

A REVIEW OF THE GENUS *Hoplomys* (THICK-
SPINED RATS), WITH DESCRIPTION OF A
NEW FORM FROM ISLA ESCUDO
DE VERAGUAS, PANAMÁ

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A specimen of the thick-spined rat, *Hoplomys gymnurus* Thomas, that Alexander Wetmore shot in a thicket on Isla Escudo de Veraguas on the morning of March 1, 1958, is probably the only mammal from this Caribbean island that is preserved in a museum. Other rats that Wetmore saw in coconut palms on the same day apparently were of another genus. No other mammals have been reported from this locality except feral hogs. Although Indians once lived on the island, human beings are now only transients there.

Escudo de Veraguas is a low island, about 1 mile wide and 2.5 miles long, in the Caribbean Sea, 11 miles off the base of the Valiente Peninsula, Province of Bocas del Toro, north coast of the Republic of Panamá. Wetmore (Smithsonian Misc. Coll., vol. 139, No. 2, 1959) has given a detailed account of the history, geography, and zoological position of the island.

Other echimyid genera, *Diplomys* and *Proechimys*, are known to occur on certain islands in the Gulf of Panamá and elsewhere, but no insular populations of *Hoplomys* have been reported. The Escudo de Veraguas *Hoplomys* differs in so many respects from other known populations of the thick-spined rat that it has prompted a brief review of the genus.

Many of the National Museum (US) specimens reported here were collected in cooperation with the Gorgas Memorial Laboratory, Panamá. I express my thanks to Carl Johnson, director, and other members of the laboratory staff for numerous courtesies and assistance in fieldwork. Some of the specimens were collected by C. M. Keenan of the Army Preventive Medicine Survey Detachment, Ft. Clayton, Canal Zone. Richard Van Gelder kindly permitted the study of specimens in the American Museum of Natural History (AMNH), New York.

Genus HOPLOMYS J. A. Allen

1908. *Hoplomys* J. A. Allen, Bull. Amer. Mus. Nat. Hist., vol. 24, p. 649.

Genotype.—*Hoplomys truei* J. A. Allen.

Distribution.—The genus has a limited distribution in Central America and northwestern South America. It is monotypic. Published records of collecting localities are mapped in figure 1. *Hoplomys* is known to occur at medium elevations (800-3,100 ft.) on the Caribbean slope of the highlands of Nicaragua and Costa Rica; near sea level on the Caribbean coast of Panamá; at medium elevations (600-4,000 ft.) on the Pacific slope of eastern Panamá, Colombia, and Ecuador; and near sea level in extreme southwestern Colombia and northwestern Ecuador. The distribution of *Hoplomys* in South America appears to be limited by the Western Andes. J. A. Allen's record for Puerto Valdivia on the Río Cauca (Bull. Amer. Mus. Nat. Hist., vol. 35, p. 207, 1916) is erroneous (the specimen is a *Proechimys*). *Proechimys cayennensis hoplomyoides* Tate (Bull. Amer. Mus. Nat. Hist., vol. 76, p. 179, 1939) from Mt. Roraima, Venezuela, appears not to be a *Hoplomys*, although a relationship has been suggested (Moojen, Univ. Kansas Publ., Mus. Nat. Hist., vol. 1, p. 324, 1948).

In the Caribbean lowlands of Panamá, where *Proechimys* is abundant and *Hoplomys* seemingly rare, I have trapped individuals of both genera under the same log on successive nights. At medium altitudes in the mountains of Panamá where *Hoplomys* is fairly common, *Proechimys* apparently does not occur.

All the *Hoplomys* that I have collected in Panamá were caught in banana-baited live traps under large decaying logs—in fairly open mature rain forest, in grassy clearings and adjacent streamside thickets, and in dense, hillside *Heliconia* thickets. Goldman (Smithsonian Misc. Coll., vol. 69, No. 5, p. 124, 1920) found *Hoplomys* associated with fallen trees and rocks in Panamanian forests.

Diagnosis.—Dorsum, flanks, and rump, in both adult and juvenile pelages, with spines 26 to 33 mm. in maximum length and 1.5 to 2.0 mm. in maximum diameter, tending to obscure soft fur. Tail shorter than head and body, scaly, and sparsely haired. Ears scantily haired. Hind feet long and narrow; fifth toe scarcely longer than first; claws relatively straight, but claw of second toe slightly expanded. Skull prominently ridged, and supraorbital shelf beaded; rostrum relatively broad at tip; auditory bullae relatively small; and infraorbital foramen without subsidiary canal on floor, and with external wall thin in lateral view. Cheek teeth with oblique folds; counterfold formula normally 4/4-4/4-4/4-4/4, rarely 4/4-4/3-4/3-4/3.

Variation.—Specimens of *Hoplomys* have never before been available in series. Fourteen specimens, seven of which are adult, recently collected on Cerro Azul, Panamá, now permit a fairly good estimate

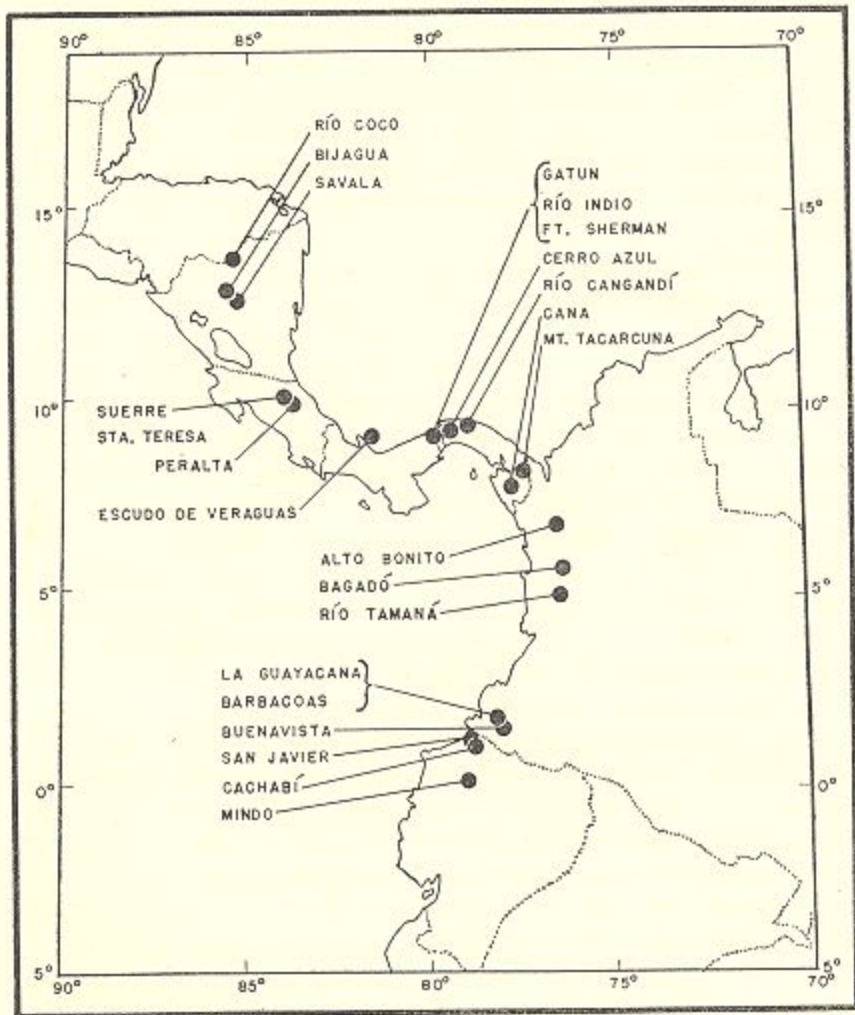


FIG. 1.—Distribution of *Hoplomys gymnurus*. All known specimen localities are indicated.

of individual variation in the genus. Eleven specimens from Darién and nine from the Canal Zone, are also helpful. In addition, random series of up to 75 specimens per sample of the closely related *Proechimys semispinosus* have been used to evaluate the variations seen in the smaller series of *Hoplomys*.

Size, flatness, and ridging of the skull increase with advancing age in *Hoplomys* and *Proechimys*. Tooth wear appears to be a reliable criterion of age. Full adult pelage usually is attained after M3 appears and before it becomes functional. Only juvenile and adult pelages have been distinguished. Specimens in which all cheek teeth are functional are considered to be adults. Generally, the largest, flattest, most heavily ridged skulls have the most worn teeth. Apparently these rodents continue to grow after all teeth are functional. Thus, there is considerable size spread among adult skulls. For this reason only maximum and minimum figures are given in the table of measurements (p. 6).

Body sizes appear to be uniform throughout the mainland range of the species, but larger on Escudo de Veraguas. The skull is narrow in the south—Ecuador, Colombia, and Darién—somewhat broader in central Panamá, Costa Rica, and Nicaragua, and broadest of all on Escudo de Veraguas. Likewise the nasals and cheek teeth are smaller in the southern populations. Size of the auditory bullae increases northward from Ecuador to Nicaragua, but the bullae are largest and most inflated anterolaterally in the Escudo specimen. Several features of the zygomatic arches vary geographically. The maxillary roots of the zygomata flare less widely and less perpendicularly from the longitudinal axis of the skull (so that the zygomata are more convergent anteriorly) from the Canal Zone southward than they do in the north. From Cerro Azul southward the maxillary roots tend to flare up, away from the ventral plane of the skull, rather than paralleling that plane as they do in the north. The jugal has a hooklike posteroventral process in most Canal Zone and Cerro Azul specimens, but not in others. Most of the specimens from Ecuador, Colombia, and Darién, and a smaller percentage of the central Panamanian specimens have a small conical projection on the dorsal edge of the zygoma at the jugal-squamosal suture. I failed to check this character in the Costa Rican and Nicaraguan specimens. There is hardly a trace of it in the Escudo individual. The nasals, broad and posteriorly truncate in the island specimen, are usually narrower and posteriorly acute in mainland populations.

Among mainland populations of *Hoplomys* flatness and ridging of the skulls of mature individuals are similar to these features in mature individuals of *Proechimys semispinosus*. None of the available *Hoplomys* or *Proechimys* closely approaches the Escudo specimen in flatness or ridging, despite the fact that the island specimen, judged by tooth wear, is a prime adult, not as old as many individuals with

which it was compared. The degree of reduction of dorsal doming and ventral depression of the brain case of the Escudo specimen is reflected in the convergence of greatest and condylobasal lengths of the skull, and in the more posteriorly oriented (as opposed to ventrally oriented) foramen magnum.

The thick spines that distinguish *Hoplomys* are longest and strongest just behind the shoulders on the upper midback, from which point they diminish in size in all directions. The spines possibly vary geographically in size. They appear to be longer and stronger toward the southern part of the range of *Hoplomys*. The Escudo specimen, although it is larger than any other, has the smallest and weakest spines. Maximum spine length varies as follows (mean, followed by extremes): 6 Ecuador 29 mm. (28-31), 4 Darién 30 (28-33), 11 Cerro Azul 28 (26-29), 5 Canal Zone 28 (27-30), 1 Escudo de Veraguas 26.

Coloration of the spines is individually variable. All specimens have all spines proximally white and distally colored. The tips of those of the dorsum are always black, but the flank spines usually are tinged with orange or banded with orange and black distally. Occasionally the flank spines are colored like the dorsal spines.

Coloration of the soft hairs of the dorsum is geographically variable. At the southern extreme they are reddish orange, especially on the shoulders. The soft hairs of the Escudo specimen are similar but darker and brighter. Costa Rican and Nicaraguan examples have the hairs more orange, and those from Panamá and northern Colombia are more yellowish on the average. The presence or absence of black ocular and crown areas appears to be individually variable throughout the range of *Hoplomys*, but only the Escudo specimen has the soft hairs blackened to form a distinct middorsal stripe from snout to base of tail.

All populations have the underparts dominantly white, and all have some individuals that show encroachment of agouti hairs of the side neck onto the throat, suggesting an incipient collar. This is well marked in the Escudo specimen; one from Río Indio, Canal Zone, has a complete collar. Nine of the 14 Cerro Azul specimens have clear orange collars, and several of them have a band of clear orange hairs separating the agouti hairs of the flanks from the white hair of the belly. Neither of these features is seen in samples of other populations. Coloration of the forefeet (usually white on the inner side, colored on the outer, occasionally colored throughout), and coloration of the cheeks (clear orange, buff, gray, or agouti) are individually variable.

TABLE I.—*External and cranial measurements of adult Hoplosternum littorale*
The minimum and maximum measurements are given in millimeters.

	Total length	Head and body length	Tail vertebrae	Hind foot (c.u., dry)	Ear (from notch)	Greatest length of skull	Condylolabial length
Escudo de Veraguas, Panamá							
1 male	498	313	185	58	23	67.2	62.0
Bijagua, Nicaragua							
1 male	—	270	—	55	—	62.1	55.0
1 female	440	240	200	52	—	60.5	54.2
Sta. Teresa Peralta, Costa Rica							
1 male	—	275	—	61	24	66.1	58.9
Canal Zone, Panamá							
3 males	454-529	221-285	200-244	59-62	24	59.7	53.0
2 females	434	259-260	174	51-59	21	61.1-63.7	54.0-56.0
Cerro Azul, Panamá							
5 males	403-530	218-275	185-255	54-61	22-30	60.6-66.3	52.7-58.3
2 females	423	233-235	188	54-57	23-25	59.6-61.3	52.6-54.2
Darién, Panamá							
6 males	443-519	224-285	181-234	51-60	—	59.5-65.7	52.7-57.6
2 females	439	243-256	196	50-51	—	58.1-62.8	51.3-54.8
S. W. Colombia and N. W. Ecuador							
3 males (only 1 skull)	392-450	243-270	149-180	51-54	22-24	58.4	50.9
4 females (only 1 skull)	396-450	238-265	158-185	50-58	21-27	60.4+	54.5+

TABLE I.—Continued.

	Zygomatic breadth	Interorbital breadth	Mastoidial breadth	Nasal length	Maxillary tooth row*	Incisive foramen length	Palate breadth †
Escudo de Veraguas, Panamá							
1 male	32.3	15.2	24.1	25.6	10.1	6.1	8.6
Bijagua, Nicaragua							
1 male	28.7	14.0	—	23.5	9.5	4.7	7.2
1 female	28.3	13.3	20.8	22.5	9.1	4.7	7.4
Sta. Teresa Peralta, Costa Rica							
1 male	30.1	14.1	22.3	22.1	9.8	5.6	8.3
Canal Zone, Panamá							
3 males	28.4-30.0	13.6-13.8	21.1-22.8	21.9-26.2	8.9-9.5	4.6-5.0	7.2-7.8
2 females	29.4-29.8	13.1-13.1	21.6-21.6	22.0-25.1	9.1-9.6	4.8-5.8	7.3-7.4
Cerro Azul, Panamá							
5 males	28.7-30.9	13.5-14.1	21.0-22.7	21.4-25.0	9.0-10.2	4.5-5.6	7.5-8.3
2 females	28.3-29.1	13.4-13.4	20.6-21.4	21.1-22.5	9.5-10.0	4.2-5.2	7.5-8.3
Darien, Panamá							
6 males	26.8-28.6	13.1-13.7	20.8-22.4	20.9-23.5	8.6-9.6	4.2-4.6	7.1-8.2
2 females	27.4-28.4	12.7-13.4	20.3-21.1	19.7-23.0	8.3-8.9	4.0-5.0	7.4-7.5
S. W. Colombia and N. W. Ecuador							
1 male	28.0	12.7	20.8	20.4	8.9	4.3	7.5
1 female	28.7	10.4	21.6	20.9†	8.6	5.1	8.0

* Alveolar length.

† Between outer margins of alveoli of P₄.

The large size of the Escudo specimen, the massiveness, broadness, and heavy ridging of its skull, the inflation of its auditory bullae, and its distinctive coloration all seem to be beyond the possibility of individual variation. This suggests that the Escudo animal is taxonomically distinct from mainland populations. That it is conspecific with them is indicated by its alignment with some of the morphological clines observed in the mainland populations. Wetmore (*op. cit.*) has named three birds (a wren, a manakin, and a tanager) collected on Escudo de Veraguas that differ from their mainland counterparts in greater size, in addition to differences in color.

Classification.—The genus *Hopломys* is represented by one species, which includes four subspecies:

HOPLOMYS GYMNURUS GOETHALSI Goldman

1912. *Hopломys goethalsi* Goldman, Smithsonian Misc. Coll., vol. 56, No. 36, p. 10 (Río Indio, near Gatun, Canal Zone, Panamá).

Characters.—Size medium; skull of medium width and ridged; brain case domed and slightly depressed; foramen magnum ventrally oriented; cheek teeth large; auditory bullae medium; zygomata converging conspicuously anteriorly, and maxillary root tending to flare up slightly from ventral plane of skull; jugal with hooklike posteroventral process and small conical posterodorsal projection; nasals long, narrow, and posteriorly acute; dorsal spines long and strong; soft hairs of dorsum appear uniform yellowish orange in mass effect.

Specimens examined.—Panamá: Cana, 2,000 ft., 5 US; Cerro Azul, 2,100 ft., 14 US; Ft. Sherman, 4 US; Gatun, 3 (2 AMNH, 1 US); Cerro Tacarcuna, 2,650 ft., 6 AMNH; Río Cangandí, 200 ft., 1 US; Río Indio, 2 US. Colombia: Alto Bonito, Antioquia, 1,500 ft., 1 AMNH; Bagadó, Chocó, 600 ft., 2 AMNH.

Additional published records.—Colombia: Río Tamaná, branch of the Río San Juan, Chocó (J. A. Allen, Bull. Amer. Mus. Nat. Hist., vol. 35, p. 207, 1916).

HOPLOMYS GYMNURUS GYMNURUS Thomas

1897. *Echimyс gymнurus* Thomas, Ann. Mag. Nat. Hist., ser. 6, vol. 20, p. 550 (Cachabí, N. Ecuador, alt. 560 ft.).

Characters.—Size medium or small; skull narrow and ridged; brain case domed and slightly depressed; foramen magnum ventrally oriented; cheek teeth small; auditory bullae small; zygomata converging conspicuously anteriorly, and maxillary root flaring up from ventral plane of skull; jugal lacking posteroventral process, but with

prominent conical posterodorsal projection; nasals short, narrow, and posteriorly acute; dorsal spines long and strong; soft hairs of dorsum giving reddish-orange mass effect, slightly darkened on shoulders.

Specimens examined.—Colombia: Barbacoas, Nariño [75 ft.], 8 AMNH; Buenavista, Nariño [1,200 ft.], 1 AMNH; La Guayacana, Nariño, 800 ft., 2 US. Ecuador: Mindo, Río Blanco [4,000 ft.], 1 AMNH; San Javier, 60 ft., 7 (1 AMNH, 6 US).

Additional published records.—Ecuador: Cachabí, 560 ft. (Thomas, *op. cit.*, p. 551).

HOPLOMYS GYMNURUS TRUEI J. A. Allen

1896. *Echinomys semispinosus* Alfaro (not Tomes, 1860, Proc. Zool. Soc. London, p. 265), Primera Exposición Centroamericana de Guatemala, Museo Nacional, San José, p. 41 (Suerre, Costa Rica).

1908. *Hoplomys truei* J. A. Allen, Bull. Amer. Mus. Nat. Hist., vol. 24, p. 650 (Savala, Matagalpa Prov., Nicaragua).

Characters.—Size medium; skull of medium width and ridged; brain case domed and slightly depressed; foramen magnum ventrally oriented; cheek teeth large; auditory bullae large; zygomata converging less anteriorly than in *goethalsi*, and maxillary root in plane of ventral surface of skull; jugal without hooklike posteroventral process; nasals long, narrow, and posteriorly acute; dorsal spines relatively short and weak; soft hairs of dorsum giving uniform dark orange mass effect.

Specimens examined.—Nicaragua: Lavala [= Savala, 800 ft., along the inner border of the low east coast region], 2 AMNH; Río Coco [800 ft.], 2 AMNH; Vijagua [= Bijagua, probably 1,500 to 2,000 ft., on eastern slope of highlands in Matagalpa Prov.], 3 AMNH. Costa Rica: Santa Teresa Peralta [3,100 ft.], 1 AMNH; Suerre, 1,500 ft. [near Jiménez], 1 AMNH.

Additional published records.—Tate (Bull. Amer. Mus. Nat. Hist., vol. 68, p. 401, 1935) supposed that True's record (Proc. U. S. Nat. Mus., vol. 11, p. 467, 1889) of *Echinomys semispinosus* in Nicaragua was the first published reference to a *Hoplomys*. The specimens, still in the U. S. National Museum, however, are *Proechimys*.

HOPLOMYS GYMNURUS WETMOREI subsp. nov.

Holotype.—U.S.N.M. No. 307057; adult male, skin and skull; collected March 1, 1958, by Alexander Wetmore; Isla Escudo de Veraguas, Prov. Bocas del Toro, Panamá; original No. 1479.

Characters.—Size large; skull broad and heavily ridged; brain case flattened dorsally and ventrally; foramen magnum posteriorly oriented; cheek teeth large; auditory bullae large and inflated anterolaterally; zygomata converging less anteriorly than in *goethalsi*, and maxillary root in plane of ventral surface of skull; jugal without hook-like posteroventral process, or conical posterodorsal projection; nasals long, broad, and posteriorly truncate; dorsal spines relatively short and weak; and soft hairs of dorsum giving dark reddish-orange mass effect (between Burnt Sienna and Sanford's Brown of Ridgway, 1912, Color Standards and Color Nomenclature), with black middorsal stripe from snout to base of tail. For measurements see table 1.

Specimen examined.—The holotype.