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**NOTES ON CLASSIFICATION OF THE
RODENT GENUS *PEROMYSCUS***

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New information which bears on classification of *Peromyscus* is the basis and reason for this report. It specifically supplements that presented a few years ago (Hooper, 1958) when two classifications of the genus were compared—one based on conventional cranial information, the other suggested by data from the glans penis. The two schemes were in general agreement but the few points of disagreement were sufficiently impressive to suggest that the classifications should again be reviewed when data on additional species had been accumulated.

We now have information on phalli of 11 additional species. Moreover, we have reviewed the earlier data (*op. cit.*) and, in addition, have examined skins and skulls of most of the kinds treated in both the 1958 and present reports. In studying the phalli of these 37 species of *Peromyscus* and *Ochrotomys* (the latter formerly in *Peromyscus*), and examining the skins and skulls of 34 of them, we conclude (1) that the phallic and cranial data are in harmony as long as no special weight is given to characters of the molar teeth and (2) that current supraspecific groupings in *Peromyscus* (Miller and Kellogg, 1955; Hall and Kelson, 1959) need revision; some make little sense from the standpoint of geographic distribution, evolution, total morphology, and biology of the species. An alternative, to us more meaningful, arrangement is suggested in the last few pages of this report.

Preceding that classification are descriptions of phalli of 18 species which received inadequate or no attention in the 1958 report. These species accounts, which are arranged to accord with the already defined phallic groups (Hooper, 1958), are based on the following specimens.

Peromyscus sejugis: México, Baja California, 2.

P. crinitus: California, Los Angeles Co., 2.

P. hylocetes: México, Michoacán, 2.

P. oaxacensis: México, Chiapas, 2; Oaxaca, 2.

- P. evides*: México, Michoacán, 9.
P. ochraventer: México, Tamaulipas, 3.
P. angustirostris: México, Hidalgo, 10.
P. zarhynchus: México, Chiapas, 8.
P. collatus: México, Sonora, 1.
P. dickeyi: México, Baja California, 2.
P. guardia: México, Baja California, 2.
P. flavidus: Panamá, Los Santos, 5.
P. pirrensis: Panamá, Darien, 6.
P. thomasi: México, Guerrero, 8.
P. banderanus: México, Colima, 2; Guerrero, 1; Michoacán, 3.
P. floridanus: Florida, Alachua Co., 4.
P. lepturus: México, Oaxaca, 8.
Ochrotomys nuttalli: Florida, Alachua Co., 1; Oklahoma, Pushmataha Co., 1.

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DESCRIPTIONS OF PHALLI

In the following accounts the species of *Peromyscus* are arranged in "divisions" and "groups" which are defined on the basis of morphology of glans and baculum (following Hooper, 1958). This differs from our revised arrangement, based on more comprehensive material and presented on pages 12-13.

MANICULATUS DIVISION

Maniculatus Group

Peromyscus sejugis.—The two phalli examined closely resemble specimens of *maniculatus*.

Intermediate Forms

P. crinitus.—After studying the available specimens, including two excellently prepared, recently acquired examples, we continue to view *crinitus* as a member of the *Maniculatus* Division, not the *Eremicus* Division where customarily it is placed. Present specimens of *crinitus* clearly fit not with examples of *eremicus* and *californicus* but with the *maniculatus-boylei* assemblages. In our opinion that is where the crania fit also.

TABLE 1
MEASUREMENTS AND PROPORTIONS OF THE GLANS PENIS IN
SPECIES OF *Peromyscus* AND *Ochrotomys*

Genus and species	Specimens	Hind foot length	Glans		Baculum, lengths		Ratios, $\times 100$			
			length	diameter	bone	cart. tip	glans/foot	diam. glans/length glans	bone/foot	
<i>Peromyscus</i>										
<i>hylocetes</i>	2	26	8.0	2.1	10.9	0.1	32	26	43	
<i>oaxacensis</i>	4	24	7.3	2.0	10.1	0.3	32	27	43	
<i>evildes</i>	5	23	8.7	2.0	12.1	0.1	38	22	53	
<i>ochraventer</i>	3	25	7.5	1.3	11.8	0.2	30	18	47	
<i>angustirostris</i>	9	30	12.6	2.0	17.1	0.3	43	16	57	
<i>zaryhinchus</i>	5	32	11.0	2.4	17.7	0.3	34	22	55	
<i>flavidus</i>	2	34	13.4	8.3	17.2	...	39	62	51	
<i>pirrensis</i>	3	36	13.3	9.2	16.4	...	37	69	46	
<i>thomasi</i>	6	32	15.2	6.1	18.5	0.7	47	40	57	
<i>lepturus</i>	7	28	5.1	1.3	7.7	0.2	18	26	27	
<i>Ochrotomys nuttalli</i>	1	18	4.9	2.2	3.8	1.0	27	45	21	

Boylei Group

P. hylocetes.—Working with a few poorly preserved phalli, Hooper (1958) could not be sure of characters of *hylocetes*. Because the comparatively short, fluted glandes, each with a short protractile segment, somewhat resembled the vase-shaped distally flared glandes of *eremicus* and *californicus*, Hooper tentatively grouped *hylocetes* in his Eremicus Division. Further study of the original somewhat distorted material together with additional specimens indicates that the glans and baculum of *hylocetes* are not like those of *eremicus* or *californicus*. Instead they fit with *oaxacensis*, and the two of them morphologically connect through *evides* (and probably *aztecus*) to *boylei*. Cranially, externally, and ecologically, also, the species *hylocetes*, *oaxacensis*, *aztecus*, and *evides* are similar.

P. oaxacensis.—The specimens of this species resemble those of *P. hylocetes*. The surface of the comparatively short glans (Table 1) is fluted, its distal border is scalloped (with no ventral flap guarding the meatus urinarius and no dorsal lappets), and its protractile segment is comparatively short. The spiny coat is like that in other species of the Maniculatus Division. The baculum is a simple osseous rod, longer than the glans (Table 1), which is expanded basally and is tipped with a cartilaginous cone.

P. evides.—In most features, the specimens of *evides* resemble those of *hylocetes* and *oaxacensis*, but they approach *boylei* in some traits. For example the protractile tip is relatively longer and the fluting is slightly less pronounced on the surface of the glans than in *hylocetes* and *oaxacensis*. In absolute lengths (Table 1) the specimens exceed those of *hylocetes*, *oaxacensis*, and *boylei*. Phallic data, in addition to cranial and ecologic information (Osgood, 1909; Hooper, 1955, 1961), indicate that *evides* is specifically distinct from *P. boylei*.

P. ochraventer.—The specimens of *ochraventer* are referable to the Boylei Group of Hooper (1958). In size they resemble examples of *P. boylei* (e.g., *levipes*), but for the most part they appear to be small versions of *furvus* or *angustirostris* (Table 1). In them, as in the examples of *furvus*, the protractile tip of the rod-like glans is relatively short and attenuate (shorter and less attenuate than in *mexicanus*, *nudipes*, and allied species), there are two prominent dorsal lappets, and a single ventral flap guards the meatus urinarius. The small, widely spaced spines that invest the surface of the glans, however, are relatively much smaller than in *furvus*. The baculum resembles that of *furvus*. Its laterally expanded and dorsoventrally flattened

base merges into a relatively gross shaft which, subapically constricted, terminates in a dorsally directed head; the head is capped with a low cone of cartilage.

P. angustirostris.—To judge from our excellent series, *angustirostris* is phallically much like *fervus*, possibly identical with it. The two forms are similar in size and proportions, and in both the baculum bears a peculiar head (unlike most other species of the genus), and the protractile distal segment of the glans appears to be rather short, shorter than in *mexicanus*, *nudipes*, *guatemalensis*, and *zarhynchus*.

P. zarhynchus.—The specimens of *zarhynchus* are morphologically near those of *guatemalensis* and *nudipes*. The long glans (Table 1) bears two prominent, relatively short, dorsal lappets, and a single ventral lip lies at the base of the protractile tip (Fig. 1). The spines of the investiture possibly are relatively smaller than in *guatemalensis* or *nudipes*. The long, slim, bowed, cone-capped baculum resembles bacula of *guatemalensis* and *nudipes*.

EREMICUS DIVISION

P. collatus.—The specimen at hand definitely belongs with samples of *eremicus* and *californicus*; it fits best with the specimens of *eremicus*.

P. dickeyi.—The specimens of *P. dickeyi* are like those of *P. eremicus*.

P. guardia.—The two specimens resemble examples of *P. eremicus*.

FLAVIDUS DIVISION

To judge from our samples of adult, well preserved specimens, *pirrensis* and *flavidus* are phallically well differentiated from other *Peromyscus*. They differ from *maniculatus* and *boylei* about as much as do *eremicus* and *californicus*; thus, they warrant division ranking if those other two pairs do. The large, cone-shaped, heavily spinous glans, with its bulbous, nonspinous, protractile mound that contains the tip of the baculum and the urethral opening (Fig. 1), is unlike other glandes of *Peromyscus*.

P. flavidus.—The examples of *flavidus* are smaller than those of *pirrensis* and there are a few other minor differences between the two samples; in essence, *flavidus* appears to be a slightly smaller replica of *pirrensis*.

P. pirrensis.—The specimens of *pirrensis*, more satisfactory than those of *flavidus*, are described in detail. The adult glans is cone-shaped, small in diameter basally and flared distally (Fig. 1), its

greatest diameter two-thirds its length and its length about one-third that of the hind foot (Table 1). Its comparatively even contours are interrupted midventrally by a slight groove which is confluent distally with a midventral notch (in the distal border or rim of the glans body) situated just proximal to a terminal mound of soft, nonspinous tissue. This mound covers the tip of the baculum and contains, immediately ventral to the baculum, the meatus urinarius. The surface, excepting that of the terminal mound, is impressively armed with large, long, sharp, proximally directed spines; these are largest in the basal half of the glans. The baculum is a long osseous rod, its basal part expanded laterad, the remainder cylindrical and but slightly tapered; its rounded tip is covered with cartilage which is diffuse, not formed as a spine or cone.

THOMASI DIVISION

P. thomasi.—Hooper's description (1958:17) of the phallus of *thomasi* was based on two ill-preserved specimens. A group of recently collected excellent specimens provides sound foundation for a more complete description of the glans and baculum of this species.

The awl-shaped glans (Fig. 1) is divisible into two topographic regions. Its basal two-thirds is fluted and densely studded with large spines (these relatively larger and shorter than those in *pirrensis* or *flavidus*); by contrast, in its distal one-third there are few flutings and few or no spines (none in a midventral sector). The position of the urethral opening apparently varies with amount of distention of the urethra. When the urethra is engorged with semen the position of the meatus is terminal and ventral to the baculum (Hooper, 1958: Pl. IX). When the urethra is not engorged, the loose spineless tissues of the ventral sector extend distad and form a hood over the baculum; then the meatus opens dorsad (Fig. 1). At about midlength in the glans the lumen of the urethra is expanded to form an elongate crater somewhat like that in *Ototylomys* or *Neotoma* (Hooper, 1960). Only the tip of the baculum is free of the crater walls; the remainder of it in the crater is bound middorsally to the crater wall and projects as a ridge into the crater. A urethral flap also is present within the crater. Insofar as known this condition—presence of internal crater with urethral flap—is unique in *Peromyscus*. It is an annectent condition between those seen in peromyscines and neotomyines. The baculum, which definitely fits with other *Peromyscus* not with neotomyines, is as described earlier (Hooper, 1958:17).

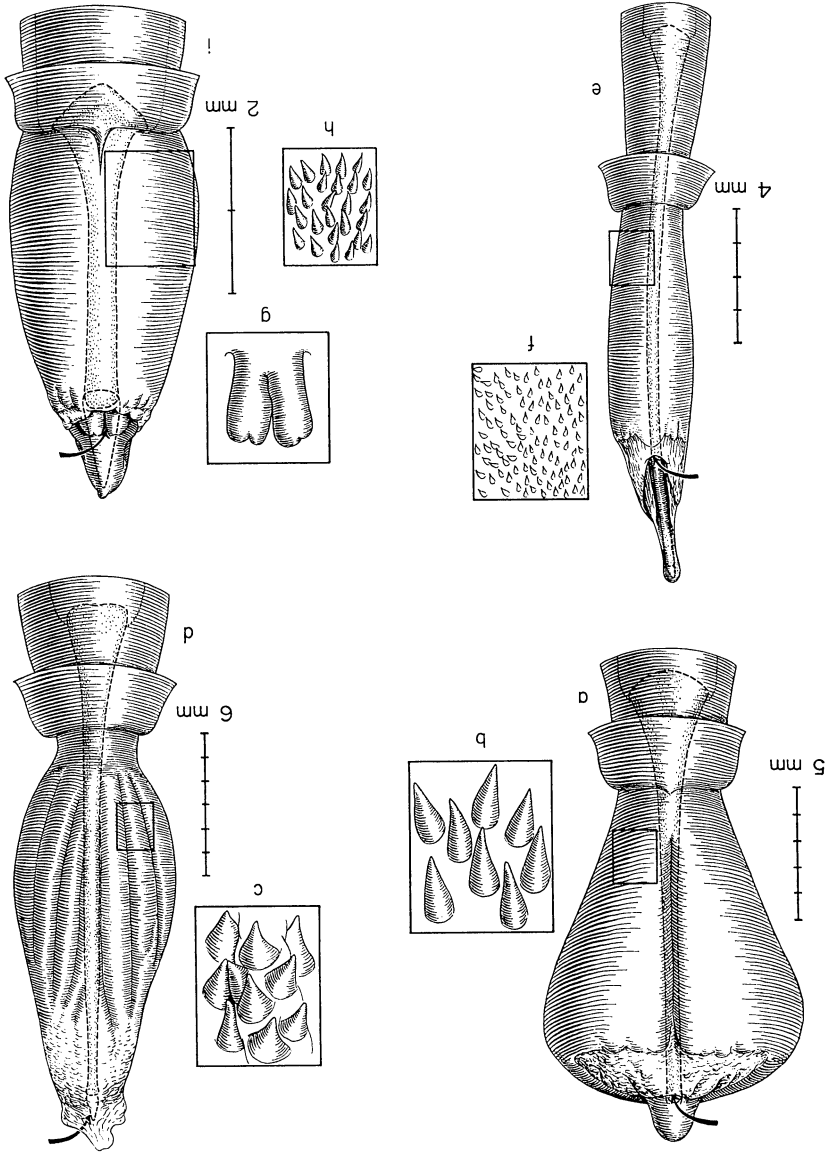


FIG. 1. Ventral view of glans penis (arrows indicate meatus urinarius), spines (enlarged to same scale), and urethral flap (enlarged, ventral aspect, g) in four species: a, b, *Peromyscus fitzingeri* (UMMZ P-3897), Panama; c, d, *P. thomasi* (UMMZ 112885), Guerrero; e, f, *P. zarhynchus* (UMMZ 10987), Chiapas; g, h, ? *Ochrotomys nuttalli* (UMMZ 110459), Florida.

BANDERANUS DIVISION

P. banderanus.—Additional examples of this species are phallically like those already described (Hooper, 1958:18), and it is now clear that the small awl-like glans with its simple bone entirely confined within it set *banderanus* apart from other *Peromyscus*. In size and shape of glans and position of meatus it resembles *Neotomodon alstoni* (Hooper, 1959:5), and in some respects its glans recalls that of *P. floridanus*. *P. banderanus* clearly is phallically peripheral to the mass of species in *Peromyscus*.

FLORIDANUS DIVISION

P. floridanus.—In recently acquired examples the glans and baculum are as described (Hooper, 1958:18, Pl. XI) except that the distal one-half and the extreme basal portion of the glans are superficially smooth, in contrast to most of the proximal one-half which is somewhat rugose and densely invested with minute spines. Phallically, *floridanus* somewhat resembles *Neotomodon alstoni* (Hooper, 1959:5) and *P. lepturus*. It, like *banderanus*, outlies the main cluster of species in *Peromyscus*.

LEPTURUS DIVISION

P. lepturus.—A series of well preserved specimens provides additional information on *lepturus*; measurements of seven adults are listed in Table 1. Characteristics of the glans and baculum are essentially as described (Hooper, 1958:19, Pl. XII). The short simple glans is slightly rugose, but completely nonspinous. The meatus urinarius is situated in the ventral sector near the tip; its ventral margin is bilobed. Lateral and proximal to the meatus is a pair of grooves. The baculum, much longer than the glans, is capped by a cone of cartilage.

OCHROTOMYS NUTTALLI

Recently received, well preserved examples of *nuttalli* provide the basis for re-illustration (Fig. 1) and a few corrections of the earlier description (Hooper, 1958:20). The first specimen figured (*ibid.*: Pl. XIV) was unnatural because it had been processed excessively; however, most essential features of the species were shown or were mentioned in the text. The present additions do not in any way modify the earlier conclusion that *nuttalli* should be divorced from *Peromyscus*.

The glans is more elongate, less like an urn, than as originally shown. Most of the surface is covered with unusually large spines; however, the short protractile tip and an adjoining portion of the glans is smooth and spineless. A bilobed urethral flap guards the meatus urinarius; when the glans is viewed ventrally the two processes of the flap are visible in the midventral notch which is situated at the base of the protractile tip (Fig. 1). The distal margin of the glans body is scalloped. The bone is capped with a long cartilaginous cone (Table 1).

CLASSIFICATION OF *PEROMYSCUS*

The current classification of *Peromyscus* (Miller and Kellogg, 1955; Hall and Kelson, 1959) is fundamentally that of W. H. Osgood (1909), the latest revisor of the genus. Like other classifications his was a best estimate of interrelationships as judged from cranial and external information. It was an excellent estimate, perhaps the best to that date in neomammalogy. It has stood the test of time and the accumulation of pertinent new information, for most of that new information has served to support, rather than to oppose, Osgood's views of the species. Some has not bolstered it. For example, a set of data regarding the molar teeth (Hooper, 1957) indicates that some of Osgood's key characters are more variable than he supposed and, therefore, that they may not warrant the reliance that he gave them in classification.

To date two important changes have been made in Osgood's scheme. First *Baiomys*, and more recently (Hooper, 1958) *Ochrotomys*, has been excluded from *Peromyscus*. These deletions make sense from the point of view of the known biology of the forms; for *Baiomys* and *Ochrotomys* morphologically and probably phyletically are no closer to *Peromyscus* (*s. s.*) than are *Scotinomys*, *Neotomodon*, and possibly *Reithrodontomys*. In effect this is to say that if the scope of *Peromyscus* includes *Baiomys* and *Ochrotomys* it also encompasses *Scotinomys*, *Neotomodon*, and possibly *Reithrodontomys*. Yet each of those groups of forms not only is morphologically distinctive but also it represents a different mode of existence and probably a separate phyletic branch. These are reasons for viewing each as a genus rather than as a subgenus of a single unwieldy genus. Divorced of all of those forms, *Peromyscus* (*s. s.*) becomes morphologically coherent and probably a close phyletic unit.

We suggest that the current classification of *Peromyscus* needs to be further modified to accord with current knowledge, and below

we present a rearrangement of the species. The basis for this reclassification is primarily data derived from the glans and baculum. But the basis is really much broader than that. It includes information from skin and skull, habits, and geographic and ecologic distribution of many of the species. Some of this information is first hand. Some is derived from the literature. All is welded into a subjective, incompletely documented estimate of interrelationships within *Peromyscus*. The estimate is subjective, nevertheless each grouping of species in the classification is definable on the basis of characters of study skin, skull, male phallus, and habitus.

This estimate is to be taken as a tentative framework, a reasonable hypothesis, against which subsequent systematic data may be tried for fit. The classification is not greatly different from the current one. Its principal feature is that it emphasizes a mosaic pattern of differentiation which appears to be typical of murid rodents. For in *Peromyscus*, as in other polytypic genera, tribes, or subfamilies of murids, most of the species cluster; morphologically they are close to one another. Only a few species, each in its own way, are set apart from the main cluster. Evolutionary dichotomy with roughly equal numbers of species of each morphologic type is atypical in *Peromyscus* and other murid groups.

A few comments regarding contrasting appearances of temperate and tropical species of *Peromyscus* may be of interest. Most, perhaps all, species of the genus which inhabit mainly temperate situations are recognizable both cranially and externally as temperate, northern species. Similarly, most tropical species are recognizable as such in characters of both skin and skull. Following are morphologic aspects typical of the temperate kinds: the tail typically is sharply bicolor; the brain case tends to be rounded, more nearly circular as viewed dorsally, and it often appears inflated; in dorsal view the interorbital area tends to be shaped like an hour-glass, evenly and strongly constricted; the ectopterygoid fossae tend to be large, usually exceeding the mesopterygoid fossa in width; the sphenopalatine vacuities are large spaces in both the basisphenoid and presphenoid bones; the auditory bullae typically are relatively large and often are highly inflated. Fitting here are the species of the following groups, all predominantly temperate: *maniculatus*, *leucopus*, *eremicus*, *crinitus*, *boylei*, *truei*, and *melanophrys*. The subtropical forms of the *boylei* group (e. g., *aztecus*, *evides*, *oaxacensis*, and *hylocetes*) and *melanophrys* group grade toward tropical species in those characters.

In tropical species the tail usually is mottled below or is essentially unicolor; the brain case tends to be more elongate and less inflated;

the interorbital area is broader, usually angular; the ectopterygoid fossae are smaller, the width of each usually is equal to or less than that of the mesopterygoid fossa; there are slight or no sphenopalatine vacuities; and the auditory bullae are moderate in size or relatively small. Belonging here are the species of the *mexicanus*, *thomasi*, and *banderanus* groups. Species of the *lepturus* group are intermediate, but are more tropical than temperate in characters. *P. floridanus* is also intermediate, possibly nearer the temperate group. We have seen no skins or skulls of the *flavidus* group.

The functional significance of these differences should be investigated. The size of the interorbital space may be related to size of olfactory lobes of the brain and, thus, to olfactory acuity. Size of ectopterygoid fossae is a function of size of the pterygoid muscles; these have to do with gnawing and mastication (Rinker and Hooper, 1950). Size of auditory bullae likely is related in some way to sound reception and transmission. Here are fertile areas for further research.

A classification of *Peromyscus* is given below, and in Figure 2 the probable position of the genus with respect to related peromyscine and neotomyine genera is indicated (Hooper and Musser, 1964). The total evidence suggests that *Peromyscus* consists of 13 groups of species. Seven of those groups comprise the main cluster, and six are peripheral in regard to amount of differentiation. In conformance with current

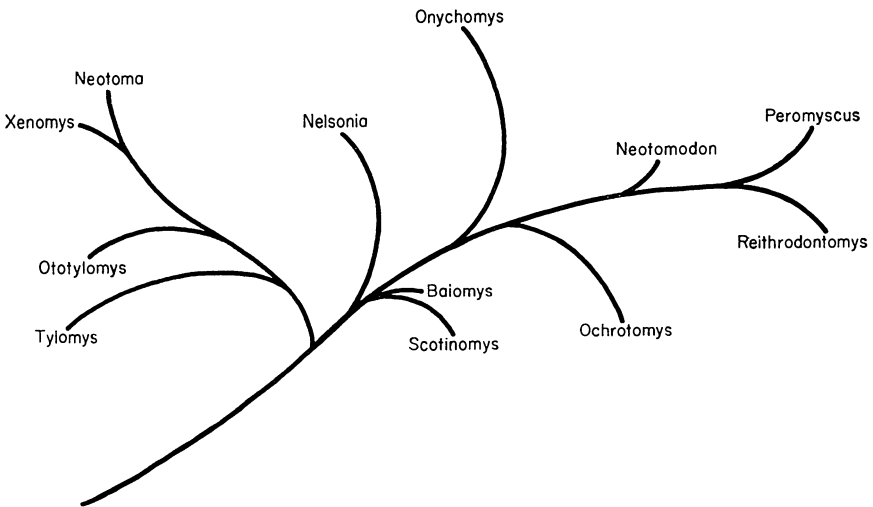


FIG. 2. Diagram of probable relationships of *Peromyscus* and other peromyscine and neotomyine rodents (see Hooper and Musser, 1964).

taxonomic practice the seven are listed as species groups of the one subgenus, *Peromyscus*; the remaining six groups are treated as subgenera. Because each subgenus is differentiated in its own way, and its probable relationships with the other forms cannot be indicated in a list, we have simply grouped the six peripheral subgenera near the end of the list. Three of the subgenera are new. The names proposed for them and the type species of each (in parentheses) are as follows: *Habromys* (*Peromyscus lepturus* Merriam), *Osgoodomys* (*Peromyscus banderanus* Allen), and *Isthmomys* (*Megadontomys flavidus* Bangs). Cranial and external characters of these forms are given by Osgood (1909) and phallic characteristics are indicated in the present report and elsewhere (Hooper, 1958). There are major doubts as to the position of a few species; these are questioned in the following list.

GENUS *PEROMYSCUS*

Subgenus *Peromyscus* Gloger

maniculatus group

polionotus (Wagner)

maniculatus (Wagner)

oreas Bangs

sejugis Burt

?*slevini* Mailliard

sitkensis Merriam

melanotis Allen and Chapman

leucopus group

leucopus (Rafinesque)

gossypinus (Le Conte)

crinitus group

crinitus (Merriam)

?*caniceps* Burt

pseudocrinitus Burt

boylei group

pectoralis Osgood

boylei (Baird)

polius Osgood

?*stephani* Townsend

evides Osgood

aztecus (Saussure)

oaxacensis Merriam

hilocetes Merriam

truei group

truei (Shufeldt)

difficilis (Allen)

bullatus Osgood

melanophrys group

?*perfulvus* Osgood

melanophrys (Coues)

?*mekisturus* Merriam

mexicanus group

ochraventer Baker

yucatanicus Allen and Chapman

?*hondurensis* Goodwin

mexicanus (Saussure)

allophylus Osgood

stirtoni Dickey

nudipes (Allen)

furvus Allen and Chapman

latirostris Dalquest

angustirostris Hall and Alvarez

altilaneus Osgood

guatemalensis Merriam

megalops Merriam

?*sloeops* Goodwin

melanocarpus Osgood

zarhynchus Merriam

grandis Goodwin

Subgenus *Haplomyiomys* Osgood

eremicus (Baird)

merriami Mearns

guardia Townsend

collatus Burt

dickeyi Burt

pembertoni Burt

californicus (Gambel)

Subgenus <i>Habromys</i> , <i>nobis</i>	<i>floridanus</i> (Chapman)
<i>simulatus</i> Osgood	Subgenus <i>Isthmomys</i> , <i>nobis</i>
<i>lophurus</i> Osgood	<i>flavidus</i> (Bangs)
<i>lepturus</i> Merriam	<i>pirrensis</i> Goldman
Subgenus <i>Osgoodomys</i> , <i>nobis</i>	Subgenus <i>Megadontomys</i> Merriam
<i>banderanus</i> Allen	<i>thomasi</i> Merriam
Subgenus <i>Podomys</i> Osgood	<i>nelsoni</i> Merriam

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