MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 105

The Male Phallus in Mice of the Genus *Peromyscus*

BY
EMMET T. HOOPER

ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
DECEMBER 29, 1958

LIST OF THE MISCELLANEOUS PUBLICATIONS
OF THE MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN

Address inquiries to the Director of the Museum of Zoology, Ann Arbor, Michigan

Bound in Paper

No. 1. Directions for Collecting and Preserving Specimens of Dragonflies for Museum Purposes. By E. B. Williamson. (1916) Pp. 15, 3 figures. $0.25

No. 2. An Annotated List of the Odonata of Indiana. By E. B. Williamson. (1917) Pp. 12, 1 map. $0.25

No. 3. A Collecting Trip to Colombia, South America. By E. B. Williamson. (1918) Pp. 24 (Out of print)

No. 4. Contributions to the Botany of Michigan. By C. K. Dodge. (1918) Pp. 14 . . . . . $0.25

No. 5. Contributions to the Botany of Michigan, II. By C. K. Dodge. (1918) Pp. 44, 1 map. $0.45

No. 6. A Synopsis of the Classification of the Fresh-water Mollusca of North America, North of Mexico, and a Catalogue of the More Recently Described Species, with Notes. By Bryant Walker. (1918) Pp. 213, 1 plate, 233 figures $5.00

No. 7. The Anculosae of the Alabama River Drainage. By Calvin Goodrich. (1922) Pp. 57, 3 plates. $0.75

No. 8. The Amphibians and Reptiles of the Sierra Nevada de Santa Marta, Colombia. By Alexander G. Ruthven. (1922) Pp. 69, 13 plates, 2 figures, 1 map $1.00

No. 9. Notes on American Species of Triacanthagyna and Gynacantha. By E. B. Williamson. (1923) Pp. 67, 7 plates $0.75

No. 10. A Preliminary Survey of the Bird Life of North Dakota. By Norman A. Wood. (1923) Pp. 85, 6 plates, 1 map $1.00

No. 11. Notes on the Genus Erythemis with a Description of a New Species (Odonata). By E. B. Williamson.
The Phylogeny and the Distribution of the Genus Erythemis (Odonata). By Clarence H. Kennedy. (1923) Pp. 21, 1 plate $1.00

No. 12. The Genus Gyrotoma. By Calvin Goodrich. (1924) Pp. 29, 2 plates $0.50

No. 13. Studies of the Fishes of the Order Cyprinodontes. By Carl L. Hubbs. (1924) Pp. 23, 4 plates. $0.75

No. 14. The Genus Perilestes (Odonata). By E. B. Williamson and J. H. Williamson. (1924) Pp. 36, 1 plate $1.00

No. 15. A Check-List of the Fishes of the Great Lakes and Tributary Waters, with Nomenclatorial Notes and Analytical Keys. By Carl L. Hubbs. (1926) Pp. 77, 4 plates $1.50

No. 16. Studies of the Fishes of the Order Cyprinodontes. VI. By Carl L. Hubbs. (1926) Pp. 79, 4 plates $1.00

No. 17. The Structure and Growth of the Scales of Fishes in Relation to the Interpretation of Their Life-History, with Special Reference to the Sunfish Eupomotis gibbosus. By Charles W. Creaser. (1926) Pp. 80, 1 plate, 12 figures $2.50

No. 18. The Terrestrial Shell-bearing Mollusca of Alabama. By Bryant Walker. (1928) Pp. 180, 278 figures $1.50

No. 19. The Life History of the Toucan Ramphastos brevicarinatus. By Josselyn Van Tyne. (1929) Pp. 43, 8 plates, 1 map $0.75

No. 20. Materials for a Revision of the Catostomid Fishes of Eastern North America. By Carl L. Hubbs. (1930) Pp. 47, 1 plate $0.75

No. 21. A Revision of the Libelluline Genus Perithemis (Odonata). By F. Ris. (1930) Pp. 50, 9 plates $0.75

No. 22. The Genus Oligoclada (Odonata). By Donald Borror. (1931) Pp. 42, 7 plates $0.50

No. 23. A Revision of the Puer Group of the North American Genus Melanoplus, with Remarks on the Taxonomic Value of the Concealed Male Genitalia in the Cyrtacanthacrinae (Orthoptera, Acrididae). By Theodore H. Hubbell. (1932) Pp. 64, 3 plates, 1 figure, 1 map. $0.75

No. 24. A Comparative Life History Study of the Mice of the Genus Peromyscus. By Arthur Svihla. (1932) Pp. 39 . . . . . $0.50

No. 25. The Moose of Isle Royale. By Adolph Murie. (1934) Pp. 44, 7 plates. $0.70

No. 26. Mammals from Guatemala and British Honduras. By Adolph Murie. (1935) Pp. 30, 1 plate, 1 map. $0.35

No. 27. The Birds of Northern Petén, Guatemala. By Josselyn Van Tyne. (1935) Pp. 46, 2 plates, 1 map $0.45

No. 28. Fresh-Water Fishes Collected in British Honduras and Guatemala. By Carl L. Hubbs. (1935) Pp. 22, 4 plates, 1 map. $0.25

No. 29. A Contribution to a Knowledge of the Herpetology of a Portion of the Savanna Region of Central Petén, Guatemala. By L. C. Stuart. (1935) Pp. 56, 4 plates, 1 figure, 1 map $0.50

No. 30. The Darters of the Genera Hololepis and Villora. By Carl L. Hubbs and Mott Dwight Cannon. (1935) Pp. 93, 3 plates, 1 figure. $0.50

No. 31. Goniobasis of the Coosa River, Alabama. By Calvin Goodrich. (1936) Pp. 60, 1 plate, 1 figure $0.35

No. 32. Following Fox Trails. By Adolph Murie. (1936) Pp. 45, 6 plates, 6 figures $1.00

No. 33. The Discovery of the Nest of the Colima Warbler (Vermivora crissalis). By Josselyn Van Tyne. (1936) Pp. 11, colored frontis., 3 plates, 1 map. $0.35

No. 34. Mollusca of Peten and North Alta Vera Paz, Guatemala. By Calvin Goodrich and Henry van der Schalie. (1937) Pp. 50, 1 plate, 1 figure, 1 map. $0.50

No. 35. A Revision of the Lamprey Genus Ichthyomyzon. By Carl L. Hubbs and Milton B. Trautman. (1937) Pp. 109, 2 plates, 5 figures, 1 map $2.00

No. 36. A Review of the Dragonflies of the Genera Neurocordulia and Platycordulia. By Francis Byers. (1937) Pp. 36, 8 plates, 4 maps $0.50

No. 37. The Birds of Brewster County, Texas. By Josselyn Van Tyne and George Miksch Sutton. (1937) Pp. 119, colored frontis., 5 plates, 1 map $1.25

No. 38. Revision of Sciurus variegatoides, a Species of Central American Squirrel. By William P. Harris, Jr. (1937) Pp. 39, 3 plates (2 colored), 3 figures, 1 map $0.50

No. 39. Faunal Relationships and Geographic Distribution of Mammals in Sonora, Mexico. By William H. Burt. (1938) Pp. 77, 26 maps $0.75

No. 40. The Naiad Fauna of the Huron River, in Southeastern Michigan. By Henry van der Schalie. (1938) Pp. 83, 12 plates, 28 figures, 18 maps $1.00

No. 41. The Life History of Henslow's Sparrow, Passerherbulus henslowi (Audubon). By A. Sidney Hyde. (1939) Pp. 72, 4 plates, 3 figures, 1 map. $0.75

No. 42. Studies of the Fishes of the Order Cyprinodontes. XVI. A Revision of the Goodeidae. By Carl L. Hubbs and C. L. Turner. (1939) Pp. 85, 5 plates. $0.90

No. 43. Aquatic Mollusks of the Upper Peninsula of Michigan. By Calvin Goodrich and Henry van der Schalie. (1939) Pp. 45, 2 maps. $0.50

No. 44. The Birds of Buckeye Lake, Ohio. By Milton B. Trautman. (1940) Pp. 466, 15 plates and a frontis., 2 maps $4.50

No. 45. Territorial Behavior and Populations of Some Small Mammals in Southern Michigan. By William H. Burt. (1940) Pp. 58, 2 plates, 8 figures, 2 maps $0.50

No. 46. A Contribution to the Ecology and Faunal Relationships of the Mammals of the Davis Mountain Region, Southwestern Texas. By W. Frank Blair. (1940) Pp. 39, 3 plates, 1 map $0.35

No. 47. A Contribution to the Herpetology of the Isthmus of Tehuantepec. IV. By Norman Hartweg and James A. Oliver. (1940) Pp. 31 . . . . . $0.35

No. 48. A Revision of the Black Basses (Micropterus and Huro) with Descriptions of Four New Forms. By Carl L. Hubbs and Reeve M. Bailey. (1940) Pp. 51, 6 plates, 1 figure, 2 maps $0.75

No. 49. Studies of Neotropical Colubrinae. VIII. A Revision of the Genus Dryadophis Stuart, 1939. By L. C. Stuart. (1941) Pp. 106, 4 plates, 13 figures, 4 maps. $1.15

No. 50. A Contribution to the Knowledge of Variation in Opheodrys vernalis (Harlan), with the Description of a New Subspecies. By Arnold B. Grobman. (1941) Pp. 38, 2 figures, 1 map. $0.35

No. 51. Mammals of the Lava Fields and Adjoining Areas in Valencia County, New Mexico. By Emmet T. Hooper. (1941) Pp. 47, 3 plates, 1 map. $0.50

No. 52. Type Localities of Pocket Gophers of the Genus Thomomys. By Emmet T. Hooper. (1941) Pp. 26, 1 map. $0.25

No. 53. The Crane Flies (Tipulidae) of the George Reserve, Michigan. By J. Speed Rogers. (1942) Pp. 128, 8 plates, 1 map. $1.25

No. 54. The Ecology of the Orthoptera and Dermaptera of the George Reserve, Michigan. By Irving J. Cantrall. (1943) Pp. 182, 10 plates, 2 maps. $1.50

No. 55. Birds from the Gulf Lowlands of Southern Mexico. By Pierce Brodkorb. (1943) Pp. 88, 1 map $0.75

No. 56. Taxonomic and Geographic Comments on Guatemalan Salamanders of the Genus Oedipus. By L. C. Stuart. (1943) Pp. 33, 2 plates, 1 map. $0.35

No. 57. The Amnicolidae of Michigan: Distribution, Ecology, and Taxonomy. By Elmer G. Berry. (1943) Pp. 68, 9 plates, 10 figures, 10 maps. $0.85

No. 58. A Systematic Review of the Neotropical Water Rats of the Genus Nectomys (Cricetinae). By Philip Hershkovitz. (1944) Pp. 88, 4 plates, 5 figures, 2 maps $1.15

No. 59. San Francisco Bay as a Factor Influencing Speciation in Rodents. By Emmet T. Hooper. (1944) Pp. 89, 5 plates, 18 maps. $1.25

No. 60. The Fresh-Water Triclads of Michigan. By Roman Kenk. (1944) Pp. 44, 7 plates, 5 figures $0.50

No. 61. Home Range, Homing Behavior, and Migration in Turtles. By Fred R. Cagle. (1944) Pp. 34, 2 plates, 4 figures, 1 map $0.35

No. 62. Monograph of the Family Mordellidae (Coleoptera) of North America, North of Mexico. By Emil Liljeblad. (1945) Pp. 229, 7 plates. $2.00

No. 63. Phylogenetic Position of the Citharidae, a Family of Flatfishes. By Carl L. Hubbs. (1945) Pp. 38, 1 figure $0.35

No. 64. Goniobasis livescens of Michigan. By Calvin Goodrich. (1945) Pp. 36, 1 plate, 1 figure, 1 map. $0.35

No. 65. Endemic Fish Fauna of Lake Waccamaw, North Carolina. By Carl L. Hubbs and Edward C. Raney. (1946) Pp. 30, 1 plate, 2 maps $0.35

No. 66. Revision of Ceratichthys, a Genus of American Cyprinid Fishes. By Carl L. Hubbs and John D. Black. (1947) Pp. 56, 2 plates, 1 figure, 2 maps. $1.00

No. 67. A Small Collection of Fishes from Rio Grande do Sul, Brazil. By A. Lourenço Gomes. (1947) Pp. 39, 3 plates, 2 figures $0.50

No. 68. The Cyprinodont Fishes of the Death Valley System of Eastern California and Southwestern Nevada. By Robert R. Miller. (1948) Pp. 155, 15 plates, 5 figures, 3 maps $2.00

(CONTINUED ON BACK COVERS)

The publications of the Museum of Zoology, University of Michigan, consist of two series—the Occasional Papers and the Miscellaneous Publications. Both series were founded by Dr. Bryant Walker, Mr. Bradshaw H. Swales, and Dr. W. W. Newcomb.

The Occasional Papers, publication of which was begun in 1913, serve as a medium for original papers based principally upon the collections of the Museum. The papers are issued separately to libraries and specialists, and, when a sufficient number of pages has been printed to make a volume, a title page, table of contents, and index are supplied to libraries and individuals on the mailing list for the entire series.

The Miscellaneous Publications, which include papers on field and museum techniques, monographic studies, and other contributions not within the scope of the Occasional Papers, are published separately, and as it is not intended they will be grouped into volumes, each number has a title page and, when necessary, a table of contents.

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 105

The Male Phallus in Mice of the Genus *Peromyscus*

BY
EMMET T. HOOPER

ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
DECEMBER 29, 1958

PRINTED IN THE UNITED STATES OF AMERICA

CONTENTS

ILLUSTRATIONS

THE MALE PHALLUS IN MICE OF THE GENUS *PEROMYSCUS**

INTRODUCTION

THE value of the male genital tract in classification of rodents has been emphasized by Gilbert (1892), Tullberg (1899), Pocock (1923), Mossman, *et al.* (1932), Burt (1936), Prasad (1957), and many others. The topography of the glans and the gross anatomy of other segments of the penis have been described for a number of species, most of them inhabitants of the Old World. In recent years attention of workers has been focused on the os penis, or baculum, and on the accessory glands of the genital tract. Studies make it abundantly clear that characters of the male genitalium are important in mammalian systematics and that they provide significant clues to interrelationships of species. The present investigation deals with the distal tract in *Peromyscus*. The distal tract is that part of the penis which extends beyond the ventral flexure (Fig. 1); it includes the glans and the baculum. In this study I have compared 27 species with regard to the structure of the glans and its contained parts. My intent is to extend this comparison to all species.

Materials and Methods

Most of the specimens used in this study are in the University of Michigan Museum of Zoology (UMMZ). The remainder came from several sources, either from other institutional collections or from individuals who trapped and preserved examples for me. I am indebted for assistance to S. Anderson, F. S. Barkalow, S. B. Benson, B. Butterworth, J. A. Davis, Jr., W. B. Davis, S. D. Durrant, G. G. Goodwin, E. R. Hall, P. Hershkovitz, J. H. Layne, R. T. Orr, J. A. Sealander, and H. W. Setzer. The illustrations were prepared by W. L. Brudon, Artist, Museum of Zoology.

The majority of the assembled lot consists of alcohol-preserved examples; a few are conventional study skins, each bearing the dried distal tract. For present purposes dessicated material is definitely less satisfactory than fresh or fluid-preserved specimens. A dry phallus is often torn and abnormally contorted. When carefully soaked in water or dilute KOH, however, it can be forced to regain much of its original shape and proportions. Almost all of the animals studied were sexually mature.

The phalli were processed in such a way that, when ready for study, both internal and external parts could be seen at the same time. The procedure followed was grossly that described by Hamilton (1946). When removed from the animal each phallus typically consisted of the entire distal tract (Fig. 1). The prepuce, accessory glands, and other tissues were stripped away exposing the glans, and, proximal to it, the stalk of the penis.

*Accepted for publication January 27, 1958.

The specimen was then placed in a 2 to 4 percent solution of KOH. There it remained at least until the baculum became faintly visible when the specimen was held before a bright light. After that it was stained in alkaline alizarin and, if necessary, returned to the 2 percent KOH to remove excess stain from the soft tissues. Finally, it was passed in three stages through increasing concentrations of glycerine, in which the tissues continued to clear, and eventually stored in pure glycerine.

The specimens were measured and drawn to scale with the aid of a camera lucida. Dimensions of external parts were taken before the example was placed in KOH. The baculum and other internal structures were assessed after the soft tissues became translucent. A few to be preserved in fluid were sketched and measured immediately after the animals were killed. These specimens served as standards and enabled me to estimate the amount of distortion to be expected in the phalli as a result of preserving and processing procedures.

The distortions that result from processing are principally these: Some layers are lost. For example, the outer layer of the glans, which in some species bears spines and tubercles, may be sloughed off; also, some soft tissues, such as those in the end of the glans of *P. nuttalli*, may be disattached. The soft parts change in dimensions. The glans swells but not in equal amounts throughout; there is little, if any, increase in length. Enlargement in diameter is least at the base of the glans and most pronounced distally. The soft tissues of the tip are particularly susceptible to change, sometimes becoming excessively turgid. Such swellings are artifacts of processing, but the dimensions of these artificially enlarged phalli probably do not differ appreciably from those in the living animal. It is not likely that the amount of enlargement in a processed phallus exceeds that which occurs naturally when the glans becomes fully distended in a sexually active animal.

Two hundred ninety-nine genital tracts were prepared. Distributed by species they are as follows: *maniculatus*, 16; *polionotus*, 5; *leucopus*, 105; *gossypinus*, 5; *pectoralis*, 12; *crinitus*, 5; *boylei*, 35; *yucatanicus*, 2; *nasutus*, 3; *truei*, 19; *perfulvus*, 3; *mexicanus*, 8; *difficilis*, 14; *melanophrys*, 5; *guatemalensis*, 1; *furvus*, 2; *nudipes*, 1; *megalops*, 7; *thomasi*, 7; *eremicus*, 14; *californicus*, 2; *hylocetes*, 4; *floridanus*, 4; *lophurus*, 2; *lepturus*, 3; *banderanus*, 9; and *nuttalli*, 7.

Measurements were taken as follows:

Length of distal tract. — Distance from the base of the flexure to the distalmost point on the glans (Fig. 1).

Length of glans. — Distance on the ventral face of the glans from its base, where the glans joins the prepuce, to its distal limits.

Diameter of glans. — Greatest diameter of the glans.

Length of baculum. — Cord length of the os penis, exluding all nonosseous parts.

Length of cartilage. — Length of the cartilaginous tip of the os penis.

Length of hind foot. — Conventional length of the foot, from heel to tip of longest claw (as recorded by the collector).

The tone drawings (Pls. I - XIV) of the glans penis are scale models of cleared specimens. Reconstructed from camera lucida sketches, they

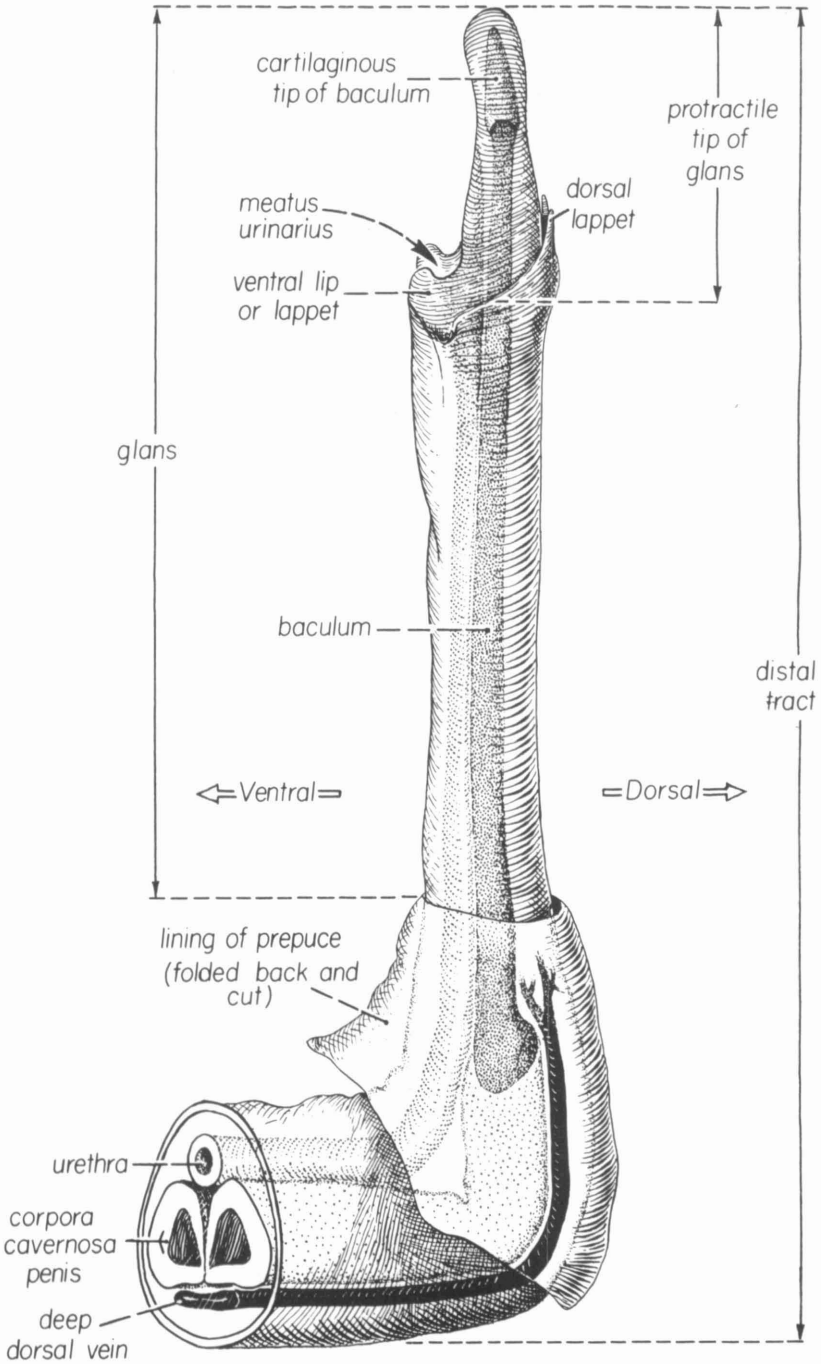


Fig. 1. Schematic view of distal tract of *Peromyscus maniculatus*.

accurately represent the observed size and shape of the whole specimen and its component parts. They are, however, somewhat schematic. Degrees of translucency have been modified in order to emphasize some diagnostic features. Moreover, any spines or tubercles which may have been present in the outer layer of the glans have been omitted. The specimens are drawn to different scales. Two vertical lines on each plate indicate the relative length of the os penis and the hind foot. Absolute size is indicated in Table I.

TABLE I

MEASUREMENTS AND PROPORTIONS OF THE GLANS PENIS AND BACULUM IN 26 SPECIES OF *PEROMYSCUS*

Species are grouped according to types of glans and within a group they are arranged in order of length of hind foot. The values are means of the adults measured.

Species	Specimens	Length(in millimeters)				Ratio X 100		
		hind foot	glans	baculum	tip	glans / foot	diameter of glans / length of glans	baculum / foot
polionotus	3	17	6.1	6.6	0.5	36	18	39
maniculatus	3	20	7.4	8.3	0.8	37	16	41
leucopus	5	21	7.8	9.0	0.8	37	24	43
gossypinus	4	23	7.4	7.1	1.0	32	22	31
pectoralis	4	22	10.6	13.4	0.9	48	18	61
crinitus	5	20	5.3	6.8	0.2	27	28	34
boylei	5	22	9.1	11.3	0.2	41	19	51
yucatanicus	2	22	10.1	12.8	0.2	46	16	58
nasutus	2	22	11.4	14.3	0.3	52	16	65
truei	4	23	10.7	13.3	0.1	47	23	58
perfulvus	2	24	9.7	12.6	0.2	40	20	53
mexicanus	3	25	11.8	15.6	0.1	47	17	62
difficilis	1	27	13.1	17.5	0.2	49	14	65
melanophrys	1	27	13.3	17.8	0.2	49	23	66
guatemalensis	1	29	11.2	16.1	0.2	39	29	56
furvus	1	30	11.5	15.2	0.3	38	17	51
nudipes	1	30	12.3	17.1	0.2	41	18	57
megalops	1	30	11.5	. . .	0.5	38	. .	. .
hylocetes	5	25	7.8	10.3	0.2	31	36	41
eremicus	6	21	7.2	8.8	0.1	34	29	42
californicus	2	26	10.9	13.4	0.1	42	32	52
thomasi	2	33	12.2	16.6	0.6	37	31	50
banderanus	6	24	6.1	4.6	0.2	25	31	19
floridanus	3	24	6.3	6.8	0.2	26	14	28
lepturus	3	27	4.5	6.8	0.1	17	27	25
nuttalli	3	18	3.3	3.0	0.1	18	52	17

ACCOUNTS OF SPECIES

The 27 species of *Peromyscus* are arranged here on the basis of the morphology of the distal tract. They have been assembled in "divisions" and "groups" according to characteristics of the tract. Species of the different divisions are markedly dissimilar in structure of phallus. Those constituting a given group (within a division) have generally similar tracts. Within each category the species have been arranged approximately in order of body size, which is indexed here by length of the hind foot. For each division and group a diagnosis is followed by a brief description of the tracts of the species comprising it.

Maniculatus Division

On the basis of similar structure of the distal tract, 18 of the 27 species of *Peromyscus* should be assembled in the same major category. These are: *maniculatus*, *polionotus*, *leucopus*, *gossypinus*, *pectoralis*, *crinitus*, *boylei*, *yucatanicus*, *nasutus*, *truei*, *perfulvus*, *mexicanus*, *difficilis*, *melanophrys*, *guatemalensis*, *furvus*, *nudipes*, and *megalops*.

In each of the 18 the glans is elongate and rod-shaped, with its extent 3 to 7 times its greatest diameter and 1/3 to 1/2 the length of the hind foot. The glans is topographically divisible into two parts (Fig. 1): (1) a main body of comparatively dense tissues and (2) a tapered, pliable tip. These parts are described in detail in the account of *P. maniculatus*. In all the species, save possibly *gossypinus*, *pectoralis*, *perfulvus*, *difficilis*, *guatemalensis*, and *furvus*, the surface of the glans body is covered with proximally directed spines. Small and dense distally, these become progressively larger and more widely spaced toward the base of the glans. In *guatemalensis* and *furvus* the nature of the surface is unknown. In *gossypinus*, *pectoralis*, *perfulvus*, and *difficilis* the glans is covered with conical tubercles, which may become spinous when the animals are sexually active. There is a strong possibility that the glans body is spiny in all species of this division.

The body of the glans terminates in two slender dorsal processes. Proximal to them and on the ventral side, there is a fleshy lip, sometimes medially cleft, that projects over the mouth of the urethra. Distal to the body is an irregular cone of soft tissue that constitutes the tip. This tip is to some extent protractile, capable of extending from or being withdrawn into the distal part of the main body, and it is without spines or tubercles. The dorsal surface is typically smooth, sloping gently to the knoblike mass that caps the baculum. Ventrally, the tissues are depressed, forming a trough which extends distad from the mouth of the urethra.

A few characters of the baculum are distinctive: (1) It is a slight simple rod; (2) its basal part is moderately expanded laterally and dorsoventrally flattened; and (3) its tip is capped with a cone of cartilage, the length of which varies with the species. In adults, length of baculum is at least 1/3 the length of the hind foot.

The Maniculatus Division is broken down into two main groups, namely, Maniculatus and Boylei. Three species do not fit precisely in either. Of

these, *pectoralis* and *crinitus* are placed between the two groups; *megalops* is listed in the Boylei Group.

Maniculatus Group

The species included here are *maniculatus*, *polionotus*, *leucopus*, and *gossypinus*. In each the glans is of moderate length, approximately 1/3 that of the hind foot; the baculum is usually no more than 2/5 the length of the foot and the cartilaginous spine capping it is always comparatively long, exceeding 1 mm. in some specimens.

Peromyscus maniculatus. — The distal tract of *maniculatus* serves as a standard and is described in detail. The gross anatomy of the penis of cricetid rodents has been outlined by Howell (1926), Tullberg (1899), and others. It need not be discussed here except to say that, from the musculus bulbocavernosus, the penis courses craniad and ventrad and then, when at rest, flexes sharply caudad. The part of the phallus that lies beyond this flexure is the distal tract. The present study is concerned only with this "distal tract" (Howell, 1926:102). In *maniculatus* the tract is 1/2 as long as the hind foot and consists mainly of the glans and structures contained therein (Fig. 1). In the resting state, the tract is directed caudad; when erected, it points ventrad and craniad, thereby topographically reversing its parts; that is, dorsal surfaces become ventral and cranial aspects become caudal. The active position of the tract is the one described on following pages.

The basal part of the tract is oval in cross section (Fig. 1). In the center lie the two, large, resilient corpora cavernosa penis. The corpora are tightly joined and appear as a single body. They insert on the base of the os penis. Ventral to them, and lying partly in a channel formed by their ventral surfaces, is the urethra. Distal to the corpora, the urethra courses along the ventral face of the os and opens to the outside by way of a bowl-shaped cavity (the meatus urinarius) located in the terminal 1/5 of the tract. This cavity continues distad as a gradually narrowed trough which terminates near the tip of the baculum. Dorsal to the corpora cavernosa is the deep dorsal vein which collects blood from the distal parts of the phallus. In the present preparations I am unable to trace its collecting vessels.

The prepuce extends well beyond the glans. Its outer surface is covered with hair and its innermost layer is a membranous tube enveloping the glans. At a plane near the base of the baculum the tube is attached to the stalk of the penis, thereby defining the proximal limit of the glans.

Specifically, in *Peromyscus maniculatus* the glans constitutes all but the basal 1/4 of the distal tract. It is a rod-shaped structure, flared medially and again distally (Pl. I). The length of the glans is approximately 1/4 that of the hind foot and its greatest diameter, in specimens at hand, does not exceed 1/4 its length. It consists of two topographic divisions: *(a)* the main body and *(b)* an attenuate tip.

The main body of the glans is tough and fibrous. Its outer surface is covered with tubercles or recurved spines, which are long and widely spaced at the base of the glans, but they become progressively smaller and

closer together distally. It is longest on its dorsal face. At its distal end there are two attenuate processes, separated middorsally by a V-shaped notch (Pl. I). The distal rim is shaped like a "W" ventrally, the lateral arms of the "W" continuing on dorsally to form the two middorsal lappets. The apex of the "W" is a short blunt, sometimes slightly cleft, lip, which closes the meatus urinarius. When the tip of the glans is extended, this lip is drawn ventrad, thereby opening the meatus.

The attenuate tip, which constitutes the terminal 1/3 or 1/4 of the glans, is unlike the main body; it resembles an irregular elongate cone. The outer surfaces are smooth and membranous. The membranes cover the flexible tip of the glans and extend tentlike to the body. This terminal part is apparently protractile, to some extent capable of extension from, and retraction into, the distal part of the main body of the glans. Unlike the main body, however, the tip apparently does not become engorged with blood. In fresh specimens of individuals of breeding age, the body of the glans is deep red, distended with blood; the tip is pale, tinted slightly by the contents of a few capillaries.

The baculum is a slight, narrow rod which is expanded basally and gradually tapered toward its tip. In adults, its length is approximately 40 percent that of the hind foot and at least 90 percent that of the distal tract. The expanded base is slightly angular. The long shaft, slightly or not at all bent, tapers gradually to an evenly rounded and slightly expanded bony tip. Capping the bony tip is a cone-shaped, cartilaginous spine, which in adults is approximately 1 mm. long, and surrounding both is the soft tissue that makes up the conical apex of the penis.

Peromyscus polionotus. — The phallus of *polionotus* is smaller than that of *maniculatus*, but the two are similar in most proportions. In both species the distal tract amounts to approximately 1/2 the length of the hind foot and the glans is long and rod-shaped. The extent of the glans is more than 3 times its greatest diameter and 1/4 the length of the hind foot. The outer surface of the glans, with the exception of the protractile tip, is covered with proximally directed spines, each of which is situated within a squarish or rhomboidal depression. These are much closer together and smaller distally than proximally.

The baculum is a slight, tapered rod. It is approximately 4/5 the extent of the distal tract and 2/5 the hind-foot length. A long cartilaginous spine extends well beyond the body of the glans.

Features that may distinguish *polionotus* from *maniculatus* are to be seen in the shape of glans and baculum. In *polionotus* the body of the glans gradually increases in diameter from base to lip; it lacks the pronounced medial flare seen in *maniculatus*. The dorsal lappets are shorter, and they are blunt instead of attenuate. The extrusible tip appears to be shorter, relative to length of glans. The baculum is more robust and thicker with respect to length; its base is relatively much broader and more angular and its terminal cartilaginous spine is shorter. In dorsal aspect of glans and in size of the basal part of the baculum *polionotus* somewhat resembles *eremicus*.

Peromyscus leucopus. — The distal tract of *leucopus* is much like that of *maniculatus* (Pl. I). The two are so similar in size, proportions, and

configuration that they are not clearly distinguishable on the basis of the few specimens studied. In all examples of *leucopus* the glans is slightly broader with respect to length, and the ventral lip is undivided. These differences, however, if real, are at best slight.

Peromyscus gossypinus. — The distal tract of *gossypinus* resembles that of *leucopus*. A few differences between them were noted. The glans of *gossypinus* is shorter with respect to length of hind foot. The baculum, likewise, is relatively shorter and its base is more angular. The surface of the glans is comparatively smooth; there are numerous small tubercles but none is definitely spinous. It is questionable whether these distinctions will hold in adequate samples of each species.

Intermediate Forms

In *Peromyscus pectoralis* and *P. crinitus* characters of the Maniculatus and Boylei groups are combined. In size and proportions *pectoralis* fits into the latter but it has a long spine on the baculum as in the former. In structure of phallus *crinitus* is perhaps most like *polionotus* or *maniculatus*. It clearly is unlike *eremicus* and *californicus*, the species with which it is currently grouped (Osgood, 1909).

Peromyscus pectoralis. — The glans of *pectoralis* is 5 to 6 times longer than its greatest diameter and about 1/3 the length of the hind foot (Pl. II). There are two dorsal lappets and a single ventral lip, sometimes lightly notched. The urethral opening lies on the ventral side at the base of a nonspiny, attenuate, apparently slightly extensible tip.

The baculum is small in diameter and relatively long, 2/3 the length of the hind foot. The base is but slightly expanded and flattened. The tip is scarcely or not at all larger than that part of the shaft immediately below it. As pointed out by Clark (1953), the tip ends in a long cartilaginous spine.

In the present specimens, some of which were from reproductively active animals, the surface of the glans is comparatively smooth, as in the examples of *gossypinus* and *perfulvus*. There are numerous minute tubercles, each set in a pit, but none of them appears to be spinous.

Peromyscus crinitus. — In characters of distal tract *crinitus* resembles species of both the Maniculatus and the Boylei groups but fits well in neither. In size and shape of glans it is much like *P. maniculatus*. The cartilaginous spine of the baculum is minute, as in *P. boylei*. Some of its proportions, however, are unlike those seen in members of either group. The distal tract is short, about 2/5 the length of the hind foot. The glans is rod-shaped, flared distally (Pl. III); its extent is 4 times its greatest diameter and 1/4 the length of the hind foot. The surface is covered with spines, the proximal slightly larger and more distantly spaced than the distal. There are two dorsal lappets, and a single ventral lip guarding the urethral opening. The cone of nonspinous soft tissue, distal to the urethral opening, is slightly protractile.

The baculum is shorter, relative to length of hind foot, than in any typical member of the Maniculatus Division; its extent is 1/3 that of the hind foot. In this respect it is closer to *gossypinus* and *polionotus* than to *truei*,

boylei, and allied species. The base is moderately expanded and flattened much as in *maniculatus*, but more so than in *boylei* and less so than in *polionotus*. Its tip is slightly expanded and is capped with a minute cartilaginous cone.

Boylei Group

This group of the Maniculatus Division includes the species *boylei*, *yucatanicus*, *nasutus*, *truei*, *perfulvus*, *mexicanus*, *difficilis*, *melanophrys*, *guatemalensis*, *furvus*, *nudipes*, and *megalops*. In each of these the glans is long, 2/5 to 1/2 the length of the hind foot. The baculum also is long, 1/2 to 2/3 the length of the foot, and its diameter apparently is smaller, relative to length, than is characteristic in the Maniculatus Group. The terminal cartilaginous cone on the baculum is minute. In some of the species it is no more than 0.1 mm. long; in *P. megalops* it is slightly longer than in the others.

Peromyscus boylei. — The glans is flared medially and again distally; in extent 5 times its greatest diameter and approximately 2/5 the length of the hind foot. The margin of the distal flare is serrate in some specimens, smooth in others. The surface of the glans is covered with recurved spines or rounded spinous nodules which are shorter and more closely spaced distally than proximally. The distal nonspinous tip appears to be slightly extensible.

The baculum is slight and long, 1/2 the length of the hind foot, and is flattened and triangular basally and is cylindrical throughout the remainder of its length. Its small knob-shaped tip is capped with a minute cone of cartilage.

Peromyscus yucatanicus. — In structure of phallus *yucatanicus* resembles *mexicanus*, *nasutus*, and other typical species of the Boylei Group. The distal tract is 2/3 the length of the hind foot. The glans is an elongate rod, 1/2 the length of the foot; its greatest diameter is roughly 1/6 its length. It consists of two areas: (1) a spine-covered body with 2 dorsal lappets and a ventral lip and (2) a smooth protractile tip. The mouth of the urethra is far removed from the distal limit of the glans; it opens into a cavity situated ventral to the baculum.

The baculum is small in diameter and long, 3/5 the length of the foot. The base is slightly expanded laterally and dorsoventrally flattened, and the tip of the narrow shaft is capped with a small cartilaginous cone.

Peromyscus nasutus. — The distal tract of *nasutus* is essentially a replica of that of *boylei* or *truei*, but larger than in either. The glans is covered with small spinous tubercles. Its distal margin, bordering its protractile tip, has two narrow dorsal lappets.

The baculum is long and slight, approximately 2/3 the length of the hind foot. Its basal part appears to be narrower, relative to length, than in *boylei* or *maniculatus*. The bone is capped distally with a minute cone of cartilage.

Peromyscus truei. — The distal tract of *truei* is similar to that of *boylei*. In both the tract is 2/3 the length of the hind foot, and the glans is a spiny, elongate rod, flared slightly distally, with a nonspinous terminal

segment (Pl. IV). The specimen illustrated in Plate IV is somewhat atypical. It is abnormally flared and swollen distally, as a result of processing. In length the glans is 4 times its greatest diameter and 1/2 the length of the hind foot. Spines occur over most of the glans except on the basal portion and on that part distal to the two dorsal lappets and the ventral lip. The conical, nonspinous tip is slightly protractile.

The baculum is similar to that of *boylei*, but is longer, approximately 3/5 the length of the hind foot. However, in all examples of *truei* the base is larger and more angular than in *boylei*. The distal cartilaginous cap is minute.

Peromyscus perfulvus. — In shape and proportions the glans of *perfulvus* is much like that of *boylei* or *truei*. It is a rod-shaped, tough-bodied organ, flared distally around a terminal segment of softer tissue. There are two attenuate dorsal processes and a ventral lip. Immediately dorsal to the lip is the urethral opening. The length of the glans is 5 times its greatest diameter and 2/5 the length of the hind foot. In the three specimens measured (2 adults, 1 subadult) the surface, unlike in *boylei* and *truei*, is comparatively smooth, with minute tubercles but no spines.

The baculum resembles that of *boylei*. It is 1/2 the length of the hind foot, and the base is moderately expanded and flattened. The tip is evenly rounded and capped by a minute cartilaginous cone, which is smaller than in *boylei*.

Peromyscus mexicanus. — The glans of *mexicanus* is an elongate rod (Pl. V), its extent 6 times its greatest diameter and 1/2 the length of the hind foot. There are two dorsal lappets and a single ventral lip at the base of a protractile tip. The surface of the glans, excluding the protractile tip, is covered with recurved spines.

The baculum is small in diameter and long, 2/3 the length of the hind foot, and courses through most of the distal tract. Its base is unusually small and but slightly expanded and flattened. A minute cone of cartilage caps the tip.

Peromyscus difficilis. — In the specimens available I find no characters, save possibly ones of size, to distinguish *difficilis* from *mexicanus* and most of the other species of the Boylei Group. The rodlike glans is long and small in diameter; its greatest diameter is about 1/7 its length. There are two acute dorsal lappets and one short broad ventral one. Minute tubercles, but no spines, cover the surface of the glans.

The baculum is long and delicate. Its base is dorsoventrally flattened and but slightly expanded and its proximal margin is convex in profile. The terminal cone of cartilage is like that in *nasutus* and *boylei*.

Peromyscus melanophrys. — In form and size the glans of *melanophrys* is similar to that of *mexicanus* and *difficilis*. It is a long tubular organ, 4 times its greatest diameter and 1/2 the length of the hind foot. The body of the glans is covered with long, proximally directed spines, which are smaller and more closely spaced distally. There are two long broad dorsal lappets at the base of a nonspinous protractile tip. Opposite the lappets, ventrally, is the fleshy lip which covers the mouth of the urethra.

The baculum is long, thin and slightly curved and more than 90 percent the length of the distal tract and 2/3 that of the hind foot. Its base is

slightly expanded and flattened. The tip is knob-shaped and capping this knob is a cartilaginous cone as minute as those in *mexicanus* and *perfulvus*.

Peromyscus guatemalensis. — One phallus of *guatemalensis* is at hand. It closely resembles the lone example of *nudipes* (Pl. VI). The extent of the glans is 3 times its diameter and 2/5 the length of the hind foot; in outline it is flared medially and again terminally. There are two small acute dorsal lappets and a ventral lip. Deep pits suggest that the surface of the glans was covered with spines, but they are now lacking. There is a nonspinous protractile tip that appears to relatively longer and perhaps capable of greater distension than in *boylei*, *truei*, and most of the other species of the Boylei Group. The urethra opens on the ventral face, well short of the extended tip.

The baculum is slight and long, 3/5 the length of the hind foot, and extends almost the full length of the distal tract. Its base is comparatively narrow. There is a minute terminal cartilaginous cone.

Peromyscus furvus. — The single available phallus of *furvus* resembles the examples of *difficilis* and *mexicanus* in shape and size. Its extent is 6 times its greatest diameter and 2/5 the length of the hind foot. The protractile tip appears to be less flexible and relatively shorter than in *guatemalensis*. There are two broad short dorsal lappets. Presumably, the surface of the glans, excepting the tip, was spinous; pits of the nature that typically contain spines are present.

The baculum is comparatively gross, its length 1/2 that of the hind foot. The base is angular and strongly expanded laterally. The shaft is comparatively large in diameter throughout its length and terminates in a broad knob which is capped by a small cartilaginous cone.

Peromyscus nudipes. — The glans of *nudipes* (Pl. VI) is an elongate rod much like that of *mexicanus*, *guatemalensis*, and *melanophrys*. In the single specimen at hand the extent of the glans is 6 times its greatest diameter and 2/5 the length of the hind foot. The protractile tip lies beyond two short dorsal lappets and a single ventral lip. The outer surface, with the exception of the tip, is spiny. The proximally directed spines are smaller and more closely spaced distally.

The baculum is long, thin, and gently curved. It is about 3/5 the length of the hind foot and extends for most of the distal tract. The base, situated several millimeters proximal to that of the prepuce, is slightly expanded and flattened and is small, relative to length of baculum, as in *mexicanus*, *guatemalensis*, and some other species of the group. A minute cartilaginous cone caps the tip.

Peromyscus megalops. — The sample of *megalops* consists of seven specimens obtained from dried study skins. Although the phalli are imperfect, each somewhat misshapen and lacking proximal parts of the tract, nevertheless, their principal features are discernible.

The glans resembles that of *mexicanus*, *difficilis*, and other large species of *Peromyscus*. It consists of the two topographical divisions that are typical of the Maniculatus Division: the rod-shaped body, covered with short recurved spines and terminating distally in two short dorsal processes and a single ventral lip, and the nonspinous, somewhat protractile, attenuate tip. At the ventral base of the tip is the mouth of the urethra

which opens into a gradually narrowed channel that terminates just short of the end of the phallus. The full extent of the glans is 2/5 the length of the hind foot.

The baculum is long and slender and ends in a cartilaginous spine 0.4 to 0.5 mm. in length. The spine is longer than in other species of the Boylei Group, but is shorter than is that in the Maniculatus Group. The extent of the os is at least 1/2 the length of the hind foot.

Eremicus Division

Three species of *Peromyscus*, namely, *eremicus*, *californicus*, and *hylocetes*, are grouped here. In each, the glans is vase-shaped, rather large in diameter, and with a pronounced distal flare (see Pl. VIII); the greatest diameter is 1/3 the length. The body of the glans is tough and resilient and, except for the extreme basal part, is covered with recurved spines. The distal border is notched middorsally and midventrally, but there are no lappets or processes as in the species of the Maniculatus Division, nor is there a protractile tip. The most distal part of the glans is either the dorsal edge of the glans body or the surface of the rounded knob that covers the baculum. This knob and the baculum beneath it apparently are not extensible.

The baculum is comparatively gross throughout its length, broad and flat at its base and large in diameter distally. Its length is 2/5 to 1/2 that of the hind foot. The cartilage over its tip is somewhat diffuse, usually forming an irregular cap rather than a distinct cone.

Hylocetes Group

In characters of phallus, *hylocetes* may fit between the Maniculatus and Eremicus divisions. Although it is here listed in the Eremicus category (as representing a group of that division), there is also justification for considering it an aberrant unit in the Maniculatus Division. Its glans is an elongate bell-shaped structure, longitudinally furrowed or fluted, and scalloped distally. The baculum and surrounding tissues project well beyond the body of the glans, though less so than in *maniculatus* or *boylei*, and there is no long protractile tip.

Peromyscus hylocetes. — The distal tract is about 1/2 the length of the hind foot. The glans is a vase-shaped structure with a distal flare (Pl. VII), approximately 1/3 the length of the hind foot and 3 times its greatest diameter. The surface is covered with short proximally directed spines. Distally there are a number of longitudinal furrows, which terminate at a scalloped border that surrounds a mound of soft, nonspinous tissue. Projecting distad from the dorsal part of this mound is a large rounded knob of soft tissues that encloses the tip of the baculum. Ventral to the baculum and within a crater in the mound is the urethral opening. The nonspinous tip is scarcely, if at all, protractile; it is closely bound to the body of the glans.

The baculum is comparatively short and gross; its length is 2/5 that of the hind foot. The base is simple in configuration, dorsoventrally flattened,

and strongly expanded laterally. The shaft is relatively large throughout its length, and its rounded tip is capped with a minute cone of cartilage.

Eremicus Group

Peromyscus eremicus and *P. californicus* form a group distinct from *P. hylocetes*. The surface of the glans is not furrowed, neither is the distal border scalloped. The fleshy mound covering the baculum is confined to the glans, rather than projecting well beyond it as in *hylocetes*. The baculum is comparatively gross throughout its length; the spatulate base is particularly large.

Peromyscus eremicus. — The phallus of *eremicus* is essentially a replica of that of *californicus* (Pl. VIII) but smaller. The glans is vase-shaped, approximately 1/3 the length of the hind foot and 2/3 that of the distal tract; its greatest diameter is about 1/3 the length. The body of the glans is covered with stubby spines. It is simple in outline and there are no lappets, nor is there a conical tip that extends well beyong the limits of the glans body. The end of the glans consists of folds of nonspinous soft tissue, a mound of which encloses the tip of the baculum. A depression in the ventral sector of the tissue marks the mouth of the urethra.

The baculum resembles that of *californicus*. It courses through approximately 3/4 of the distal tract. The bone is 2/5 the length of the hind foot, and has a flat, broad base. The shaft is large in diameter throughout its length and terminates in a rounded tip covered by a cap of cartilage.

Peromyscus californicus. — The glans is vase-shaped, narrow at its base and flared medially and again distally (Pl. VIII). In length it is approximately 3 times its greatest diameter and 2/5 that of the hind foot. The surface, except for the basal sixth and the terminal face, is covered with recurved spines, which are longer and more widely spaced proximally than distally. The distal border, or rim, of the glans body is shallowly notched middorsally but it is not prolonged into distinct lappets; it curves gently around soft nonspinous tissues which enfold the baculum and close the end of the glans. Near the rim on the ventral side is the mouth of the urethra.

The baculum is comparatively gross, in length 3/4 that of the distal tract and 1/2 that of the hind foot. The basal part is paddle-shaped, thin dorsoventrally, and broad laterally. The shaft and tip are also comparatively broad. The blunt tip is surrounded by a thick layer of soft tissue, little, if any, of which is cartilaginous; a cartilaginous cap is indistinct or absent.

Thomasi Division

Peromyscus thomasi is unlike the other species studied. It warrants division rating. Diagnostic characters include: a bulbous, fluted glans that is covered with long conical spines; a subterminal meatus urinarius; and a broad-based baculum equipped distally with a long cartilaginous spine.

Peromyscus thomasi. — The distal tract of *thomasi* is approximately 3/5 the length of the hind foot. The glans is a bulbous structure, of

greatest diameter about midway in its length (Pl. IX), its extent 3 times its greatest diameter and approximately 2/5 the length of the foot. The outer layers form a series of longitudinal channels and ridges which extend from the base of the glans almost to the meatus urinarius. The surface is covered with conical, proximally directed spines, which are larger than in any other species studied. The urethral opening lies on the ventral side, 1 or 2 mm. short of the end of the glans. Distal and dorsal to the opening is a knoblike process that contains the cartilaginous tip of the baculum. The tissues distal to the proximal border of the urethral opening are non-spinous. There are no dorsal or ventral lappets.

The baculum is slight and long, extending almost the full length of the distal tract. It is approximately 1/2 as long as the hind foot. The base is dorsoventrally flattened and strongly expanded laterally; the proximal border is truncate. The cylindrical shaft tapers slightly distad to terminate in a small rounded head. Capping the head is a slender cartilaginous cone, 5 to 7 mm. long, which is longer, relative to length of os, than in the other large species of *Peromyscus* studied excepting possibly *P. megalops*.

Banderanus Division

In structure of phallus *P. banderanus* is markedly different from all species of *Peromyscus*, save possibly *P. lepturus*. The minute baculum and small simple glans with the urethral opening at its tip are the principal diagnostic characters.

Peromyscus banderanus. — The distal tract of *banderanus* is only 2/5 the length of the hind foot. The glans is a small awl-shaped structure (Pl. X) which in size and shape somewhat resembles the glans of *Neotomodon alstoni* and that of *P. lepturus*. It is simple in form, lacking both the protractile tip and the lappets and other processes seen in most species of the genus. The urethra opens at the tip of the glans. The glans is approximately 3 times longer than its greatest diameter and 1/4 the length of the hind foot. The surface, except at the extreme tip and base, is covered with recurved spines, which are longest proximally.

The baculum is a slight rod, only 1/5 as long as the hind foot. It is confined entirely to the glans. Its base is not much larger than the shaft; the lateral diameter is slightly greater than the dorsoventral one. Its knob-shaped tip is capped with a small cartilaginous cone.

Floridanus Division

Among the characters of the distal tract that set *Peromyscus floridanus* apart from other species of the genus are: the small size, smooth surface and simple form of the glans; the terminal meatus urinarius; and the small simple baculum.

Peromyscus floridanus. — The distal tract of *floridanus* is short, only 1/3 the length of the hind foot. The glans is awl-shaped, widest nearest its base, and tapered gradually to a blunt or acute tip (Pl. XI). It is approximately 7 times longer than its greatest diameter and 1/4 the length of the hind foot. The terminal part consists of two lobes: (1) a blunt dorsal lip

and (2) a longer triangular ventral process which can be both extended and folded. When the process is extended, its margins are curled dorsad, forming a triangular trough continuous with the meatus urinarius; when folded, it is a rounded mass which opposes the dorsal lip and closes the meatus. When the ventral process is folded the mouth of the urethra is terminal in position; when the process is extended the mouth is on the dorsal side, slightly short of the tip. The surface of the glans is smooth in all specimens; there are no spines or rugosities.

The baculum is a slightly curved rod, its length approximately equal to that of the glans and about 1/4 that of the hind foot. The base is slightly flattened dorsoventrally and but little expanded laterally. The tip, scarcely larger than the shaft, is capped by a cartilaginous spine 0.1 to 0.2 mm. long. This spine terminates short of the tip of the glans.

Lepturus Division

The species *P. lepturus* and *P. lophurus* are placed together, because both have a small, simple and apparently spineless glans, a subterminal meatus urinarius, and a short, comparatively thick baculum that terminates in a rounded head capped with a mound of cartilage. When the characters of their phalli are better known, either one or both may be arranged with *banderanus* or *floridanus*.

Peromyscus lepturus. — The three specimens of *lepturus* were recovered from study skins; hence, their proportions may be slightly distorted. In each, the glans is small, its length only 1/6 that of the hind foot. It resembles the glans of *banderanus* and is a simple awl-shaped structure (Pl. XII) of greatest diameter near its base and tapered distally to a blunt tip. The surface is smooth, without spines or prominent tubercles. The urethral opening lies on the ventral side a short distance from the tip; leading distally from the opening is a gradually narrowed channel.

The baculum is comparatively large, much longer than the glans and approximately 1/4 the length of the hind foot. The base is spatulate, moderately expanded laterally and concave on dorsal and ventral faces. The shaft, relatively large in diameter throughout its length, terminates in a distinct head that is capped by a layer of cartilage.

Peromyscus lophurus. — The sample of *lophurus* consists of two specimens, each the distal part of a phallus removed from a dried study skin. These are fragmentary and somewhat twisted but, although far from satisfactory, they still show several principal features. The glans somewhat resembles those of *lepturus* and *floridanus*. It is a simple tubular structure (Pl. XIII), without spines or tubercles, terminating in a rounded lobe that apparently should be dorsal in position but is twisted to the side in my material. The ventral face of the lobe is convex and forms a channel that leads from the mouth of the urethra. The urethral opening, on the ventral side just short of the tip, is guarded ventrally by a crescentic lip.

The shaft of the baculum is of moderate diameter. Its tip is enlarged, forming a distinct head, which is capped with a narrow layer of cartilage. The base of the os is missing.

Nuttalli Division

In its short urn-shaped glans, with its fleshy bilobed process and small peculiarly shaped baculum, *nuttalli* stands in sharp contrast to all other species currently included in *Peromyscus*.

Peromyscus nuttalli. — In *nuttalli* the distal tract is 1/4 or 1/3 the length of the hind foot. The glans is minute and barrel- or urn-shaped (Pl. XIV), its length twice its greatest diameter and about 1/6 that of the hind foot. Its surface is covered with stubby, broad-based, conical, recurved spines, each seated in a pit. There is no protractile tip. The distal rim of the glans surrounds a mound of nonspinous soft tissue. Distally through this tissue two structures extend: (1) a bilobed process of soft tissue near the ventral rim and (2) through the dorsal part, the membrane-covered tip of the baculum. Between the bilobed process and the baculum is the mouth of the urethra, which is thus terminal in position.

The baculum is somewhat ornate. Its length is 1/5 or less that of the hind foot and about equal to that of the glans. The base is spade-shaped, expanded laterally, flattened dorsoventrally, and concave ventrally. The distal part of the bone is club-shaped, that is, blunt and comparatively broad, and is covered with a narrow layer of cartilage, which in turn is capped with a cone of less dense tissue (Pl. XIV) about 0.3 mm. long.

DISCUSSION

Types of Phallus

The 27 species of *Peromyscus* studied have been segregated in seven divisions each of which is characterized by a distinctive phallus. The division comprised of *P. lophurus* and *P. lepturus* is based on insufficient evidence and may not hold up. The other six are clearly distinct, each differing from the other in size and shape of the phallus and in arrangement of its component parts. The chief characteristics of the divisions are given below. The divisional names are strictly utilitarian; no taxonomic usage is implied.

Maniculatus Division. Eighteen of the 27 species exhibit the same type of phallus. All of the 18 have an elongate rod-shaped glans which consists of two topographic divisions: (1) a fibrous body that ends in two dorsal lappets and a ventral lip and (2) a cone-shaped, nonspiny, somewhat protractile tip which terminates in a knob of tissue surrounding the apex of the baculum. The urethral opening lies in the ventral sector, comparatively far removed from the end of the glans.

Observed distinctions between any of the 18 species are principally ones of absolute or relative size of one or more parts of the glans or baculum. On this basis two groups have been segregated within the division. In the Maniculatus Group the glans and bone are comparatively short and there is a long cartilaginous spine capping the bone. In the Boylei Group, by comparison, the glans and bone are actually and relatively longer and the cartilaginous spine is much shorter. Three species — *crinitus*, *pectoralis*, and *megalops* — share characters of both groups. The glans of

crinitus is relatively small, as typical of the Maniculatus Group, but the distal spine on the baculum is as short as in *P. boylei* and related species. Both *pectoralis* and *megalops*, the former especially, have a spine like that in *maniculatus*, but in dimensions of glans and bone they match or exceed *boylei*.

Eremicus Division. A second type of phallus is seen in *P. eremicus* and *P. californicus*, and a variant of it, apparently, is exhibited by *P. hylocetes*. *P. hylocetes* is, and probably should be, grouped with *eremicus* and *californicus* because it resembles those species more than the others; however, it apparently is unique in a few features. In these three species the glans is vase-shaped, broader with respect to length and more strongly flared distally than in the Maniculatus Division. There is no protractile distal cone, nor are there dorsal or ventral processes, and the baculum is comparatively gross. The urethra opens ventrally and subterminally. The type of phallus seen in *eremicus* and *californicus* is well differentiated from that of the Maniculatus Division. The distinction between *hylocetes* and that division is less pronounced.

Thomasi Division. A third type of phallus, exhibited by *P. thomasi*, may be interpreted as a modification of the type characteristic of the Maniculatus Division. Structurally, it is more similar to the *maniculatus* type than to that seen in the Eremicus Division. In *thomasi* the glans is bulbous, fluted, and covered with large spines, the baculum is broad basally and terminates in a long cartilaginous spine, and the urethral opening is on the ventral side near the end of the glans.

In all species of the foregoing three divisions the glans is relatively long, the baculum extends almost the full length of the distal tract, and the urethral opening lies well back of (basal to) the end of the glans. Quite different shapes and proportions are seen in the following five species. In them the glans and baculum are relatively short and slight and the urethra opens at or very near the tip of the glans. In morphology of phallus these five species are set apart from all foregoing species.

Banderanus Division. A fourth pattern of phallus is evident in *P. banderanus*. Here, the glans is a small, awl-shaped structure, simple in form (Pl. X), the urethra opens at its tip and the os penis is a slight rod no longer than the glans. The base of the os is unusually narrow and the tip is expanded to form a distinct head.

Floridanus Division. The phallus of *floridanus* is grossly similar to that of *banderanus*, but the two organs are distinguishable in size, shape, and structure of the tip of the glans and in dimensions of the baculum. In *floridanus* the glans is awl-shaped, simple and small (Table I), its greatest diameter no more than 1/5 its length. The surface of the glans is smooth, without spines or prominent tubercles and the urethral opening is terminal. The baculum is slender throughout its length, its basal part but slightly expanded.

Lepturus Division. The phalli of *lepturus* and *lophurus*, the two apparently much alike, may constitute a separate type of phallus, as here recognized, or they may prove to be generally similar to that of either *banderanus* or *floridanus*. They are morphologically unlike any species, other than those two, examined to date. Available data on *lophurus* and *lepturus* are incomplete and inadequate.

Nuttalli Division. A seventh category includes the one species, *nuttalli*. In shape and structural plan of phallus this species is unique. The short, urn-shaped glans, equipped with a fleshy bilobed process, the small peculiarly shaped baculum (Pl. XIV) and other characters serve to set this species well apart from all the others. In structure of phallus *nuttalli* resembles species of other genera more closely than any species of *Peromyscus* yet examined.

Classification of the Species

Osgood's classification of 1909 is current for *Peromyscus*. There have been taxonomic changes in the genus since 1909, for example the species of *Baiomys* have been excluded, but those changes are of no immediate importance here. The 27 species that I examined are arranged in Osgood's list (1909:28) in 5 subgenera as follows: *Podomys (floridanus)*; *Ochrotomys (nuttalli)*; *Megadontomys (nelsoni)*; *Haplomylomys (crinitus, eremicus,* and *californicus)*; and *Peromyscus* (the remaining 21 species studied). The 21 species represent all of the eight species groups that go to make up Osgood's subgenus *Peromyscus*.

My arrangement of the 27 species that is based on structure of the phallus agrees in some respects with Osgood's classification and in other respects disagrees importantly with it. The two schemes are compared below.

Three categories correspond exactly. *Podomys* is equivalent to my Floridanus Division, and *Ochrotomys* matches my Nuttalli Division. There is only one species in each category. *Megadontomys* corresponds with the Thomasi Division. I have examined only one species, *thomasi*, that belongs here. Osgood lists two others, namely *nelsoni* and *flavidus*. There is major agreement, too, between his *Haplomylomys* and my Eremicus Division. Both are comprised of *eremicus*, *californicus*, and *goldmani*. I have examined *goldmani* but have not described it; it clearly fits here. The three species belong together. There is lack of agreement with respect to two other species. Osgood's *Haplomylomys* includes *crinitus* and it excludes *hylocetes*, the latter being listed in the subgenus *Peromyscus*. In structure of phallus *crinitus* belongs in *Peromyscus*, and *hylocetes* probably should be shifted from *Peromyscus* to *Haplomylomys*.

There is some disagreement as to allocation of the remaining 20 species. Osgood arranges them in eight groups within the one subgenus *Peromyscus*. The data obtained from the phallus indicate that all of those species do not belong together. The species *banderanus*, *lepturus*, and *lophurus* definitely do not fit in this group of 20, unless the group be expanded to include both *nelsoni* and *floridanus*. It reasonably may be questioned whether *nelsoni* and *floridanus* each should rate a subgenus. If they do, then *banderanus* likewise warrants one, and perhaps the pair *lepturus* and *lophurus* does too.

As to matching of species groups within the subgenus *Peromyscus*, my Maniculatus Group — consisting of *maniculatus*, *polionotus*, *leucopus* and *gossypinus* — is equivalent to the *maniculatus* and *leucopus* groups, the two combined, of Osgood. The Boylei Group — made up of *boylei*, *truei*, *nasutus*,

mexicanus, *yucatanicus*, *difficilis*, *melanophrys*, *guatemalensis*, *furvus*, and *nudipes* — draws species from five of Osgood's groups. The status of three other species — *pectoralis*, *crinitus* and *megalops* — is not satisfactorily resolved in my classification. Each of those clearly belongs in *Peromyscus*; however their precise positions within it are not clearly indicated by the data at hand. Thus within this subgenus, the two schemes of classification do not closely jibe. Perhaps they should not be expected to do so, for the following reason. The phalli of closely related species, such as those listed here, are probably closely similar. Their interspecific differences, if present at all, are subtle, requiring refined techniques and large samples to be seen and accurately defined. For such purposes, the methods and samples used here are scarcely adequate. They reveal principally gross differences. The data produced here appear to be most useful in distinguishing subgenera and other higher taxonomic groups.

Only one change in classification is called for now. *Ochrotomys* should be raised to generic level. Students of *Peromyscus* have long been aware of many characteristics of *P. (Ochrotomys) nuttalli* that set it apart from other species of the genus. Osgood listed many distinctions and Blair (1942) pointed out the peculiarities of its baculum and suggested that *Ochrotomys* should have generic status. I have additional data, yet unpublished, which further indicate that the hiatus in kinship between *nuttalli* and the other species is a long one, longer than reasonably can be spanned by a single generic term. In light of all evidence now available, it is clear that *nuttalli* should be removed from *Peromyscus* and should be listed as *Ochrotomys nuttalli* (Harlan).

Although the data given here do not provide sufficient reason for rejecting the whole presently accepted classification of *Peromyscus*, they appear sufficiently impressive to suggest that the current arrangement is due for a critical review and probably a major overhaul.

LITERATURE CITED

Blair, W. Frank
1942 Systematic Relationships of Peromyscus and Several Related Genera as Shown by the Baculum. Jour. Mammal., 23:196-204, 2 figs.

Burt, William H.
1936 A Study of the Baculum in the Genera Perognathus and Dipodomys. Jour. Mammal., 17:145-56, 6 figs.

Clark, William K.
1953 The Baculum in the Taxonomy of *Peromyscus boylei* and *P. pectoralis*. Jour. Mammal., 34:189-92, 1 fig.

Gilbert, Th.
1892 Das Os priapi der Saugethiere. Morph. Jahrb., 18:805-31, 1 pl.

Hamilton, William J., Jr.
1946 A Study of the Baculum in Some North American Microtinae. Jour. Mammal., 27:378-87, 3 figs.

Howell, A. Brazier
1926 Anatomy of the Wood Rat. Baltimore: Williams & Wilkins Co. Pp. x + 225, 37 figs.

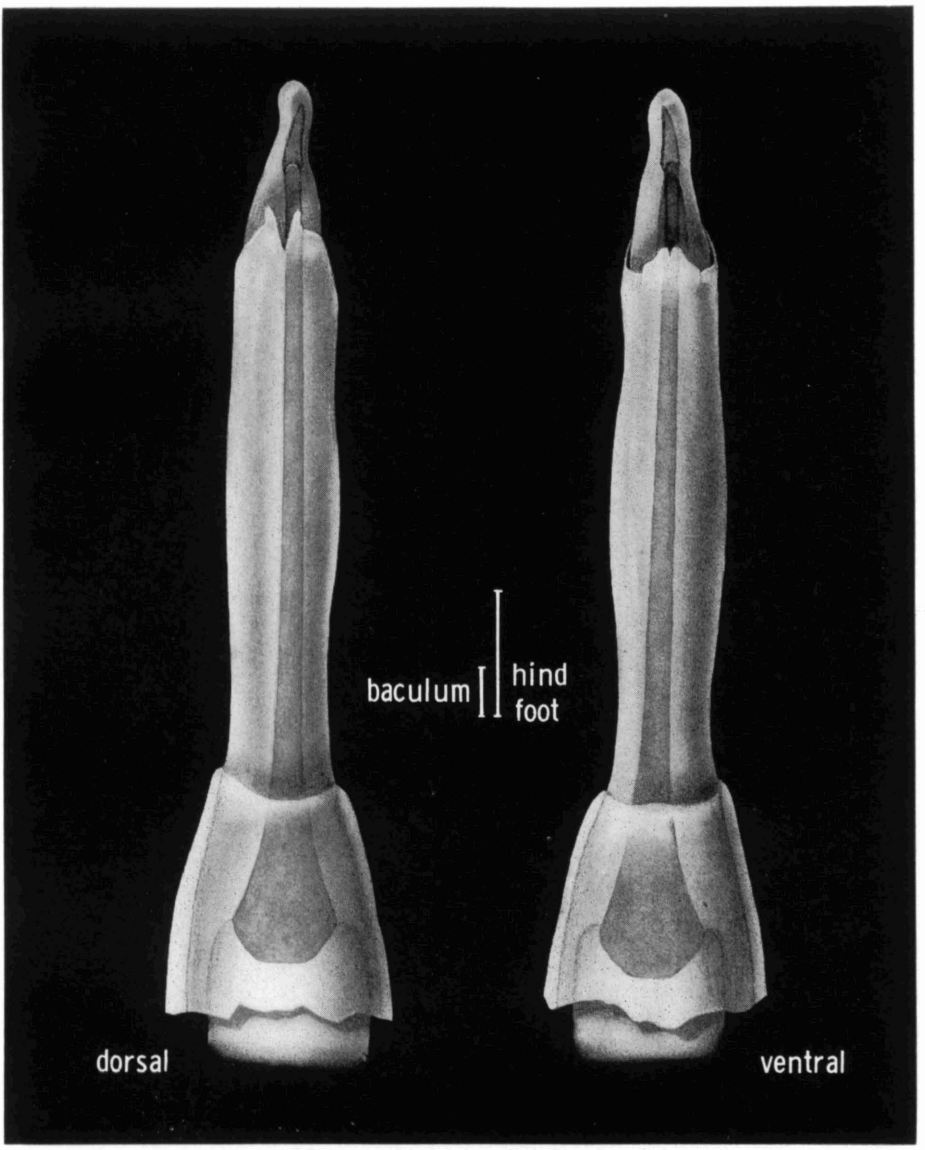
Mossman, Harland W., J. W. Lawlah, and J. A. Bradley
1932 The Male Reproductive Tract of the Sciuridae. Amer. Jour. Anat., 51:89-155, 7 pls., 16 figs.

Osgood, Wilfred H.
1909 Revision of the Mice of the American Genus Peromyscus. N. Amer. Fauna, 28:1-285, 8 pls., 11 figs.
Pocock, R. I.
1923 The Classification of the Sciuridae. Proc. Zool. Soc. London, pp. 209-46, 12 figs.
Prasad, M. R. N.
1957 Male Genital Tract of the Indian and Ceylonese Palm Squirrels and Its Bearing on the Systematics of the Sciuridae. Acta Zool., 38:1-26, 19 figs.
Tullberg, T.
1899 Über das System der Nagathiere, eine phylogenetische Studie. Kongl. Vetensk. Soc. i Upsala, ser. 3, 18, Sec. Med. Hist. Nat., pp. 1-514, 57 pls.

PLATES I–XIV

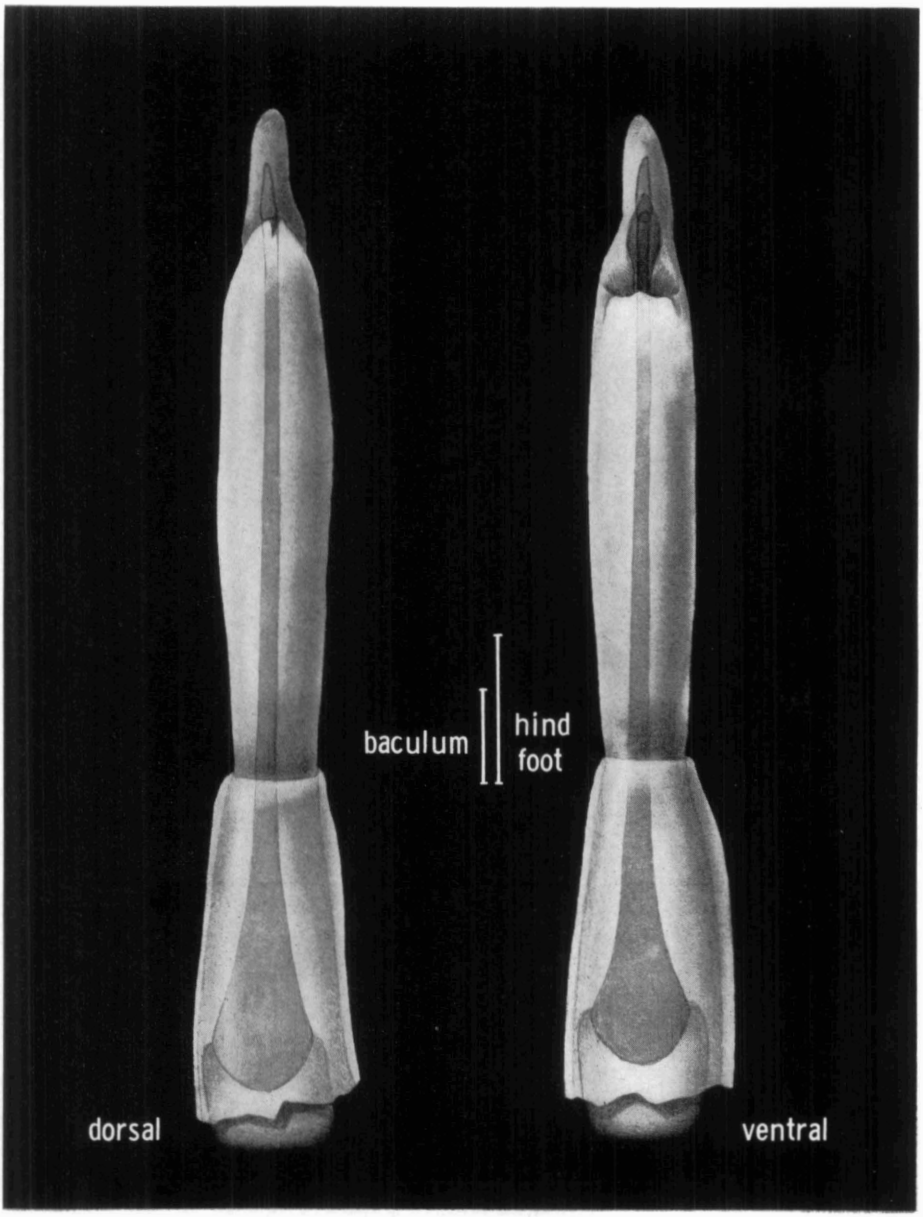
Translucent views of distal tracts in fourteen species of *Peromyscus* (see text for explanation).

PLATE I



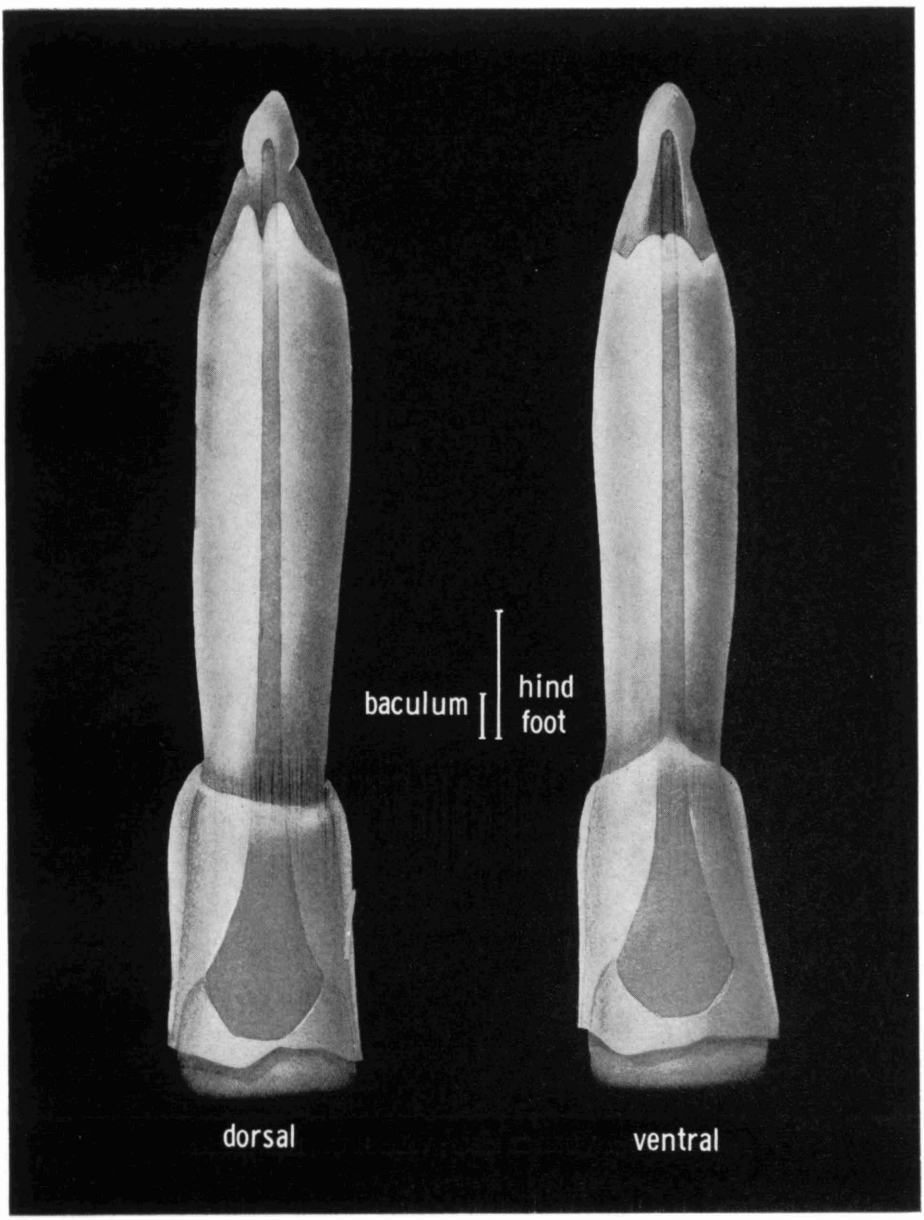
Peromyscus maniculatus, UMMZ 103718; Pierce Co., Washington.

PLATE II



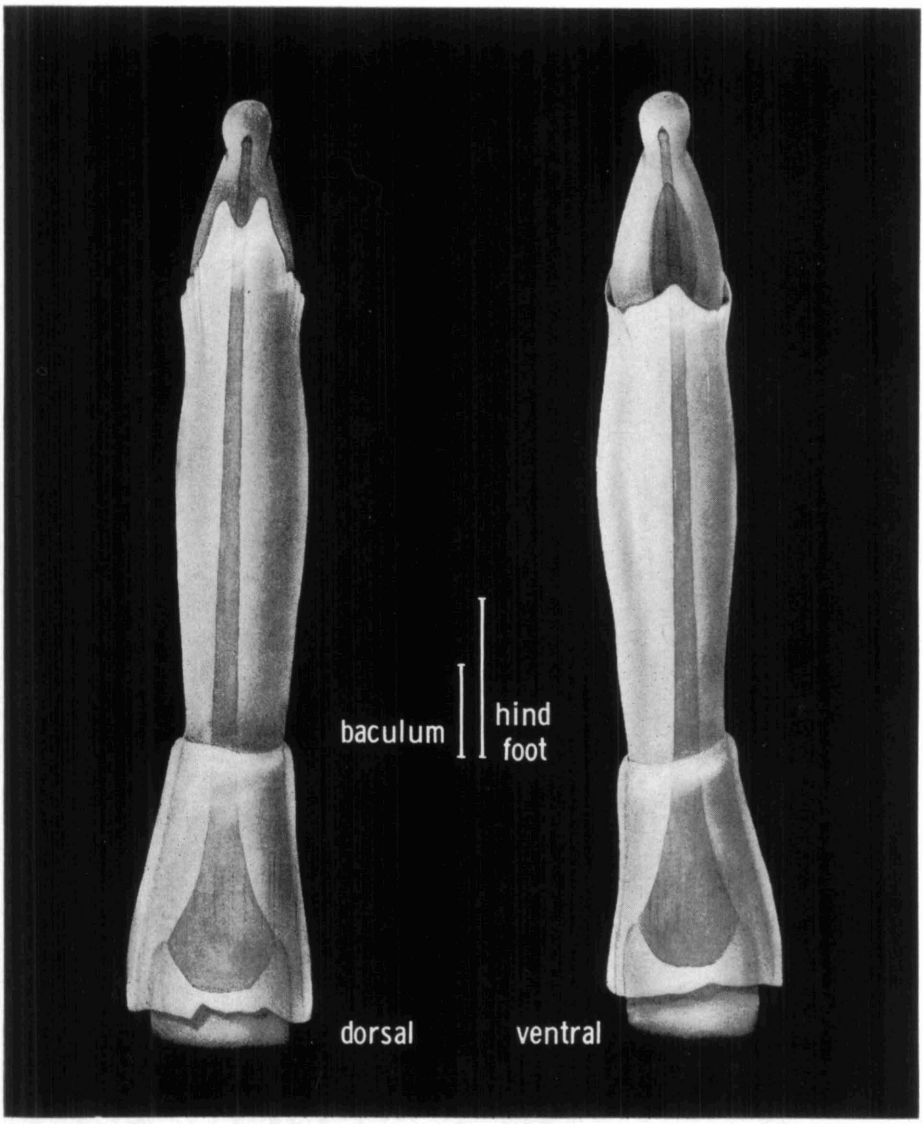
Peromyscus pectoralis, UMMZ 101684; Brewster Co., Texas.

PLATE III



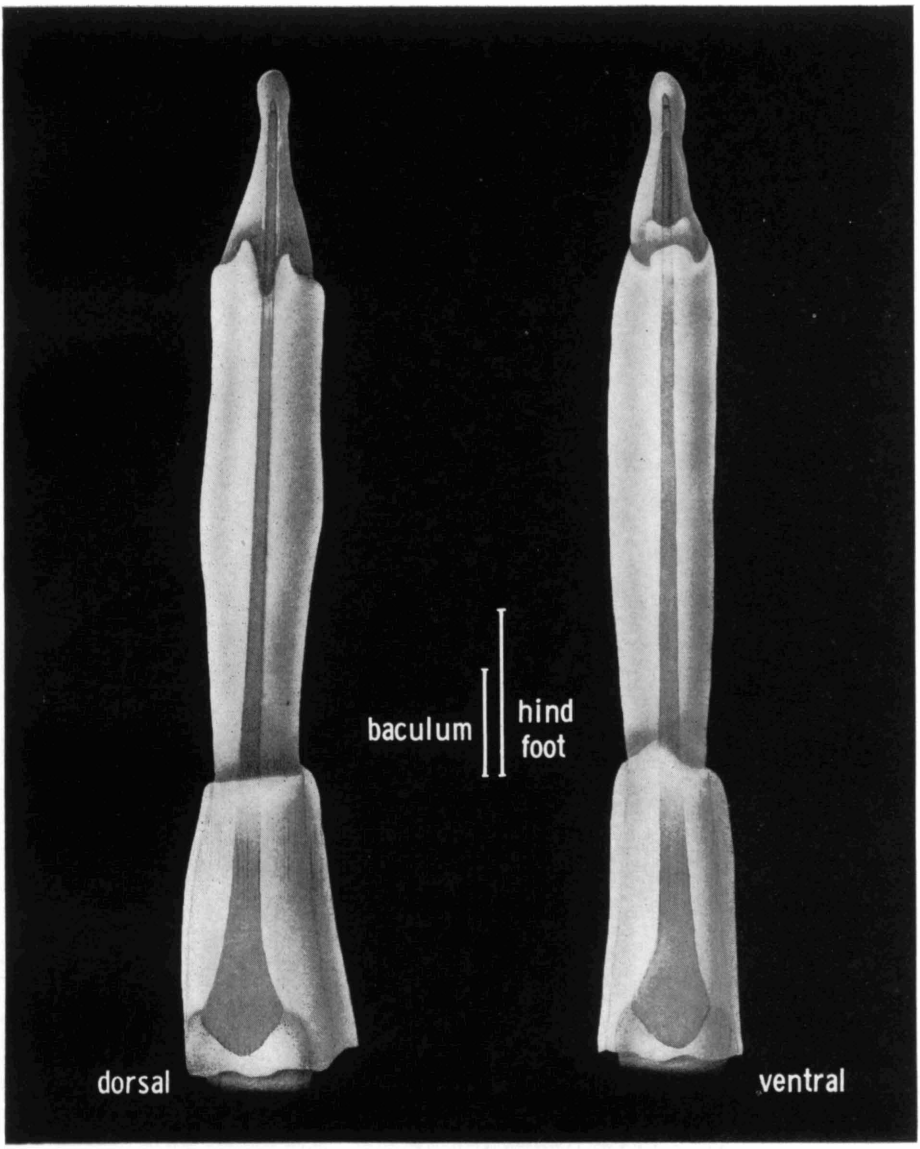
Peromyscus crinitus, UMMZ 103740; Tooele Co., Utah.

PLATE IV



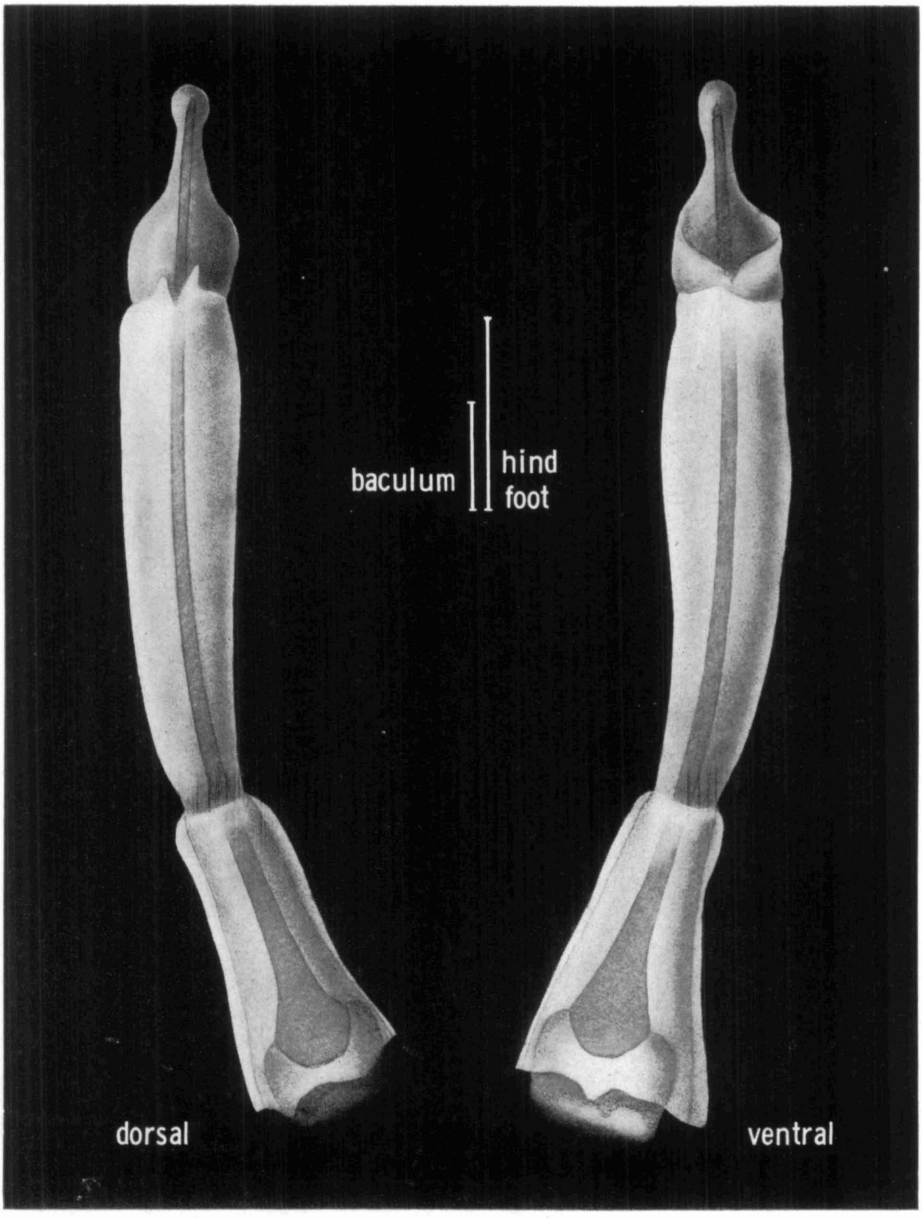
Peromyscus truei, UMMZ 83663; Valencia Co., New Mexico.

PLATE V



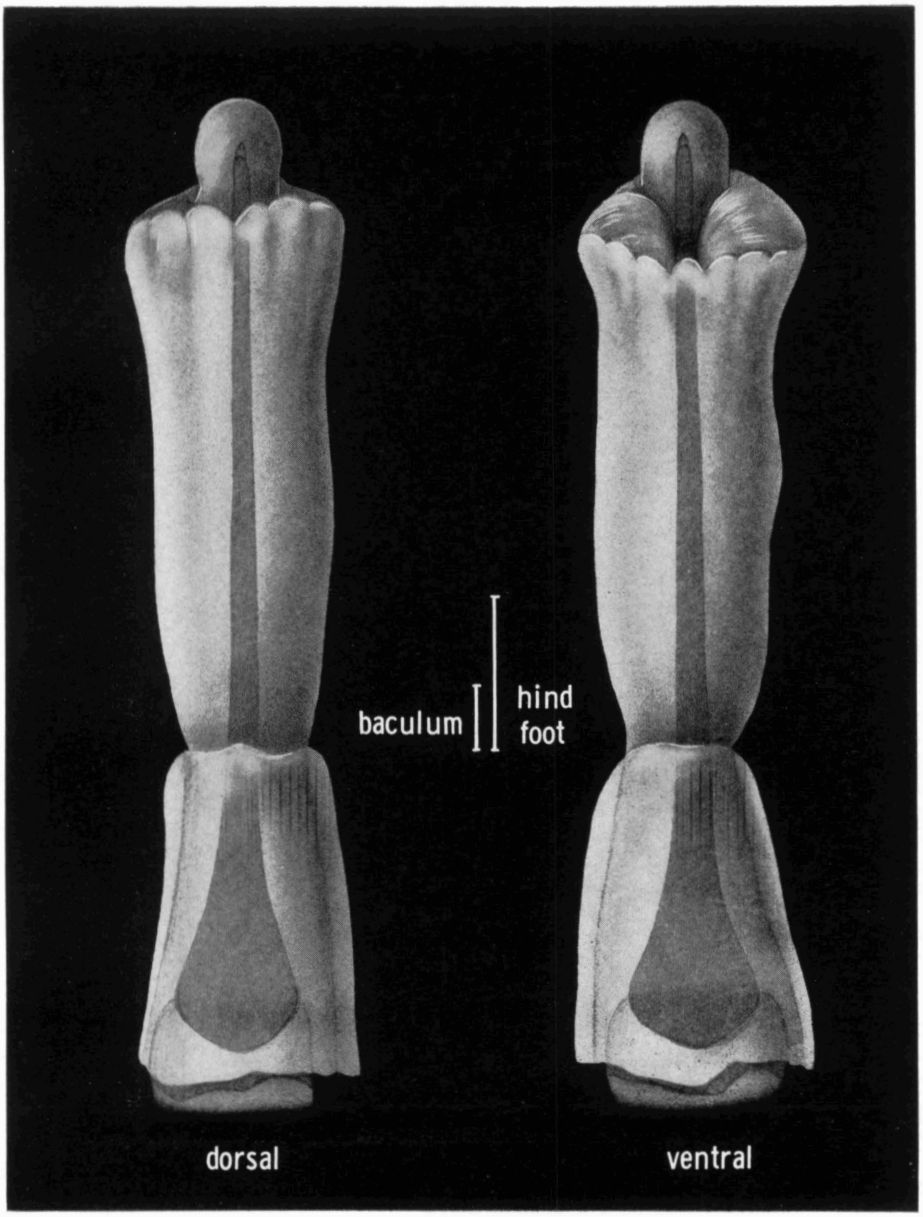
Peromyscus mexicanus, CNHM 56054; Presidio, Veracruz.

PLATE VI



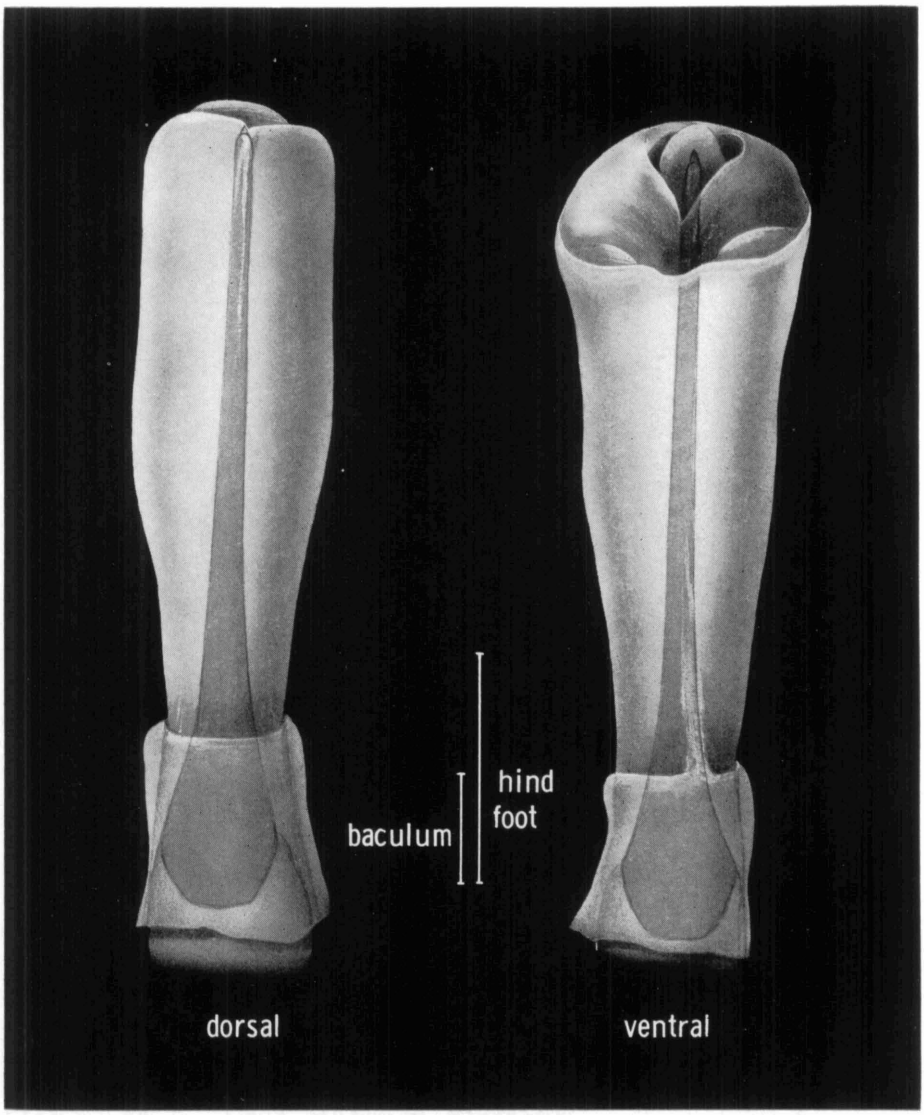
Peromyscus nudipes, KMNH 39254; 30 km. S. San José, Costa Rica.

PLATE VII



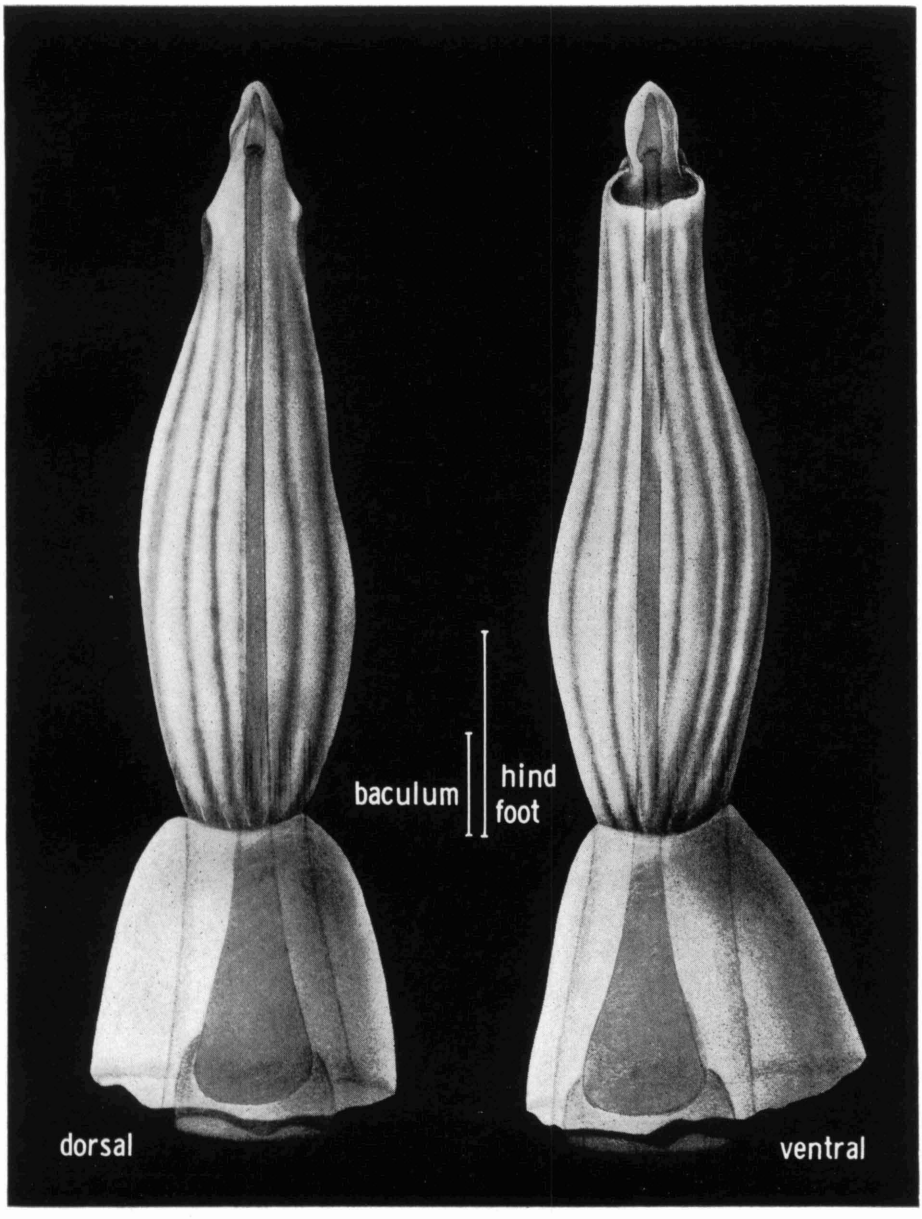
Peromyscus hylocetes, UMMZ 95330; Sierra de Autlán, Jalisco, México.

PLATE VIII



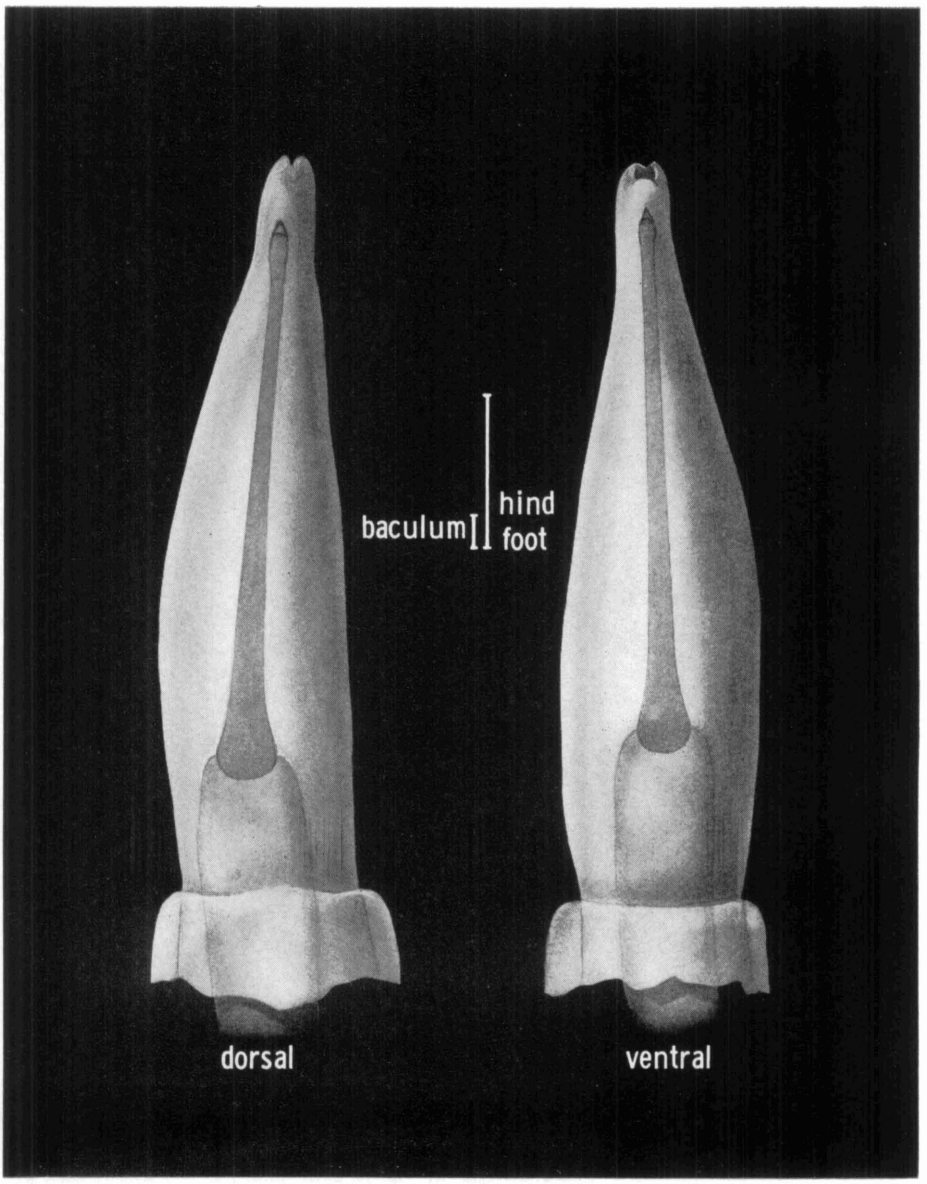
Peromyscus californicus, UMMZ 103726; Alameda Co., California.

PLATE IX



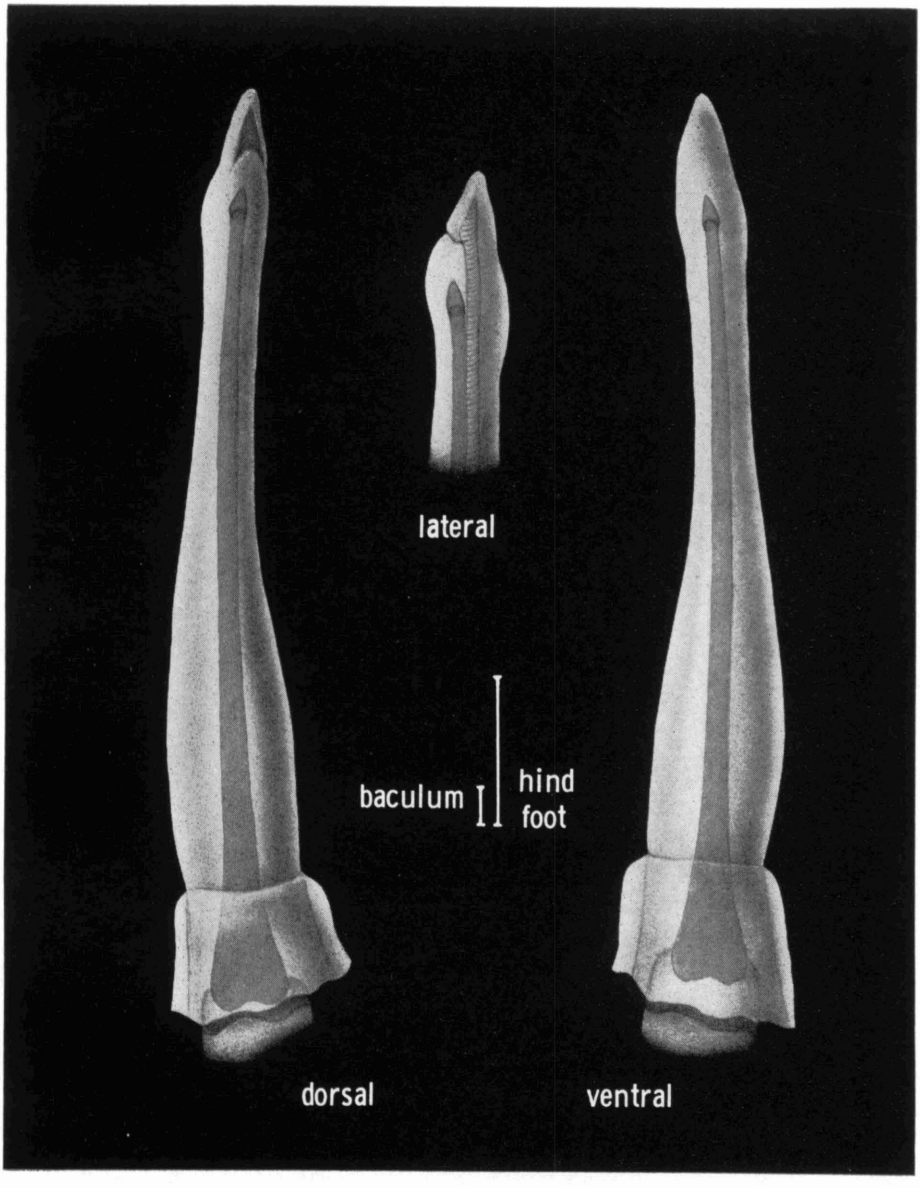
Peromyscus thomasi, MVZ 113564; 3 mi. W. Omilteme, Guerrero, México.

PLATE X



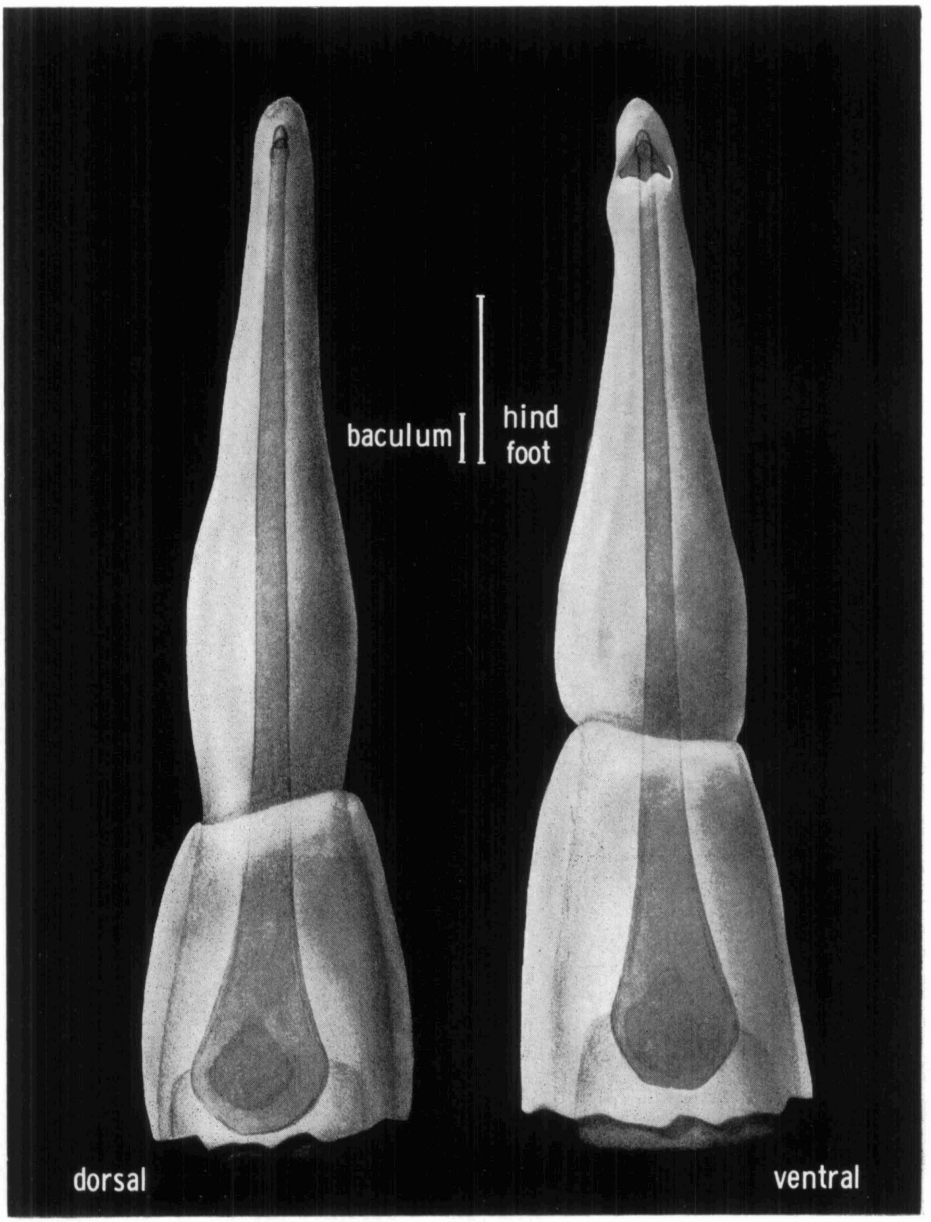
Peromyscus banderanus, AMNH 172068; Pueblo Juárez, Colima, México.

PLATE XI



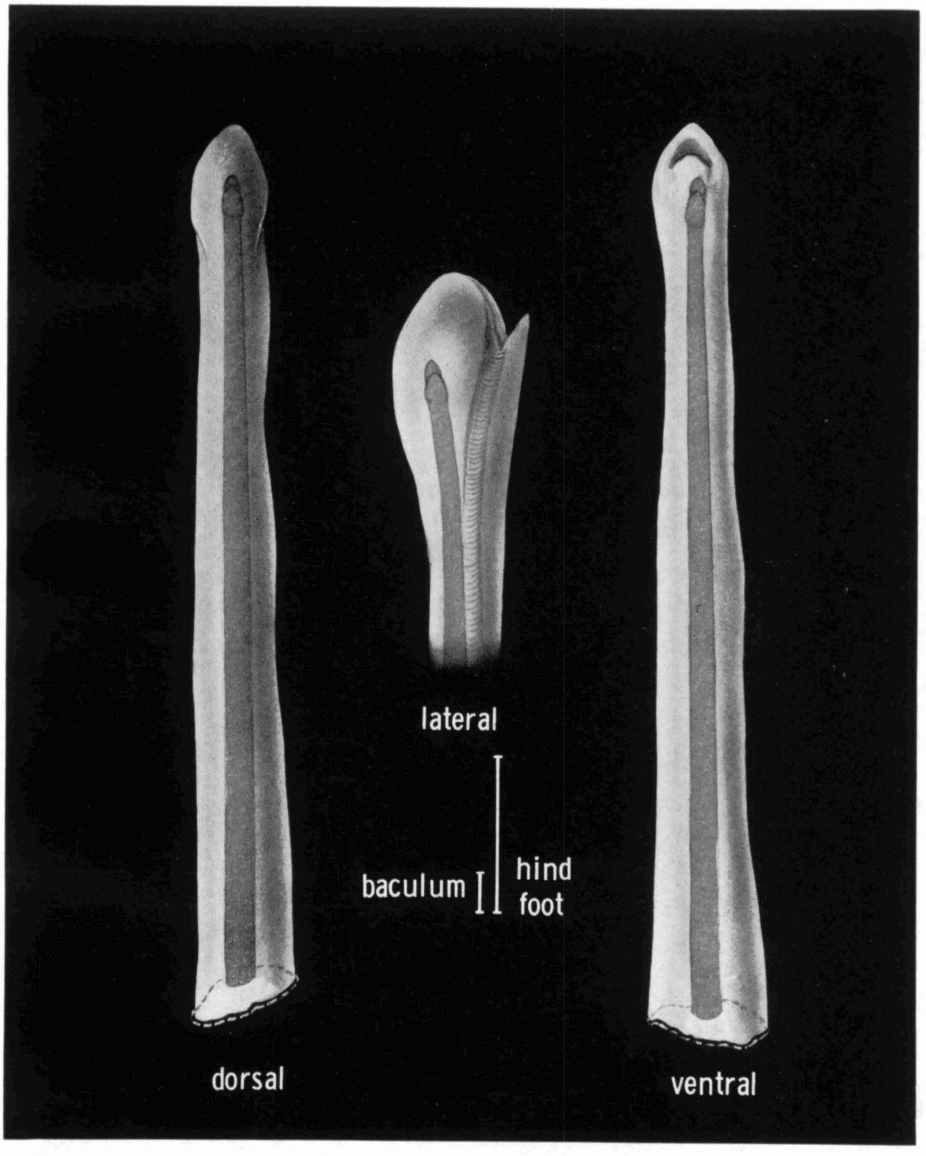
Peromyscus floridanus, UMMZ 103733; Alachua Co., Florida. Tip in lateral aspect.

PLATE XII



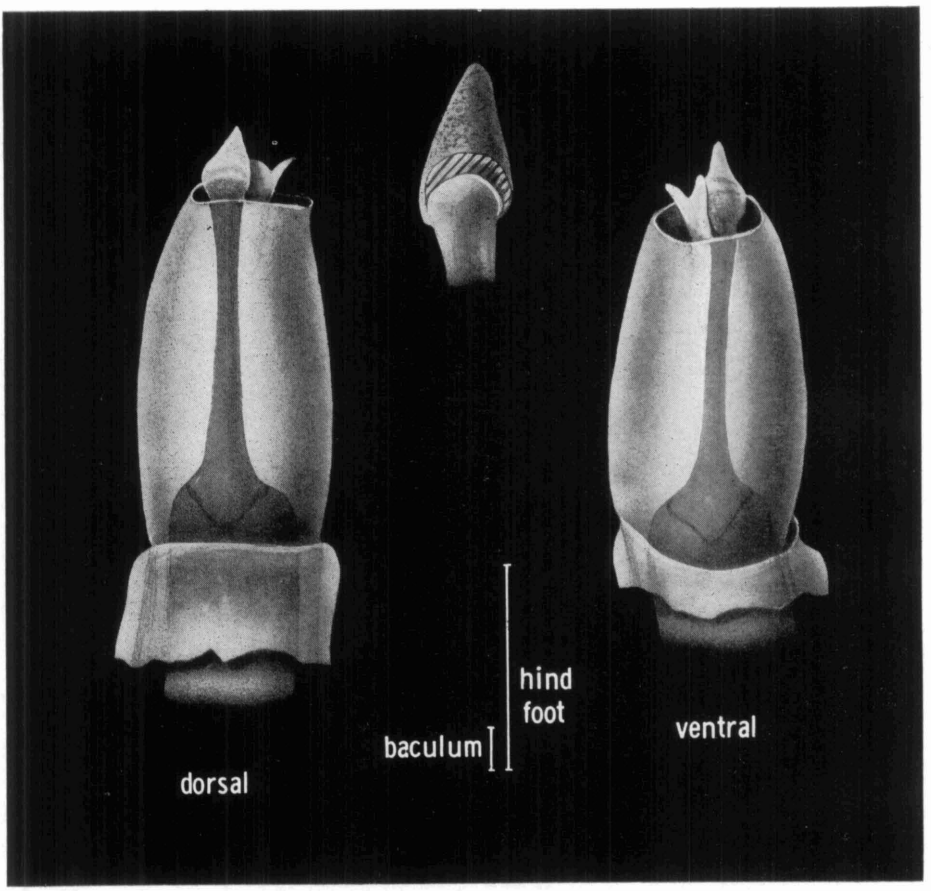
Peromyscus lepturus, USNM (F. & W. Coll.) 68642; Totontepec, Oaxaca.

PLATE XIII



Peromyscus lophurus, D. R. Dickey Coll. 12546; Los Esesmiles, El Salvador. Part of glans penis; tip in lateral aspect.

PLATE XIV



Peromyscus nuttalli, UMMZ 98990; Wake Co., North Carolina.

No. 69. The Amphibians and Reptiles of Alta Verapaz, Guatemala. By L. C. Stuart. (1948) Pp. 109, 10 figures, 1 map. $1.50

No. 70. The Land and Fresh-water Mollusks of Puerto Rico. By Henry van der Schalie. (1948) Pp. 134, 15 plates, 4 figures, 64 maps $2.50

No. 71. The Animal Life of Temporary and Permanent Ponds in Southern Michigan. By Roman Kenk. (1949) Pp. 66, 3 plates, 7 figures, 1 map $1.00

No. 72. Faunal Relationships of Recent North American Rodents. By Emmet T. Hooper. (1949) Pp. 28 . . . . . $0.35

No. 73. A Study of Small Mammal Populations in Northern Michigan. By Richard H. Manville. (1949) Pp. 83, 4 plates, 6 figures, 1 map. $1.25

No. 74. Studies of the Nesting Birds of the Edwin S. George Reserve. Part I. The Vireos. By George M. Sutton. (1949) Pp. 37, 5 plates. $1.00

No. 75. The Birds of Michigan. By Norman A. Wood. (1951) Pp. 559, 16 plates, 1 map $6.00

No. 76. Studies of the Black Swamp Snake, Seminatrix Pygaea (Cope), with Descriptions of Two New Subspecies. By Herndon G. Dowling. (1950) Pp. 38, 6 figures, 1 map $1.25

No. 77. A Systematic Review of the Harvest Mice (Genus Reithrodontomys) of Latin America. By Emmet T. Hooper. (1952) Pp. 255, 9 plates, 24 figures, 12 maps $4.00
Cloth bound. $4.60

No. 78. Studies of Cyprinodont Fishes. XX. A New Subfamily from Guatemala, with Ctenoid Scales and a Unilateral Pectoral Clasper. By Carl L. Hubbs. (1950) Pp. 28, 4 plates, 1 map. $1.25

No. 79. An Analysis of Some Physical Factors Affecting the Local Distribution of the Short-tail Shrew (Blarina brevicauda) in the Northern Part of the Lower Peninsula of Michigan. By William O. Pruitt, Jr. (1953) Pp. 39, 9 figures $0.75

No. 80. A Comparative Study of the Osteology and Myology of the Cranial and Cervical Regions of the Shrew, Blarina brevicauda, and the Mole, Scalopus aquaticus. By George R. L. Gaughran. (1954) Pp. 82, 67 figures $1.00

No. 81. A Systematic Study of the Avian Family Fringillidae, Based on the Structure of the Skull. By Harrison B. Tordoff. (1954) Pp. 42, 77 figures. $0.75

No. 82. The Meibomian Glands of Voles and Lemmings (Microtinae). By Wilbur B. Quay. (1954) Pp. 24, 3 plates, 3 figures $0.25

No. 83. The Comparative Myology of the Mammalian Genera Sigmodon, Oryzomys, Neotoma, and Peromyscus (Cricetinae), With Remarks on Their Intergeneric Relationships. By George C. Rinker. (1954) Pp. 124, 18 figures $1.50

No. 84. The Burrowing Beetles of the Genus Mycotrupes (Coleoptera: Scarabaeidae: Geotrupinae). By Ada L. Olson, T. H. Hubbell, and H. F. Howden. (1954) Pp. 59, 8 plates, 3 figures. $0.60

No. 85. The Myology of the Pectoral Appendage of Three Genera of American Cuckoos. By Andrew J. Berger. (1954) Pp. 35, 4 figures $0.50

No. 86. The Anatomy of the Diastemal Palate in Microtine Rodents. By Wilbur B. Quay. (1954) Pp. 41, 4 plates, 12 figures $0.50

No. 87. Records of Fishes in the John N. Lowe Collection From the Upper Peninsula of Michigan. By William Ralph Taylor. (1954) Pp. 50, 1 map $0.50

No. 88. An Annotated List of the Moths of Michigan Exclusive of Tineoidea (Lepidoptera). By Sherman Moore. (1955) Pp. 87. . . . . $0.90

No. 89. Anatomy, Life History, and Evolution of the Mites Parasitizing Fresh-water Mussels. By Rodger D. Mitchell. (1955) Pp. 28, 6 figures. $0.50

No. 90. The Crane Flies of Alaska and the Canadian Northwest (Tipulidae, Diptera). The Genus Erioptera Meigen. By C. P. Alexander. (1955) Pp. 33, 38 figures $0.50

No. 91. A Brief Review of the Guatemalan Lizards of the Genus Anolis. By L. C. Stuart. (1955) Pp. 31 . . . . . $0.50

No. 92. A Systematic Review of the Middle American Fishes of the Genus Profundulus. By Robert Rush Miller. (1955) Pp. 64 . . . . . $1.00

No. 93. Variation and Systematic Significance of Vertebral Counts in the American Fishes of the Family Percidae. By Reeve M. Bailey and William A. Gosline. (1955) Pp. 44 . . . . . $0.50

No. 94. The Anatomy of the Head of Ctenosaura pectinata (Iguanidae). By Thomas M. Oelrich. (1956) Pp. 122, 59 figures $1.85

No. 95. Survival Rates, Longevity, and Population Fluctuations in the White-footed Mouse, Peromyscus leucopus, in Southeastern Michigan. By Dana P. Snyder. (1956) Pp. 33, 3 figures $0.50

No. 96. The Frogs of the Hylid Genus Phrynohyas Fitzinger, 1843. By William E. Duellman. (1956) Pp. 47, 6 plates, 10 figures, 4 maps $0.70

No. 97. Variation and Relative Growth in the Plastral Scutes of the Turtle Kinosternon integrum Leconte. By James E. Mosimann. (1956) Pp. 43, 1 plate, 24 figures $0.75

No. 98. A Synopsis of the Tabanidae (Diptera) of Michigan. By Kirby L. Hays. (1956) Pp. 79, 3 plates $1.15

No. 99. Dental Patterns in Mice of the Genus Peromyscus. By Emmet T. Hooper. (1957) Pp. 59, 24 figures $0.75

No. 100. Aspects of the Biology of Pomatiopsis lapidaria (Say) (Mollusca: Gastropoda: Prosobranchia). By Dee Saunders Dundee. (1957) Pp. 65, 14 plates, 1 figure, 2 maps. . . $1.00

No. 101. A Biogeography of Reptiles and Amphibians in the Gómez Farías Region, Tamaulipas, México. By Paul S. Martin. (1958) Pp. 102, 7 plates, 7 figures, 4 maps. $1.50

No. 102. Great Blue Heron: Behavior at the Nest. By W. Powell Cottrille and Betty Darling Cottrille. (1958) Pp. 15, 7 figures. $0.35

No. 103. Life History and Ecology of the Chipmunk, Eutamias amoenus, in Eastern Washington. By Harold E. Broadbooks. (1958). Pp. 48, 3 plates, 6 figures $0.95

No. 104. Catalogue of the Odonata of Michigan. By Edward J. Kormondy. (1958) Pp. 43, 1 map. . . $0.65

No. 105. The Male Phallus in Mice of the Genus Peromyscus. By Emmet T. Hooper. (1958) Pp. 24, 14 plates, 1 figure $1.15