom extends onto cheeks and ankles); having a relatively well-haired tail with a conspicuous terminal tuft (the tail in *H. desmarestianus* is sparsely haired, without a conspicuous terminal tuft); and in having a baculum with a relatively narrow shaft (Engstrom et al., 1987; Genoways, 1973; Goldman, 1911). *H. gaumeri* has a diploid number of 56 chromosomes whereas *H. desmarestianus* and all other members of the subgenus *Heteromys* have a diploid number of 60 (Engstrom et al., 1987; Rogers, 1989).

GENERAL CHARACTERS. *Heteromys gaumeri* (Fig. 1) is a medium-sized orange-buff to gray spiny pocket mouse. In general coloration, it resembles *Liomys pictus* and *L. spectabilis* more than other species of *Heteromys*. Engstrom et al. (1987:301) described *H. gaumeri* (Figs. 1, 2) as follows: "Dorsal coloration of adults ranges from dark to medium gray, with heavy admixture of orange buff hairs lending an overall ochraceous cast to the otherwise gray dorsum (adults in worn pelage appear more ochraceous and molting individuals often have a 'salt and pepper' appearance); rich orange buff lateral line, usually broad and conspicuous, extending from cheeks to base of tail, ochraceous hairs often extending onto dorsal and ventral surfaces of ankle; margins of forearm orange buff, interrupted on dorsal surface by white line; venter and feet white; tail well haired, grayish brown above, dull white below, with conspicuous terminal tuft of hairs; ears dusky, lightly edged with dull white; sole of hind foot haired, posteriorly. Subadults medium to dark gray above, dorsum without ochraceous hairs; ochraceous lateral line faint and narrow. Juvenile pelage similar to that of subadults, but spiny hairs on dorsum absent. Tail longer than head and body; soles of hind feet with six tubercles; body size medium for the genus. Skull size medium, with relatively large auditory bullae; lower permanent premolar with three lophs; upper and lower molars with three lophs, enamel island formed between metaloph (id) and cingulum disappearing quickly with wear."

In Gaumer's spiny pocket mouse, males average larger than females for most external and cranial characters, however, sex accounts for only a minor component (average 0.9%) of total variance within samples. Most external and cranial measurements vary significantly with age and age contributes the major component (average of 53.1%) of total within-sample variance. Although levels of age and sexual variation are comparable to other heteromyines, most mensural and pelage characters do not vary geographically. In contrast to other heteromyines, those characters that are significantly heterogeneous among localities appear to lack any spatial pattern (Engstrom et al., 1987).

Means and ranges (in parentheses) of selected external and cranial measurements (in mm) of adult males and females (Engstrom et al., 1987) are: total length, 261.2 (235 to 288); length of tail, 145.5 (137 to 159); length of hind foot, 34.2 (32 to 36); length of ear, 17.4 (17 to 19); greatest length of skull, 35.2 (33.9 to 37.5); zygomatic breadth, 16.1 (15.3 to 16.7); mastoid breadth, 15.3 (14.8

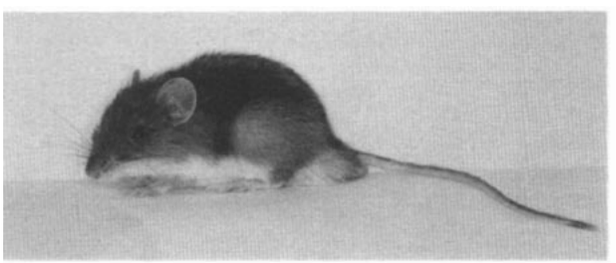

FIG. 1. Adult male *Heteromys gaumeri* from 27.5 km S Constitucion, Campeche, México. Photograph by M. D. Engstrom.

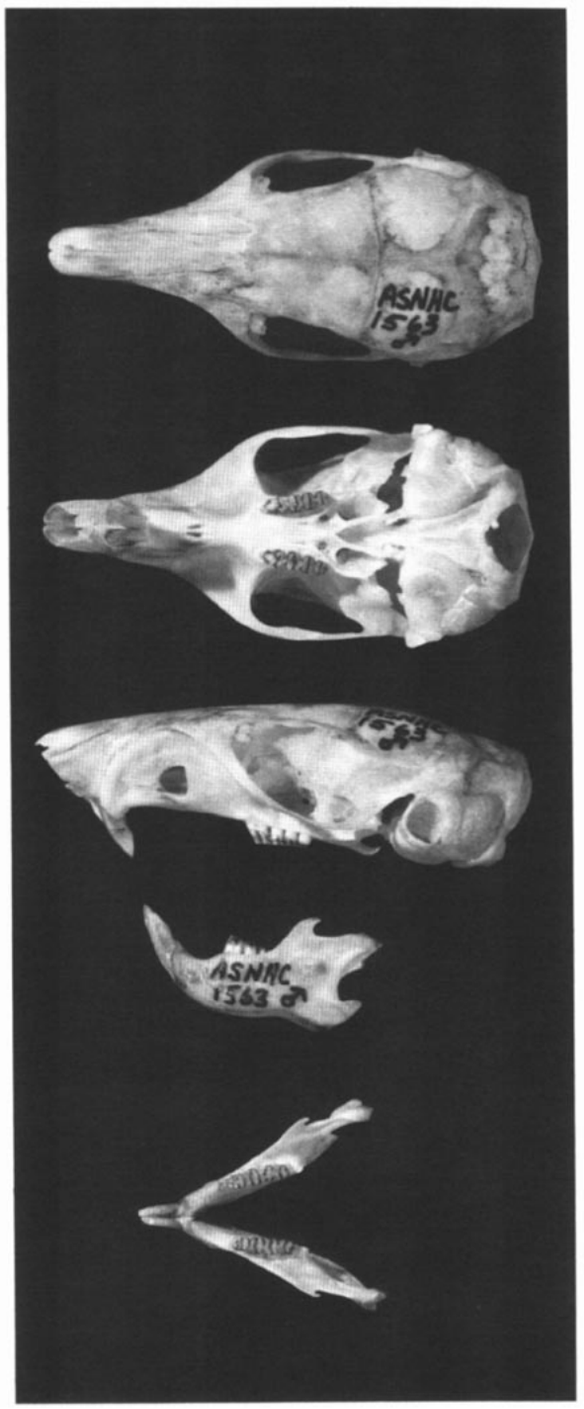

FIG. 2. Dorsal, ventral, and lateral views of the cranium, and lateral and dorsal views of the mandible of an adult male *Heteromys gaumeri* from 7.9 km E Sihochac, Campeche, México (Angelo State Natural History Collections 1563). Greatest length of skull is 35.6 mm.

to 15.9); length of nasals, 14.3 (13.2 to 15.6); length of maxillary toothrow, 4.9 (4.7 to 5.2); depth of braincase, 9.0 (8.5 to 9.5). Means and ranges (in parentheses) of weights (in g) for four adult males and six adult females (Birney et al., 1974) are, respectively, 70.7 (62.0 to 85.4) and 56.6 (43.2 to 65.3).

DISTRIBUTION. *Heteromys gaumeri* is endemic to the Yucatán Peninsula and has been taken there at elevations from sea level to 100 m. The geographic range of *H. gaumeri* (Fig. 3) includes: northern Belize; El Petén, Guatemala; eastern Tabasco, México; and

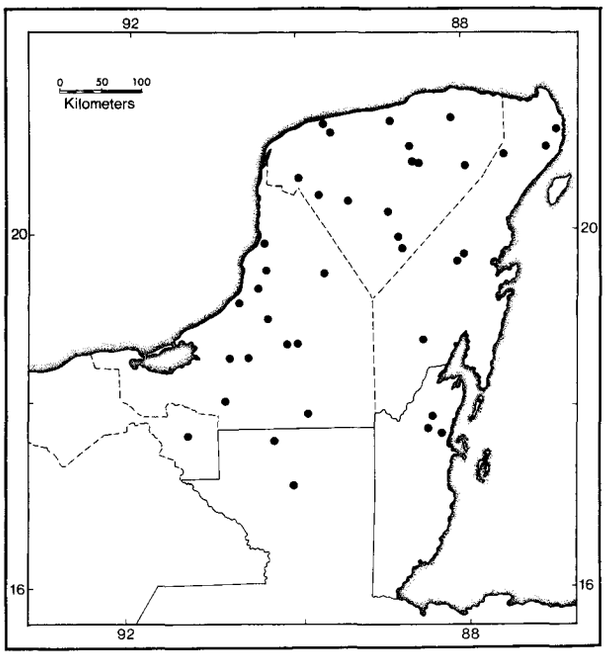

FIG. 3. Distribution of *Heteromys gaumeri* on the Yucatán Peninsula of North America. Collecting localities indicated by solid circles (modified from Engstrom et al., 1987).

the Mexican states of Campeche, Quintana Roo, and Yucatán (Dowler and Engstrom, 1988; Engstrom et al., 1987; Izor and McCarthy, 1984; Jones et al., 1974; Ryan, 1960).

FOSSIL RECORD. Alvarez (1982) reported fossil remains (primarily postcranial material and mandibles) of *H. gaumeri* from Pleistocene and Holocene cave deposits in Loltún, Yucatán. Hatt et al. (1953) reported sub-Recent deposits from several other caves in the state of Yucatán.

FORM. The dental formula of *H. gaumeri* is i 1/1, c 0/0, p 1/1, m 3/3, total 20. The upper premolar consists of a protoloph, metaloph, and posterior cingulum. The protoloph and metaloph are each composed of three cusps and the two lophs are separated by a Y-shaped median valley of enamel, the lingual portion of which persists in some specimens until they are old adults. The posterior cingulum is well-developed and is separated from the hypocone of the metaloph by a lingual re-entrant angle of enamel which, upon wear, forms an island of enamel surrounded by dentine. This island persists for some time with further wear, but does not persist as long as the enamel valley between the protoloph and metaloph (Genoways, 1973).

The lower premolar is composed of three lophs, an anterior cingulum, protolophid, and metalophid. The anterior cingulum is well-developed and composed of two or more cusps. The protolophid comprises three united cusps, anteroconid, protoconid, and mesoconid. With wear, the anteroconid is the first cusp to be united (along its lingual margin) to the anterior cingulum. The metalophid is composed of two united cusps and is separated from the protolophid by a deep, median valley of enamel. There is no posterior cingulum (Genoways, 1973).

The upper and lower molars are composed of three lophs(ids), a protoloph(id), metaloph(id), and posterior (upper) or anterior (lower) cingulum. The cingulum is well-developed in both the upper and lower molars; it is nearly as long as the metaloph and about half the length of the metalophid. The cingulum is connected to the metaloph(id) along the lingual margin of the tooth, but separated from that loph(id) along the labial margin at early stages of wear. The two lophs(ids) are united along their labial margins as wear progresses, isolating one or more islands of enamel between them. These islands disappear with further wear, and, in the upper molars, persist for a much shorter period of time in *H. gaumeri* than in *H. desmarestianus* (Genoways, 1973).

The baculum is similar to that of *H. desmarestianus* and has

a broad base comprising about one-third the total length of the bone. A narrow oval shaft (almost needle-like in some specimens) makes up the remaining two-thirds and ends in a slightly upturned tip. Selected bacular measurements (in mm) of two adult *H. gaumeri* are: length of baculum, 8.1, 8.8; height of base, 1.65, 1.75; and width of base, 1.25, 1.45 (Genoways, 1973).

Soles of the hind feet in *H. gaumeri* have six plantar tubercles and are haired posteriorly (Genoways, 1973; Goldman, 1911). Overhairs taken from the dorsum of the body are widely and deeply troughed on the dorsal surface. The ventral hair surface is domed, but flattened near the ridges of the dorsal trough. Individual hairs consist of a narrow base that quickly flares to a broad shaft and then tapers gradually to the tip. Overhairs of *H. gaumeri* are longer and wider than other species of *Heteromys*; lengths and widths (in mm) of individual hairs range from 12.5 to 14.0 and 0.26 to 0.37, respectively (Homan and Genoways, 1978).

REPRODUCTION. *Heteromys gaumeri* appears to have a relatively distinct breeding season beginning near the end of the dry season, continuing through the wet season, and perhaps ending in January. Reproduction appears to be "asynchronous" with females in all stages of reproduction present in one population. Testes sizes of subadult and adult *H. gaumeri* caught between 23 April and 10 May ranged (in mm) from 6 by 3 for a subadult to 21 by 13 for an adult. Four of 11 females collected during the same period were pregnant (Birney et al., 1974). A pregnant female taken on 26 December and males with enlarged testes in March, April, July, and August were reported by Genoways (1973). None of seven females collected in Tabasco in July was pregnant, although both scrotal and nonscrotal males were present in the same population (Dowler and Engstrom, 1988). Gaumer (1917) stated that females of *H. gaumeri* gave birth to four young, although litter sizes ranging from two to four have subsequently been reported (Birney et al., 1974; Genoways, 1973).

ECOLOGY. *Heteromys gaumeri* occurs in a variety of habitats on the Yucatán Peninsula from tall to medium-height subdeciduous-subperennial tropical rainforest in the south and east, to short tropical deciduous forest and thorn forest in the north and northwest (Miranda and Hernandez X., 1963). This species often is common in cultivated areas. *H. gaumeri* has been reported from the following habitats: herbaceous vegetation along roadsides and bordering sugarcane fields in Yucatán and Quintana Roo (Hatt and Villa, 1950); dense thorn forest and cornfields surrounded by thorn forest in Yucatán (Birney et al., 1974); secondary deciduous forest and brushy areas near a river in eastern Tabasco (Dowler and Engstrom, 1988); along fallen logs and in dense vegetation at the base of trees within primary forest in Petén, Guatemala (Ryan, 1960); and in riparian deciduous seasonal forest in Belize (Izor and McCarthy, 1984). In Belize, *H. gaumeri* was collected in broadleaf forest characterized by the occurrence of the trees *Achras zapota, Bursera simaruba, Guazuma* sp., *Acacia* sp., and *Lonchocarpus* sp.; palms (*Sabal* sp. and *Crysophila* sp.) also were present, but less abundant (Izor and McCarthy, 1984). Other species of rodents taken in association with *H. gaumeri* include: *Sciurus yucatanensis, S. deppei, Orthogeomys hispidus, Sigmodon hispidus, Oryzomys melanotis, O. couesi, O. fulvescens, Ototylomys phyllotis, Otonyctomys hatti, Reithrodontomys gracilis, Peromyscus leucopus, P. yucatanicus, Mus musculus, Rattus rattus, Dasyprocta punctata, Agouti paca*, and *Coendu mexicana* (Birney et al., 1974; Dowler and Engstrom, 1988; Izor and McCarthy, 1984; Jones et al., 1974).

Heteromys gaumeri is known to harbor the following ectoparasites: mites, Trombiculidae (*Cordiseta mexicana, Ectonyx fusicornis, Fonsecia gurneyi, Leptotrombidium panamense, Odontacarus cayolargoensis, Pseudoschoengastia extriseca, P. scitula*; Loomis, 1969), Laelapidae (*Androlaelaps fahrenholz, Eubrachylaelaps jamesoni, Hypaspis lubrica, H.* sp., *Steptolaelaps heteromys*: Genoways, 1973), and Glycyphagidae (*Dermacarus ornatus, Neolabidophorus yucatanensis*; Pence and Genoways, 1974); ticks, Ixodidae (*Amblyomma* sp., *Ixodes* sp.; Genoways, 1973); and anopluran lice, Hoplopleuridae (*Fahrenholzia ferrisi*; Emerson, 1971). No endoparasites have been reported from Gaumer's spiny pocket mouse.

GENETICS. The karyotype (Fig. 4) has a diploid number of 56 and a fundamental number of 76. The autosomal complement consists of a graded series of 11 pairs of large to small-sized metacentric and submetacentric chromosomes and 16 pairs of large to small-sized acrocentrics or subtelocentrics (here scored as uniarmed in the calculation of the fundamental number). The sex chromosomes consist of a large submetacentric X and a medium-sized subtelocentric Y. No chromosomal variation has been noted among individuals or populations (Engstrom et al., 1987).

FIG. 4. Karyotype of a male *Heteromys gaumeri* from 7.5 km W Escárcega, Campeche, México (Engstrom et al., 1987).

Levels of genetic variation within populations of *H. gaumeri*, as measured by protein electrophoresis, are comparable to values reported for most heteromyine rodents, but low when compared to rodents in general. In four populations of *H. gaumeri*, mean proportion of polymorphic loci per population was 0.025 and average proportion of loci heterozygous per individual was 0.002. Genetic distances among these populations (average Rogers $D = 0.025$) also were small (Patton and Rogers, in press *a*).

REMARKS. The number of species currently recognized within the genus *Heteromys* varies among authors. For example, Hall (1981) and Honacki et al. (1982) included 10 nominal species in the genus (although Hall, 1981, suggested that the genus was in need of revision), whereas Best (in press), Patton and Rogers (in press *a*, in press *b*), and Rogers (1989) recognized only seven described species. Additionally, Patton and Rogers (in press *a*) noted the presence of two undescribed species, one from Costa Rica and one from Panama. In this review, we followed the last group of authors and the seven described species are included in the key to species.

Subgeneric affinities within *Heteromys* also are unclear. Patton and Rogers (in press *a*, in press *b*) and Rogers (1989) questioned the monophyly of the subgenus *Xylomys* and noted that chromosomally, *H. oresterus* is more similar to members of the subgenus *Heteromys* than to *H. nelsoni* (the other member of the subgenus *Xylomys*). Goldman (1911) included *H. gaumeri* within the *desmarestianus* species group in the subgenus *Heteromys* for convenience, but noted that it was not closely related to any living species of *Heteromys*. On the basis of morphological and karyotypic differences, Engstrom et al. (1987) recommended that *H. gaumeri* be removed from the *desmarestianus* group and suggested that it might warrant recognition as a subgenus distinct from other *Heteromys*.

The generic name, *Heteromys*, is from the Greek for different or other (*Hetero*) and mouse (*mys*) in reference to the original description of the type as *Mus anomalus*. The specific name, *gaumeri*, was named in honor of George F. Gaumer, naturalist and student of the flora and fauna of the Yucatán Peninsula. The Mayan vernacular name for *H. gaumeri* is "puten put."

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