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MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 120

**A Synopsis of Recent North American
Microtine Rodents**

BY

EMMET T. HOOPER

AND

BARBARA S. HART

ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
JUNE 26, 1962

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A SYNOPSIS OF RECENT NORTH AMERICAN MICROTINE RODENTS

TULLBERG (1899), Bittera (1918), Tokuda (1934, 1941), Ognev (1948, 1950) and others have described the glans penis in various species of microtines and have employed the resulting data in systematic analyses of the rodent fauna of Europe and Asia. As a result of their efforts there is a sizable body of information regarding Old World microtine glandes and their usefulness in classification. There are no comparable data on North American microtines although there are several studies of the structural core of the glans which indicate that the baculum provides useful clues to affinities of microtine species. The most important of these studies are by Hamilton (1946), Dearden (1958), and Anderson (1960).

Described here are glandes of 33 species of microtines, 25 of them North American and eight of the Old World. Most of the North American species are represented, and our study is focused on them, but also it necessarily was extended to some Old World species. In addition to describing and comparing the glandes, we have attempted to couple those data with information derived from skins and skulls and thereby to form an opinion as to classification of New World microtines. As here understood the sub-family Microtinae is as defined by Hinton (1926) and Simpson (1945).

MATERIALS AND METHODS

The glandes which were measured and sketched and served as the prime source of new basic data are listed below (New World species arranged in systematic order following Hall and Kelson, 1959, and Old World species listed alphabetically by genus). Other specimens, which were incomplete or poorly preserved or which were used as supplementary material, are excluded here but are mentioned in the text.

NORTH AMERICA.

Clethrionomys gapperi: Ontario, 1. Colorado, Rocky Mt. Park, 1. Montana, Park Co., 3.

Clethrionomys rutilus: Alaska, 2.

Phenacomys intermedius: Montana, Missoula Co., 2; Madison Co., 1. Colorado, Rocky Mt. Park, 1.

Phenacomys longicaudus: California, Sonoma Co., 4.

Microtus pennsylvanicus: Michigan, Shiawassee Co., 7; Washtenaw Co., 1.

M. montanus: Montana, Carbon Co., 1. Wyoming, Johnson Co., 2.

M. californicus: California, Contra Costa Co., 2.

M. townsendi: Washington, Mason Co., 2. Oregon, Clatsop Co., 1.

M. oeconomus: Alaska, 5.

- M. longicaudus*: Montana, Carbon Co., 3. Washington, Chelan Co., 1.
M. mexicanus: Mexico, Vera Cruz, 2.
M. fulviventer: Mexico, Oaxaca, 4.
M. (Aulacomys) richardsoni: Wyoming, Teton Co., 1. Montana, Park Co., 1; Carbon Co., 2.
M. (Chilotus) oregoni: Washington, Mason Co., 1; Olympic Natl. Park, 1. California, Humboldt Co., 1. Oregon, Clatsop Co., 1; Tillamook Co., 1.
M. (Stenocranius) miurus: Alaska, 3.
M. (Herpetomys) guatemalensis: Guatemala, Chemal, 1; Todos Santos, 9.
M. (Pedomys) ochrogaster: Illinois, Macowpin Co., 1. Missouri, Boone Co., 2. Montana, Carbon Co., 2.
M. (Pitymys) pinetorum: North Carolina, Wilkes Co., 4.
Lagurus curtatus: Idaho, Butte Co., 1. Washington, Kittitas Co., 4.
Neofiber alleni: Florida, Alachua Co., 4.
Ondatra zibethica: Michigan, Washtenaw Co., 5.
Lemmus sibiricus: Alaska, Pt. Barrow, 7.
Synaptomys (Synaptomys) cooperi: Michigan, Washtenaw Co., 3.
S. (Mictomys) borealis: Alaska, 2.
Dicrostonyx torquatus: Alaska, 2. Manitoba, 2.

EUROPE AND ASIA.

- Antelionomys smithi*: Japan, Shikoku, 2.
Arvicola terrestris: Europe, 2.
Ellobius talpinus: U.S.S.R., Tien-Shan, 1; West Kazakstan, 1.
Eothenomys melanogaster: Burma, Chimeli Pass road, 1. China, Yunnan, 1.
Lemmus lemmus: Norway, Mjøsen Lake, 2.
Microtus arvalis: Germany, Holstein, 1; Saxonia, 1. Hungary, Herceghalom, 1.
Microtus oeconomus: Hungary, Kis-Balaton, 1.
Prometheomys schaposchnikowi: U.S.S.R., Georgia, 1.

Most of the glands are contained in the University of Michigan Museum of Zoology, but a few are in collections of W. B. Quay, the American Museum of Natural History, and the U. S. National Museum. Curators of those collections and a number of other persons have graciously taken special effort to provide us with specimens we could not otherwise have obtained. For such consideration we are indebted to: S. Anderson, F. S. Barkalow, Jr., D. Birkenholz, C. Buckner, C. O. Handley, Jr., R. S. Hoffmann, E. W. Jameson, M. L. Johnson, W. Z. Lidicker, W. O. Pruitt, W. B. Quay, R. L. Rausch, D. R. Roberts, H. E. Stark, R. Van Gelder, and N. Vorontsov. This project received financial support from the National Science Foundation.

The processing of formalin-preserved specimens has already been described in detail (Hooper, 1958, 1959). The phalli were cleared in KOH solutions, stained with alizarin, and preserved in glycerine. Sketches and measurements were made with the aid of a camera lucida and an ocular grid. The measurements in Tables 1 and 2 are of specimens known to be adult, and do not include all the phalli examined. Those of *M. guatema-*

lensis are of phalli obtained from dry study skins and subsequently processed in fluid, consequently the dimensions of soft parts may not bear fine comparison with those of other species. The measurements are as follows:

LENGTH OF GLANS.—Distance from the glans-prepuce junction to the most distal part of the organ, measured along the dorsal midline.

DIAMETER OF GLANS.—Greatest diameter of the glans.

PROXIMAL BONE.—Length of the main bone, the basal segment of the baculum.

MEDIAL OSSICLE.—Length of osseous formation in the medial digit.

MEDIAL ROD.—Length of entire medial digit, including both cartilage and bone.

LATERAL OSSICLE.—Length of bone in the lateral digit.

TOTAL BACULUM.—Distance from the proximal face of the main bone to the tip of the cartilage of the medial distal segment of the baculum.

Orientation is the same as that adopted by most authors. Ventral is that side of the glans which lies against the body of the animal when the organ is not erect. In reference to the baculum, ventral is that side which faces the urethra. Other terms requiring clarification are treated in Figure 1.

The illustrations are the work of Suzanne Runyan, staff artist of the Museum of Zoology. Figures 2–11 were rendered directly from camera lucida tracings from which most artifacts had been removed. They are scale models of translucent specimens, designed to show a few diagnostic features of the glans and its components. Horizontal bars which indicate relative sizes of whole specimens do not apply to parts shown as insets on the plates. Absolute sizes as well as proportions are stated in Tables 1 and 2.

Responsibilities are divided in this project. The junior author focused her efforts on the basic data. She processed, measured, and sketched many of the specimens; assembled and analyzed the data on the microtine phallus; and prepared much of the descriptive part of this report. The senior author participated in those procedures and analyses, and in addition he studied skins and skulls of North American microtines, reviewed pertinent literature, and prepared the other sections and final copy of this report.

In describing the glandes we have relegated the Old World species to a separate section of this report and have assembled the North American kinds in three groups (I–III). These are groups of convenience, established to facilitate and reduce the amount of description of the glandes, but they also obviously bring together species with more or less similar glandes.

The sequence of groups together with the arrangement of species within them have further significance. In Group II the glans tends to be large and elaborate, with all components present and well developed, while in groups I and III it tends to be simpler. The groups are not discrete; they can not be in view of the reticulate pattern of variation which is observed in the Microtinae. Within each group the species are arranged roughly in order

of degree of resemblance of glans, and since the groups themselves are ordered to indicate directional trends, the species within them follow in line with those trends. Thus, species placed at the end of Group I tend to resemble species in the beginning of Group II, and those at the end of Group II morphologically approach the first in Group III. The arrangement is indicated in Tables 1 and 2. Within each group, a given species account qualifies the general description given for that group; that is, the characters of a group apply to all species of that category unless indicated to the contrary in the species account.

FEATURES OF THE GLANS PENIS IN THE MICROTINAE

In contrast to some other groups of cricetid rodents in which there is considerable diversity in form and size of the glans (Hooper, 1958, 1959, 1960), the Microtinae exhibit a rather bland assortment of glandes which typically are stubby and truncate and are equipped with a shallow terminal crater and various internal structures centered on a compound baculum. Features of the microtine glans, as observed in the forms studied but excluding *Ellobius*, are described below.

At maximum, the length of the glans is one-fourth the length of the hind foot. Rarely is it less than one-fifth, and a range of 10 per cent includes even the most divergent species. The ratio of diameter to length is more variable, bounded by the percentages of 50 and 75.

The glans is rather barrel-like, its contours slightly interrupted mid-dorsally by a shallow trough and midventrally by a raphe which terminates proximally as a small frenum that connects the glans with the prepuce. Small, single-pointed spines cover the entire surface except for a narrow band just distal to the prepuce junction. The rim of the barrel, which separates the tougher epidermis from the soft tissues within the crater, is divisible into three structural sectors. The dorsal sector, which frequently takes the form of an enlarged prominence and is referred to as the "dorsal lobe" (Fig. 1), is generally furrowed by the middorsal trough which terminates as a crevice or V-shaped nick at the crater's edge.

In many species the crater rim carries fingerlike processes which rise bare-sided from the edge and terminate in a spine. Although these papillae are not always present, and vary considerably in number, their distribution nevertheless follows a pattern; when they are few they are situated at each side of the dorsal lobe, when more numerous they also occur farther ventrad, and at maximum they line both ventrolateral sectors of the rim. A few species also have papillae on the dorsal lobe, but this occurs only when most of the remainder of the rim is papillose.

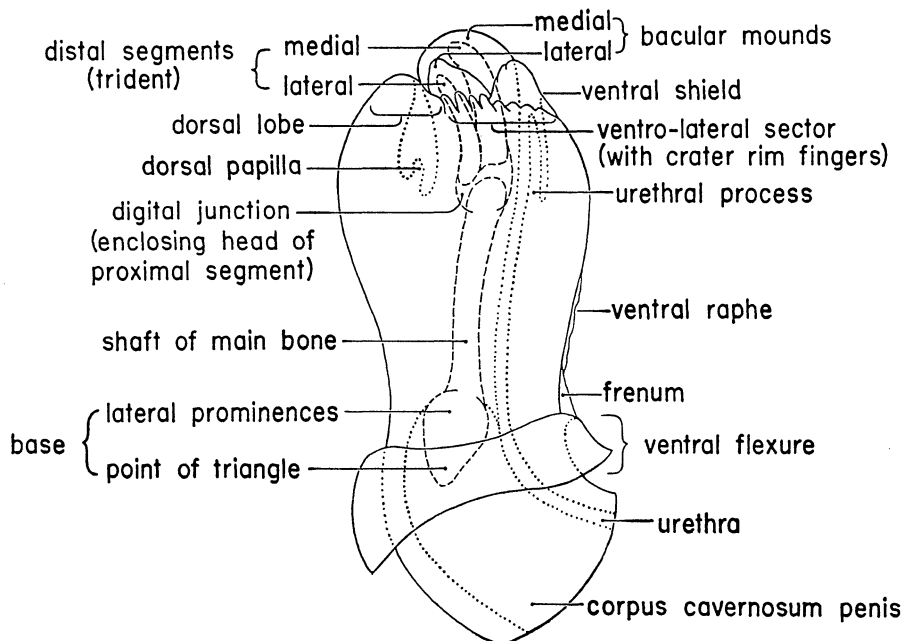


FIG. 1. Schematic lateral view of a microtine glans penis.

A conspicuous structure within the crater is the large mound of smooth-skinned tissue which houses the medial process of the trident baculum and which without exception is partly uncovered and exposed beyond the crater rim. Flanking the central mound on either side are smaller mounds which enclose the lateral digital units of the baculum. The medial mound is round and globular; the lateral mounds are shaped more like a candle flame—obovate, ovate, or lanceolate—with the tips directed distad. Directly dorsal to the medial mound there is a protuberance which, for lack of a functional connotation, we have referred to simply as the “dorsal papilla.” These three mounds and one papilla are, respectively, the papillae “centralis,” “lateralis,” and “dorsalis” of Tullberg (1899) and Tokuda (1934). Except for single spines accentuating certain prominences, all spines within the crater are localized in two areas between the dorsal papilla and the lateral bacular mounds. Single spines usually occur on the tips of the dorsal papilla, the lateral bacular mounds, and the urethral process (see below). Immediately ventral to the medial mound is the meatus urinarius. Projecting from its ventral lip is a multishaped structure, the “urethral process,” or “papilla lingualis” of Tullberg and Tokuda; its characteristics suggest that it may serve to protect the aperture or, because it is erectile, to

TABLE 1
MEAN MEASUREMENTS (MM.) OF THE GLANS PENIS IN 25 SPECIES OF NORTH
AMERICAN MICROTINES

Abbreviations are as follows: prox., proximal; med., medial; lat., lateral; oss., ossicle;
* questionable measurements

Species	specimens	Hind Foot length	Glans		Baculum, lengths				
			length	diameter	prox. bone	med. rod	total	med. oss.	lat. oss.
GROUP I									
<i>D. torquatus</i>	4	21	4.3	2.4	3.4	0.7	4.1	0.4
<i>N. alleni</i>	4	43	7.6	4.3	4.1	1.9	6.0	0.4	0.7
<i>P. longicaudus</i>	4	20	2.8	1.6	2.1	0.5	2.6	0.1
<i>S. cooperi</i>	3	18	3.5	1.8	2.3	0.7	3.0	0.5	0.2
<i>S. borealis</i>	1	18	4.0	1.9	2.6	0.9	3.5	0.8	0.9
<i>P. intermedius</i>	3	17	3.7	2.0	2.0	1.1	3.1	0.9	0.8
<i>L. sibiricus</i>	4	21	4.9	3.1	2.8	1.5	4.3	1.2	1.0
<i>L. curtatus</i>	4	17	3.3	2.0	2.4	1.2	3.6	1.0	0.8
GROUP II									
<i>C. gapperi</i>	4	18	4.2	2.5	2.3	1.4	3.7	1.1	0.9
<i>C. rutilus</i>	1	21	4.8	2.8	2.9	1.5	4.4	1.2	1.1
<i>O. zibethica</i>	2	81	11.2	6.8	5.6	3.2	8.8	2.8	1.2
<i>M. pennsylvanicus</i>	4	21	5.3	3.6	2.6	1.6	4.2	1.4	1.1
<i>M. montanus</i>	3	18	4.6	2.8	2.4	1.3	3.7	1.0	0.8
<i>M. townsendi</i>	3	26	5.4	3.5	3.1	1.6	4.7	1.3	0.9
<i>M. oeconomus</i>	4	21	4.7	2.8	3.3	1.3	4.7	1.0	0.6
<i>M. longicaudus</i>	2	21	4.8	2.8	3.0	1.4	4.4	1.3	0.8
<i>M. oregoni</i>	4	17	3.2	1.9	2.2	0.8	3.0	0.9	0.7
<i>M. miurus</i>	1	18	3.9	2.6	2.9	1.2	4.1	1.1
GROUP III									
<i>M. richardsoni</i>	3	26	5.5	3.4	4.5	1.1	5.6	0.9
<i>M. californicus</i>	2	23	3.8	2.4	2.8	0.9	3.7	0.8
<i>M. guatemalensis</i>	2	21	3.2*	2.4*	3.2	0.8	4.0	0.8	0.4
<i>M. ochrogaster</i>	4	19	4.1	3.0	2.9	0.8	3.7	0.6	0.2
<i>M. pinetorum</i>	4	16	3.0	2.2	2.8	0.6	3.4	0.5
<i>M. mexicanus</i>	2	19	3.8	2.6	3.1	0.7	3.8	0.4
<i>M. fulviventer</i>	4	18	3.6	2.7	2.9	0.7	3.6	0.5

TABLE 2
 RATIOS (PER CENT) OF MEASUREMENTS LISTED IN TABLE 1
 Excepting those in one column (diameter: length of glans), all ratios are of
 lengths as indicated

Species	Glans	Diam. Glans	Baculum	Baculum	Med. Rod	Med. Oss.	Lat. Oss.
	Foot	Len. Glans	Glans	Foot	Baculum	Baculum	Baculum
GROUP I							
<i>D. torquatus</i>	21	55	95	20	17	10
<i>N. alleni</i>	18	57	78	14	32	7	12
<i>P. longicaudus</i>	15	58	92	13	19	4
<i>S. cooperi</i>	20	50	83	17	23	17	7
<i>S. borealis</i>	22	48	88	19	26	23	26
<i>P. intermedius</i>	22	55	85	19	35	29	26
<i>L. sibiricus</i>	24	64	88	21	35	28	23
<i>L. curtatus</i>	20	62	110	21	33	28	22
GROUP II							
<i>C. gapperi</i>	24	60	88	21	38	30	24
<i>C. rutilus</i>	23	58	92	20	34	27	25
<i>O. zibethica</i>	14	61	79	11	36	32	14
<i>M. pennsylvanicus</i>	25	66	79	20	38	33	26
<i>M. montanus</i>	26	61	82	21	35	27	22
<i>M. townsendi</i>	21	64	86	18	34	28	19
<i>M. oeconomus</i>	23	61	100	22	30	21	13
<i>M. longicaudus</i>	24	59	91	22	32	30	18
<i>M. oregoni</i>	19	60	93	17	27	30	23
<i>M. miurus</i>	22	68	105	23	29	27
GROUP III							
<i>M. richardsoni</i>	22	63	103	22	20	16
<i>M. californicus</i>	17	64	99	16	24	22
<i>M. guatemalensis</i>	15*	78*	131*	20	20	20	10
<i>M. ochrogaster</i>	22	74	90	20	22	16	5
<i>M. pinetorum</i>	19	75	115	21	18	15
<i>M. mexicanus</i>	21	68	99	21	18	11
<i>M. fulviventor</i>	23	72	101	20	19	14

guide fluid flow from the urethra. A fan-shaped mass of soft tissue extrudes itself between the urethral process and the wall of the crater; this is designated the "ventral shield" (Fig. 1).

The microtine baculum has already been adequately described (Hamilton, 1946; Anderson, 1960). When most complete it consists of a proximal segment and three distal units joined by a mass of cartilage. The proximal unit is bone in all species. The trident is osseous or cartilaginous, or a combination of both. A formation of vascular tissue parallels or surrounds each of the distal units; if the lateral digits are absent the tissue can still be discerned extending from the dorsal side of the main bone out into the lateral bacular mounds.

DESCRIPTIONS OF GLANDES

NORTH AMERICAN SPECIES

As explained above, and emphasized here, the following three categories are principally groups of convenience, designed to minimize repetitive description and eliminate the confusion of cross-references; in consequence, they will also facilitate comparisons of species. The nucleus of each group is a cluster of species which are generally similar in structure of glans. The peripheral species diverge from the central type in varying amounts and, in regard to some characters, may fit as well or better in another group.

GROUP I

Species included are as follows: *Dicrostonyx torquatus*, *Neofiber alleni*, *Phenacomys longicaudus*, *Synaptomys cooperi*, *S. borealis*, *Phenacomys intermedius*, *Lemmus sibiricus*, and *Lagurus curtatus*.

In these species the glans is approximately one-fifth the hind foot in length, and its diameter-length ratio ranges between 50 and 60 per cent. As a whole, the glans is slender and straight-sided without localized swellings or distinct indentations. The dorsal lobe is generally narrower and longer than in other groups and marginally it is set off from the remainder of the rim by nicks in the crater's edge. The rim tends to be smooth-edged and nonpapillose. The dorsal papilla is typically a single conule of moderately large size; it bears one spine on its tip. The lateral bacular mounds are long. The urethral process, while species-variable, is most frequently a lobate flap which is greater in length than width.

The ratio of baculum to glans ranges between 80 and 90 per cent. The shaft of the proximal bone is relatively straight, and may be slightly swollen in the distal half. The base is biconcave, the two surfaces having about equal curvatures. The head of the bone, when set off by a stricture, is

equally developed both dorsally and ventrally, forming a simple globe. The cartilage of the digital junction is square-heeled, and the three distal units are long and straight; the medial one tapers distad to a point.

Dicrostonyx torquatus.—The frenum which joins the midventral basal part of the glans to the prepuce continues its attachment along the midventral line for about half the length of the glans (Fig. 2). The dorsal lobe is indicated only by slight undulations in the otherwise smooth rim, although occasionally there may be one stubby papilla on either side of the lobe. The crater is notably shallow and it, together with its rim and an adjoining narrow band of epidermis, is smooth and spineless. A dorsal papilla was not observed in any of the four specimens at hand. Lateral mounds are present beside, and flattened into, the medial mound; these are indistinct, but they appear to be pointed with the tips directed dorsad. Since in form they exactly coincide with the cartilage within them, they probably are counterparts of lateral mounds in other species, but they are scarcely discrete units. The urethral process consists of a pair of simple elongate lobes, each blunted at the tip; in one specimen of four there are small lobules on the distal edge of each lobe. The process projects beyond the edge of the ventral shield despite the large size of that structure.

The baculum is thick and gross. Its base is slightly longer than wide and rounded on the proximal edge; the ventral surface is more deeply concave than the dorsal one. The straight shaft is squared off sharply at the head and sometimes the flatness of the head extends into small lateral protuberances. The cartilage of the distal parts, which encloses the head of the bone, has the shape of a shamrock which is almost as wide as it is long, but the medial segment is thicker and distally more rounded than the lateral ones; the lateral units curve dorsad. In two of seven specimens there is a minute ossicle in the medial process; the lateral ones are entirely cartilaginous. Both Anderson (1960) and Hamilton (1946) found lateral ossicles, but no medial ones, and it has been suggested that the medial unit does not ossify in *Dicrostonyx*.

This species differs from all other North American kinds in the absence of a dorsal papilla, length (but not breadth) of the ventral frenum, the peculiar formation of the lateral bacular mounds, size and configuration of the urethral process, and the entire conformation of the baculum. In the absence of spines on the crater walls it is matched only by *Phenacomys longicaudus*. It fits in Group I by virtue of its shape and diameter-length proportions. Within that group it is most like *Phenacomys longicaudus* in baculum-to-glans ratio, and like both species of *Phenacomys* in the nature of the rim papillae and in the elongate shape and bilateral symmetry of the urethral process. Similar elongation of the urethral process is seen also in

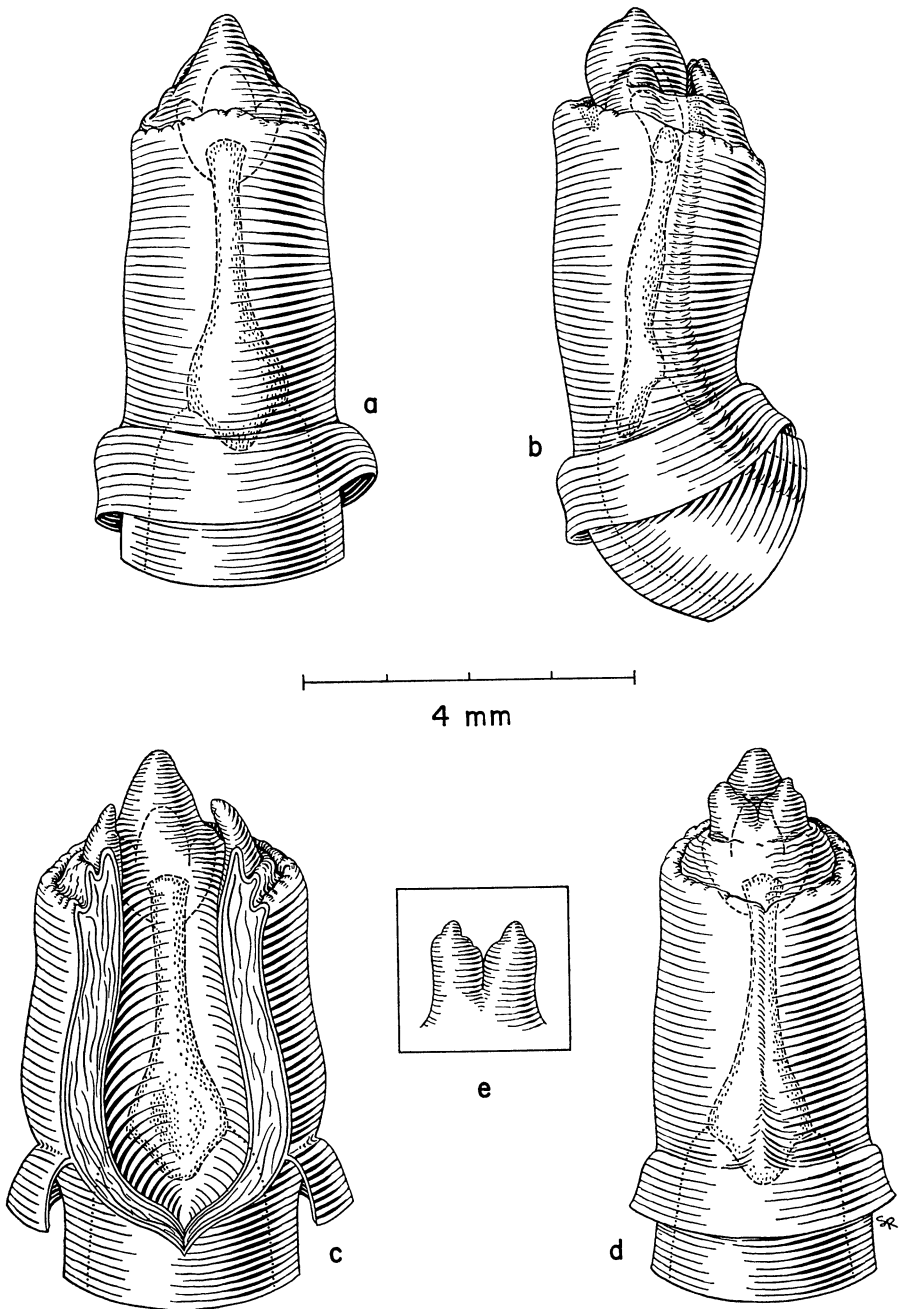


FIG. 2. Views of glans penis of *Dicrostonyx torquatus*: a, dorsal; b, lateral; c, incised midventrally exposing urethra; d, ventral; e, urethral process, enlarged, ventral aspect (110463), Alaska.

both species of *Synaptomys*. It resembles Group III species in: (1) absence or scarcity of rim papillae and (2) incomplete digits of the baculum.

Neofiber alleni.—The glans has its greatest diameter medially, about at the distal limits of the long thick frenum which extends as much as halfway up the glans (Fig. 3). The dorsal lobe is not elevated distad; it is distinguishable from the remainder of the nonpapillose rim by slight lateral nicks. The tissues lining the crater are heavily wrinkled and occasionally extrude into a secondary wall above the crater edge proper. There are spines in the dorso-lateral areas within the crater as usual, but they are few. The dorsal papilla generally consists of three long conules arranged in a dorsoventral row (one specimen of four carries four conules), and they are all enmassed in tissue folds of the medial bacular mound. The lateral bacular mounds are pointed and leaf-shaped in younger specimens and flaccid in adults. The urethral process, essentially a slender cone, bears a pair of small lateral projections at its base, and on its ventral surface are one to three small tubercles; in old specimens the tip of the cone is slightly cleft. This proportionally quite small process is hidden behind a short, wide, ventral shield.

As viewed ventrally, the base of the baculum has a rounded outline which in some instances forms a smooth semicircle; from the lateral prominences the outline turns almost directly into the shaft. The shaft is almost straight and often slightly swollen in the distal half; it terminates in a small globular head within the cartilage of the digital junction. One specimen of four has an ossicle in the cartilage of the long pointed medial rod. Three of four specimens have ossifications in the lateral processes which in ventral aspect are ovoid or bluntly triangular, but in lateral view they are square and serrate along the distal edge. Others (Hamilton, 1946; Anderson, 1960) who have studied the species also find medial ossification infrequent and occurring only when lateral ossicles are present.

The glans of *Neofiber alleni* is unique in external form, in size and shape of the ventral frenum (approached only by *Dicrostonyx*), and in the cone-like arrangement of the urethral process. According to the present and other studies of the baculum, the medial digital rod of *Neofiber* ossifies later than the lateral rods, and it is not known that this order of ossification occurs in any other species except *Lagurus* (Dearden, 1958). Similarities with other species of Group I are seen in the nonpapillose rim (approached by *Phenacomys* and matched by *Synaptomys cooperi*) and the longer than wide—somewhat flaplike—urethral process (the tapered form of the process is closely comparable only to *Phenacomys longicaudus*).

It coincides with Group II in carrying two or more conules in the dorsal papilla (particularly like *Ondatra*, but three conules also sometimes

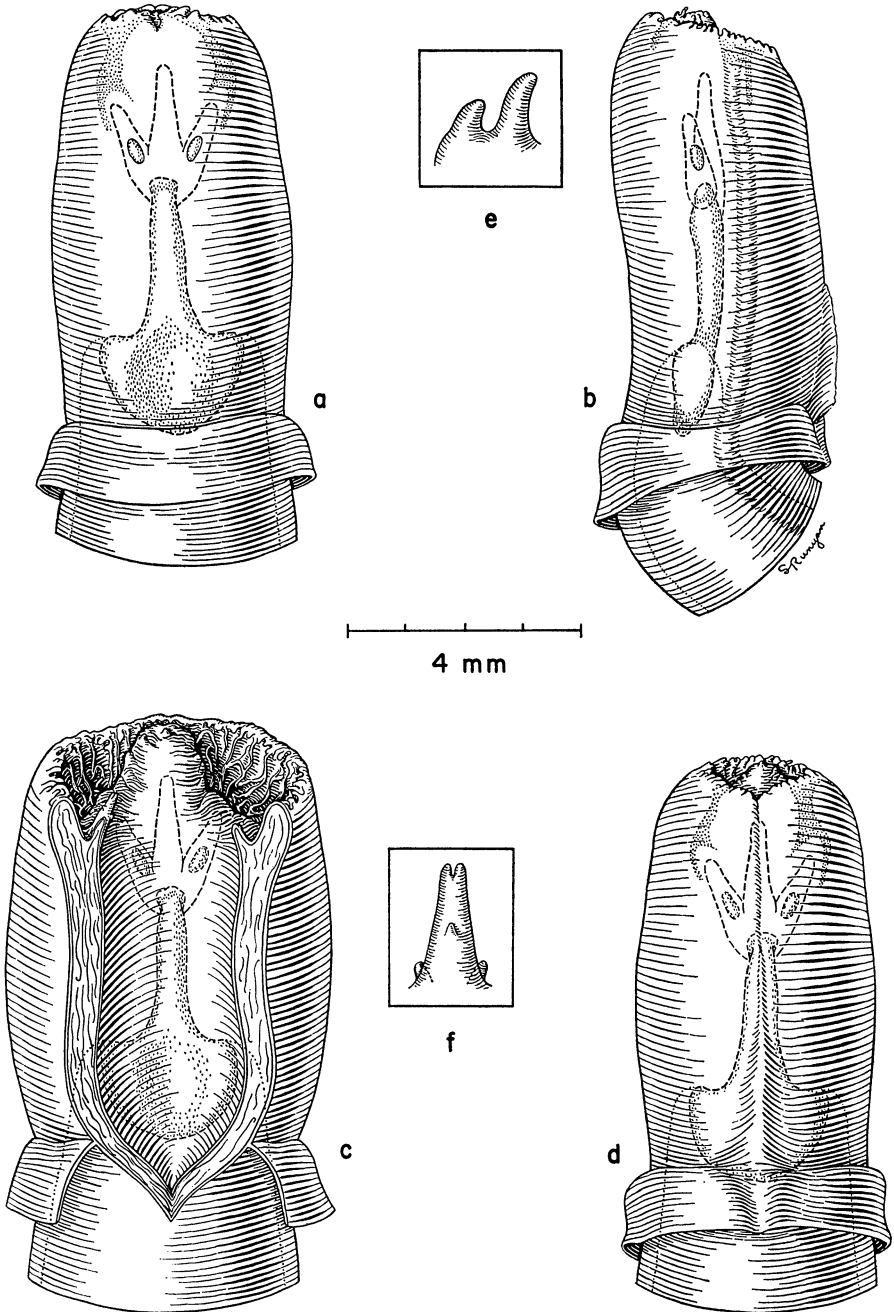


FIG. 3. Views of glans of *Neofiber alleni*: *a*, dorsal; *b*, lateral; *c*, incised midventrally exposing urethra; *d*, ventral; *e*, dorsal papilla, enlarged, lateral aspect; *f*, urethral process, enlarged, ventral aspect (110456), Florida.

occur in *Clethrionomys* and *M. pennsylvanicus*) and in baculum-to-glans ratio. It could be assigned to Group III only on the basis of its nonpapillose rim and incompletely ossified digits of the baculum.

Phenacomys longicaudus.—The ratio of glans to hind foot length is small in this species (Table 2). In lateral view the glans is slightly sway-backed, its external shape coinciding with the heavily bowed baculum (Fig. 4). The spiny vestiture is exceptionally extensive, in some specimens attaining the basal limits of the glans. The dorsal lobe, the shortest part of the rim, dips below the remainder of the rim. On each side of the lobe there is a single spinetipped peripheral process, the only protuberances on an irregular but otherwise nonpapillose rim. The crater is shallow, and the soft tissue within is often extruded as a secondary wall above the crater rim. There are no spines within the crater; the dorsal papilla is a short simple conule, and the lateral bacular mounds are moderately long and distally rounded. The large urethral process, which reaches almost to the top of the medial bacular mound, is tonguelike in shape and slightly cleft distally into four parts; because of peculiarities of the ventral shield it appears to rise directly from the ventral rim of the crater. The ventral shield consists of two wings of tissue which extend laterad and dorsad over the lower corners of the urethral process (Fig. 4).

The base of the baculum is generally wider than long and highly irregular along its proximal edge, but disregarding irregularities its outline appears to be nearer round than triangular. The base is biconcave, deepest ventrally. Emerging from the base the shaft gradually arches ventrad and narrows distad to a neck directly beneath a spatulate, almost trilobed head. There is no ossification in the medial unit in any of the five specimens at hand, but in two examples the lateral rods show some bone tissue, which lies close to the head of the proximal bone, and in one of these one lateral ossicle is fused to the proximal bone. In specimens examined by Dearden (1958) there were no lateral ossicles, but there was a small one in the proximal end of the medial process. More complete ossification, and perhaps the condition typical of old animals, is figured by Hamilton (1946), in which all three processes are bony and proximally ankylosed to the main shaft.

The glans of *P. longicaudus* is unique in several respects: external conformation, extensive distribution of spines over the exterior surface, shortness of the dorsal lobe, the spatulate character of the head of the proximal bone of the baculum, and the arrangement of the digital junction.

Most of its similarities lie with Group I species. The absence of spines on the floor of the crater is a character shared only with *Dicrostonyx*. The simple cone of the dorsal papilla, the single rim process, and the four blunted lobes of the urethral process point to *Phenacomys intermedius*. A simple

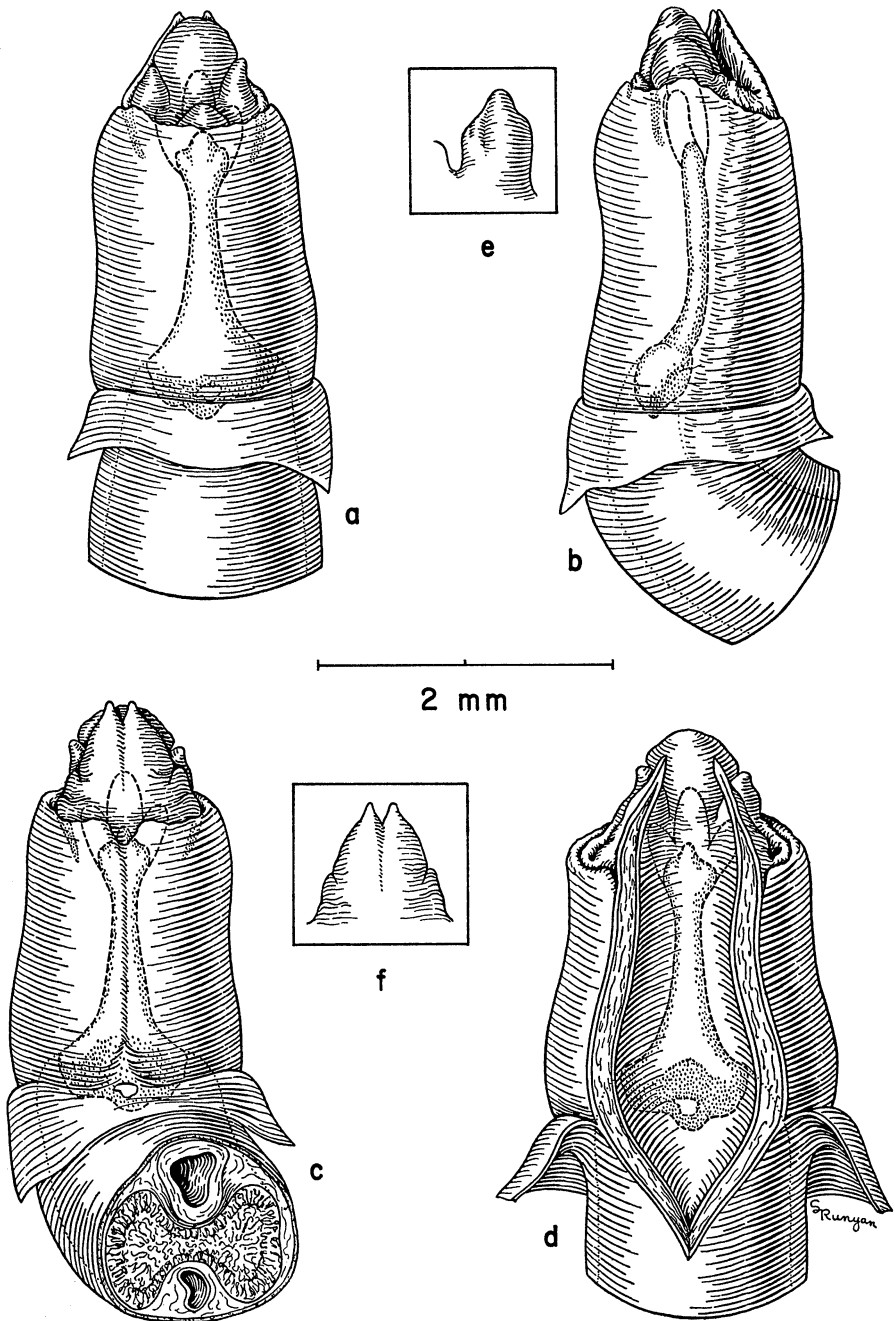


FIG. 4. Views of glans of *Phenacomys longicaudus*: a, dorsal; b, lateral; c, ventral; d, incised midventrally exposing urethra; e, dorsal papilla, enlarged, lateral aspect; f, urethral process, enlarged, ventral aspect (P-3925), California.

dorsal papilla is also seen in both species of *Synaptomys*, and the general lack of rim papillae again suggests *S. cooperi*. Similarities with Group III species are: absence of rim papillae, ratio of baculum to glans, and the pronounced ventral bowing of the baculum. All characters considered, *P. longicaudus* belongs in Group I, but (like *Neofiber alleni* and, to a lesser extent, *Dicrostonyx torquatus*) it is strongly differentiated and doesn't fit closely with those or other species. We view it as a divergent form of *P. intermedius*.

Synaptomys cooperi.—The dorsal lobe is double-peaked, and, like the remainder of the rim, nonpapillose (Fig. 5). The dorsal papilla is a single cone and the short lateral bacular mounds are usually hidden in folds of tissue. The urethral process, which is almost as wide as long, is divided distally into three pointed lobes, of which the lateral ones are longer.

The base of the baculum is variable in shape, but tends to round out on the proximal edge and in one specimen it has a medial notch; its distal face curves gently into the essentially straight shaft which terminates in a head that may have a slight dorsal swelling. In both ventral and lateral aspects the medial rod tapers from a wide base. The lateral rods are short and mostly cartilaginous, although there is some ossification—a sliver—in all specimens; they are similar to the medial rod in thickness and length.

For comparisons, see accounts of *Phenacomys intermedius* and other species.

Synaptomys borealis.—The dorsal lobe is double-peaked and non-papillose, but ventral to the lobe each side of the crater rim bears four to eight slight and indistinct papillae (Fig. 5). The dorsal papilla is a single short conule. The urethral process is a flap, distally trilobed, the short median lobe bounded by pointed lateral arms which are as long as the medial bacular mound.

As viewed ventrally the base of the baculum is sharply defined by three points; the line between the medial point and each lateral prominence decurves to about the same degree as the line connecting the lateral points with the sides of the shaft. In ventral aspect the medially constricted shaft enlarges gradually to the point where it is engulfed by the cartilage of the digital junction; its distal border is a smooth semicircle. In lateral view the sides of the shaft are parallel to each other and there is no indication of a head. The medial rod is moderately long and generally fusiform, though the base may be slightly flared. The lateral rods are also fusiform except for some curvature in them proximally, and they are as long as, or longer than, the medial one.

For comparisons, see account of *Phenacomys intermedius* and other species.

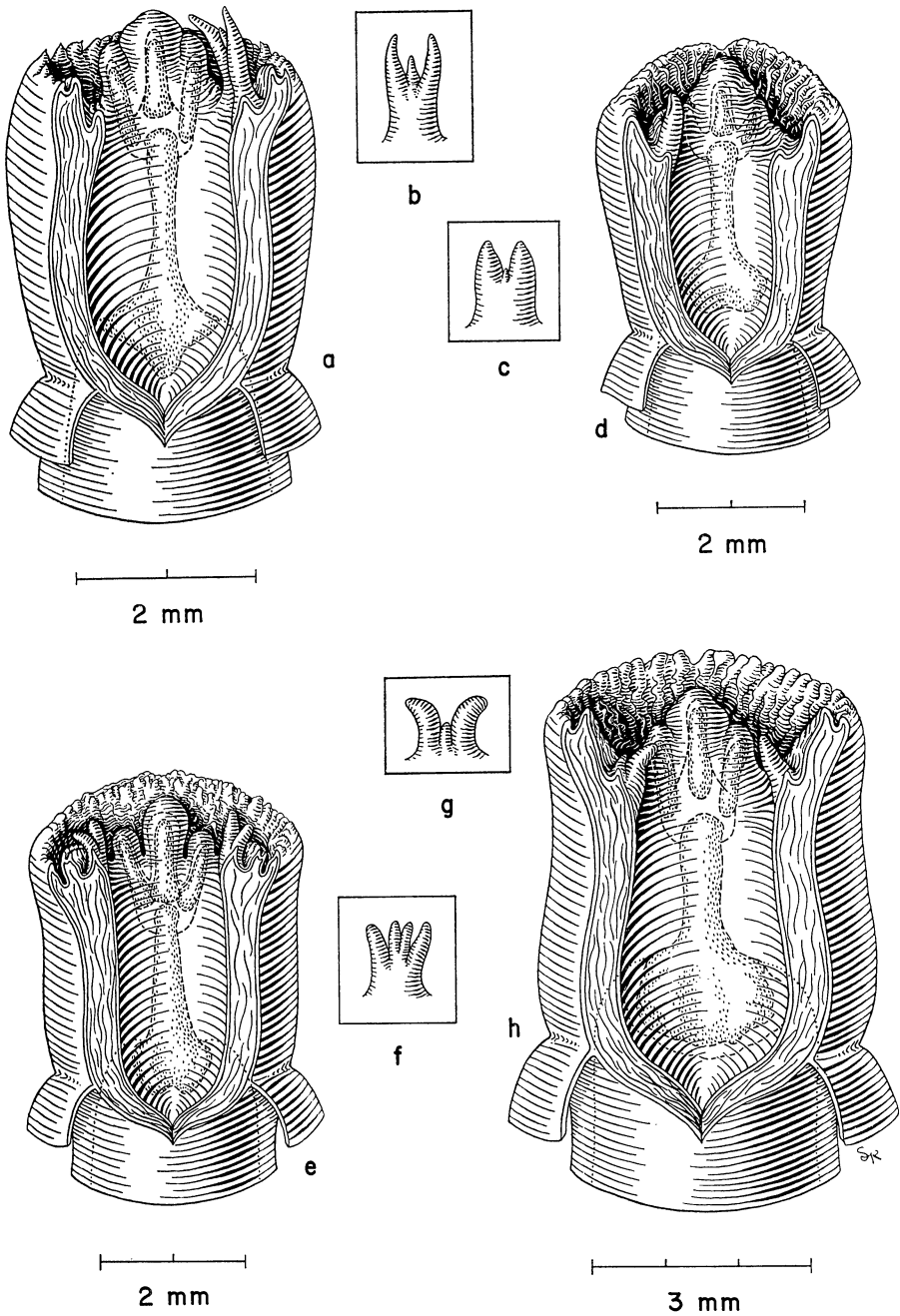


FIG. 5. Ventral views of glans (incised midventrally) and urethral process (enlarged) of: a, b, *Synaptomys borealis* (P-3996), Alaska; c, d, *S. cooperi* (108544), Michigan; e, f, *Phenacomys intermedius* (P-3917), Montana; g, h, *Lemmus sibiricus* (110465), Alaska.

Phenacomys intermedius.—The edge of the dorsal lobe is double-peaked and smooth; it is flanked on each side by one or two spine-tipped papillae, while the remainder of the rim is crenate but not papillose (Fig. 5). The dorsal papilla is a single relatively long conule, not enfolded in a mass of tissue. The urethral process is a flap split distally into four blunt lobes of almost equal size.

The baculum is slender. In the three specimens at hand the base is notched rather than pointed at its proximal median, and from the widest lateral points its outline curves sharply into the shaft. In one specimen the shaft is slightly bowed ventrally, but usually it is straight; it terminates in a head which is distinguished not by swelling but rather by a narrow neck at its base. The ventrally bowed medial digit tapers from a wide base to a blunt tip; in one specimen the digit has a midbasal bump suggesting a keel. The lateral rods are compressed distally in the dorsoventral plane so that they appear tapered in ventral view but of the same thickness from end to end in lateral view; these also are bowed ventrad.

Synaptomys cooperi, *Synaptomys borealis*, and *Phenacomys intermedius* form a loose group by reason of their resemblances in shape of glans, diameter-length ratio, proportions of the urethral process (longer than wide and essentially flap-like), simplicity of the dorsal papilla, and other details. Various characters of each, however, are approached or matched in other species; for example the glans shape, particularly shape of dorsal lobe, is somewhat like that of *Clethrionomys*, and a similar dorsal papilla and a flap-like urethral process are seen in *P. longicaudus*; the three pointed urethral lobes of both *Synaptomys* and the poorly ossified digits of the baculum of *S. cooperi* are reminiscent of Group III species; the number of rim papillae of *S. borealis* likens it to *Lagurus*, *Clethrionomys*, and *Ondatra*; and in total characters of the baculum *S. borealis* is rather similar to *Clethrionomys*, although more like *P. intermedius*.

The two species of *Synaptomys* differ from *P. intermedius* in number of rim papillae and number and shape of urethral lobes, and each *Synaptomys* is further separable from *intermedius* in other characters. *S. borealis* differs from *S. cooperi* in number of rim papillae and several characters of the baculum.

Lemmus sibiricus.—The dorsal lobe is generally smooth-edged, but in one of six specimens it carries well-formed papillae. Each ventrolateral sector of the rim bears seven to nine short blunt fingers (Fig. 5), the dorsal four of which are distinctly larger. The dorsal papilla has two conules, the posterior one noticeably the shorter. The lateral bacular mounds are straight and distally squared off. The urethral process is trilobed and

strikingly compact; the lateral lobes are curved slightly to the sides and the medial lobe may be either shorter or longer than the lateral pair.

The baculum is notable for straightness in all aspects. The proximal outline of the base is usually a smooth crescent, although an occasional specimen shows the triangle point. The base grades gently into the stocky shaft which bears a more or less flattened head that is distinguished by lateral inflations within the cartilage. Seen ventrally, the medial rod tapers very slightly from proximal to distal end, but in lateral view it is the same thickness throughout. The lateral digital processes are straight and simply fusiform with equal thicknesses in all views but slightly more pointed at the distal end.

For comparisons, see accounts of *Lagurus curtatus* and other species.

Lagurus curtatus.—The short dorsal lobe is defined laterally by notches in the crater rim, but it is not well elevated above the papillose ventrolateral sectors of the rim. Each ventrolateral sector carries four short fingers, and there may be additional less distinct ones. The dorsal papilla has two short conules; one of five specimens has a single conule. In two of five specimens the lateral bacular mounds are lobulate distally. The stocky and compact urethral process is divided into three subequal lobes (Fig. 6), the lateral lobes slender and slightly curved to the side and the medial one thick and erect.

The baculum exceeds the glans in length. The proximal bone is slender and straight-sided, its base wider than long and frequently square in outline, and its shaft is straight and terminally rounded or flattened into a knob-like head. The medial digital process is widened basally and while tapered in some specimens is straight-sided and blunt in others. It arches dorsad from its point of attachment, and in lateral view is of the same thickness from end to end; occasionally it bears a small ventrobasal keel. One specimen has no medial ossification despite the presence of thick lateral processes (cf. development of the baculum in *Lagurus*, Dearden, 1958). The lateral rods are either blunt or sharp at their tips, laterally compressed, and directed dorsad in more of a slant than a curve.

The glandes of *Lemmus sibiricus* and *Lagurus curtatus* are similar in shape, diameter-length ratio, dorsal papilla (double cone, the two parts tending to be unequal), and configuration of the urethral process (short, compact, and trilobed with slight curvatures of the lateral arms), and in those same respects both *sibiricus* and *curtatus* resemble some species of Group II. *Lemmus* particularly resembles *M. pennsylvanicus* and *M. townsendi* in number of papillae, in bearing papillae on the dorsal lobe, and also in the ventral aspect of the main bone of the baculum, but in baculum-glans ratio it is perhaps most like *Clethrionomys*.

Lagurus has more points of resemblance with Group I than does *Lemmus*, for example in shape and elongation of the dorsal lobe (which is similar to *Synaptomys*) and in the number of rim papillae (which is particularly like *S. borealis*). But the same characteristics also match *Lagurus* with *Clethrionomys* and *Ondatra* of Group II, and the overall character of the baculum is very close to *M. pennsylvanicus*. In ratio of baculum to glans *Lagurus* is approached by *M. miurus* in Group II and by Group III species of *Microtus*.

GROUP II

The following species are included: *Clethrionomys gapperi*, *C. rutilus*, *Ondatra zibethica*, *Microtus pennsylvanicus*, *M. montanus*, *M. townsendi*, *M. oeconomus*, *M. longicaudus*, *M. oregoni*, and *M. miurus*.

It is among these species that the glans reaches its largest relative size, the length approximating one-fourth that of the hind foot and the diameter-length ratio generally between 60 and 70 per cent (Tables 1, 2). The dorsal lobe is prominent not only at the crater's edge, but it also bulges dorsally, the swellings set off by a pair of shallow lateral troughs and a middorsal groove. In all species the rim carries papillae on its ventrolateral sectors. The dorsal papilla consists of two small spine-tipped conules, one set dorsal to the other; when retracted they are engulfed in a mass of wrinkled tissue. The lateral bacular mounds are long. The urethral process shows species differences, but generally it has two longer lateral lobes which curve to the sides and a lesser medial process; frequently it bears other small lobules or tubercles.

The baculum, in length, equals 80–90 per cent of the glans. The shaft of the proximal bone, as seen from the side, is either straight or very slightly S-shaped—the distal end inclined ventrad. The base is biconcave, the ventral surface having the shallower concavity. The head tends to be squared off and blunt, rarely swollen, but it frequently shows slight irregularities on the sides where the cartilage leaves that bone to join the digital processes. The cartilage of the digital junction (Fig. 1) characteristically has square corners. The lateral ossifications are either straight or curve slightly inward; they are long, slender, and laterally compressed in the distal half. The medial segment, also long, tapers from a flared base to a slender but blunt tip which usually hooks dorsad, and there is a prominent tendency within this Group for the segment, when well ossified, to bear a medial ventral keel.

Clethrionomys gapperi.—The distinct long narrow dorsal lobe occurs as either two sharp-pointed smooth-edged peaks or a single flat-edged prominence. It is flanked on each side of the crater rim by four to six

spined fingers (Fig. 6). The dorsal papilla is unencumbered by surrounding folds of skin, and in one of five specimens it consists only of a single conule. The urethral process has two curved lateral arms and a medial finger, each arm about twice the length of the finger and each carrying a small tubercle on the distal crest of its curve.

The baculum appears to be considerably less variable than in many species of the group. In all specimens examined the base is a long triangle frequently notched on each side of the proximal point; specimens examined by Dearden (1958) and others, however, are "subrectangular to cupped." In lateral view the shaft is straight; but seen ventrally it is slender and either narrows off to a point or forms a small but distinct head. The medial rod is large and well formed, tapering from a wide base as it curves dorsad, and there is a distinct keel on its ventral surface. The long lateral bones are deeper than wide and are compressed particularly in the distal half. Each curves dorsad from its proximal attachment and has a squared-off appearance in lateral aspect; frequently it bears a small notch in its proximal ventral edge.

For comparisons, see accounts of *Ondatra zibethica* and other species.

Clethrionomys rutilus.—In the two specimens at hand, the dorsal lobe, well set off by deep lateral indentations in the rim, rises in a pair of sharp-pointed peaks. Some features of the glans are sufficiently different in the two specimens to warrant separate description. One phallus, from an animal captured by W. H. Dall in 1868, at Nulato, Alaska, carries four or five papillae on each ventrolateral sector of the rim. Its dorsal papilla has three conules arranged in a dorsoventral row, and the urethral process consists of two long lateral arms curving away from a long medial lobe which is split at the tip (Fig. 6). In the other example, from St. Lawrence Island, the rim bears two papillae on each side of the dorsal lobe, the dorsal papilla has four conules in a row, and the lateral bacular mounds are lobulate along the distal edge. The elaborate urethral process consists of two long curved lateral arms, a pair of shorter medial processes, and a midventral lobe which is exceptionally long and is split distally into a distinct hammerhead (Fig. 6). The above listed differences may be intraspecific, but it is noteworthy that Tokuda's figures (1941) for *C. rufocanus* fit the St. Lawrence Island specimen.

The two bacula are similar. In both the base is wider than long, and rather than coming to a proximal point it is divided by a notch between lateral condyles. According to Anderson (1960) and Ognev (1950) this formation is atypical, and the basal tuberosities of the stalk are "medially confluent." In lateral aspect the bone is S-shaped in some slight degree; the shaft is slender and the head is laterally rounded out within the cartilage

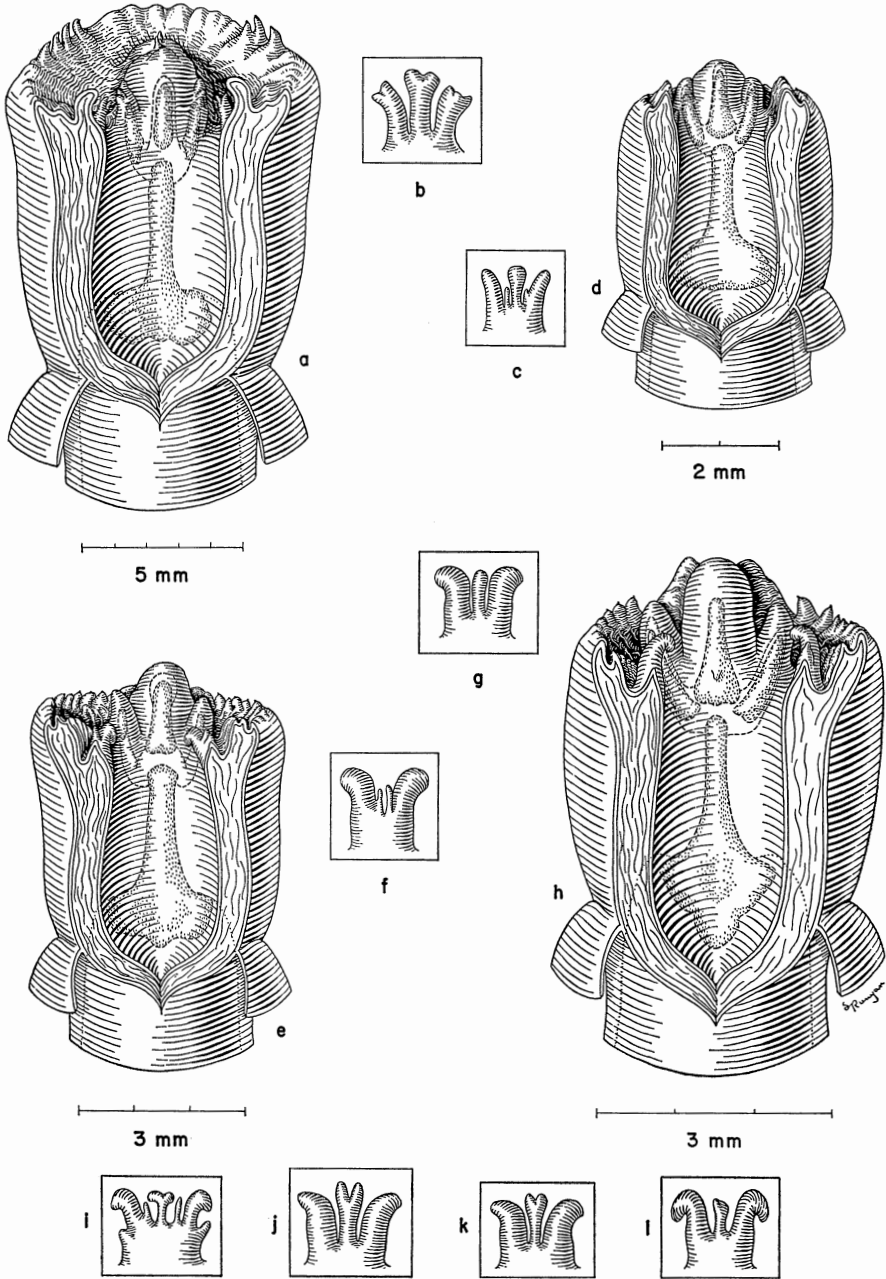


FIG. 6. Ventral views of glans (incised midventrally) and urethral process (enlarged) of: a, b, *Ondatra zibethica* (P-3921), Michigan; c, d, *Lagurus curtatus* (78505), Idaho; e, f, *Microtus longicaudus* (110250), Montana; g, h, *Clethrionomys gapperi* (110212), Montana; i, *C. rutilus albiventer* (P-3916), Alaska; j, *M. townsendi* (P-3970), Washington; k, *M. montanus* (110265), Wyoming; l, *C. rutilus dawsoni* (P-3953), Alaska.

of the digital junction. The medial rod is moderately wide basally, keeled and arched, and blunt terminally. Each lateral segment, as long as the medial one, is angular and distally compressed into a blade which is wide in the dorsoventral plane.

For comparisons, see accounts of *Ondatra zibethica* and other species.

Ondatra zibethica.—The glans is small in proportion to the size of the animal (Tables 1, 2), but in other measurements there is no unusual divergence from the Group pattern. The dorsal lobe is double-peaked and smooth-edged and on each side of it three or four slender fingers rise from the rim (Fig. 6). The dorsal papilla carries an array of four conules in a dorsoventral row; these are situated closer to the medial bacular mound than to the crater wall. That wall carries spines middorsally as well as dorsolaterally. The lateral bacular mounds are lobulate along the distal edge. The urethral process is trilobed; each lateral lobe is divided distally into two horns of equal size, the medial lobe longer than the lateral ones and often split distally into a hammerhead. In one specimen the urethral process has five lobes, an extra pair of lateral ones. The short ventral shield does not reach above the crater rim.

The baculum is comparatively slender, but its base is much wider than long and in the five specimens at hand is unusually constant in shape—a large rectangle with either a small medioproximal point (set off by a pair of notches in the straight line of the basal edge) or simply one central notch instead of a point. Base becomes shaft with almost a 90 degree angle. The proximal portion of the shaft is arched ventrad; the distal half, often slightly swollen, is constricted immediately under the round head. The head is inclined ventrad in most specimens, its shape suggesting an S. The medial rod is straight-sided in ventral view; in lateral view it has a pronounced dorsal hook at the distal end. Each lateral rod is distally curved dorsad, compressed laterally, and flat-topped; occasionally the top edge is serrate, the serrations coinciding with lobules in the tissue of the mound enclosing it.

There are resemblances of *Clethrionomys gapperi*, *Clethrionomys rutilus*, and *Ondatra zibethica* in the diameter-length ratio, the elongate shape of the dorsal lobe, the number of rim papillae, and the trilobed urethral process. In each of these points the species are also similar to *Lagurus curtatus* although the urethral process in *Lagurus* is distinctly different in its general proportions. The dorsal papilla of *C. gapperi* has two cones, as does that of *L. curtatus*, and in both species apparently there is a tendency toward a single cone. The two species of *Clethrionomys* resemble each other especially in length and slenderness of the lobes of the urethral process and the pronounced hooking in the lateral pair of lobes, and in characters of the baculum; in characters of the urethral process (lateral hooking and long

distally split medial process) they approach *Microtus montanus* and *M. townsendi*. *C. rutilus* is unlike *C. gapperi* in having three or four conules in the dorsal papilla, in which respect it resembles *O. zibethica*, and the two together would compare with the *Microtus* species *pennsylvanicus*, *montanus*, and *townsendi*, some specimens of which have more than two conules in the papilla; *Neofiber* also carries more than two conules. *O. zibethica* and *C. rutilus* are further alike in that in both there are small accessory lobules on the urethral process and serrate edges on the lateral digits which are surmounted by lobate bacular mounds; the lateral view of the baculum and its curvature perhaps bears as strong a resemblance between those two species as between *C. gapperi* and *C. rutilus*. *Ondatra* is individually distinctive in the forking (rather than hooking) of the lateral arms of the urethral process, in absolute size, and in a few other characters.

Microtus pennsylvanicus.—The dorsal lobe is papillose, its papillae ranging in number from four to ten (Fig. 7), and each ventrolateral sector carries between four and eight long fingers, with additional smaller ones ventrally. In one of five specimens the dorsal papilla has three conules rather than two, and in another specimen the lateral bacular mounds are lobulate. The urethral process varies considerably; in most examples each lateral arm bears a small tubercle on the crest of the outward curve, and the medial lobe, which is one-half the length of the lateral pair, is divided into two processes; two of five specimens have a single medial lobe, and in one example there is an extra pair of lateral lobes.

The main bone of the baculum is heavy and broad. The base is triangular (though not with a sharp proximal point) or almost square in ventral aspect; Dearden (1958) describes it as generally being cup-shaped. Lateral subterminal indentations in the shaft faintly set off a head within the cartilage of the digital junction. The medial ossicle, 33 per cent of the total baculum in length—larger than in any other microtine studied—is distinctly tapered in ventral view, but noticeably less so in lateral aspect; it bears a midventral keel. The lateral digits also are comparatively large; they are either straight in all views or they arch laterad and ventrad.

For comparisons, see accounts of *Microtus townsendi* and other species.

Microtus montanus.—The dorsal lobe is double-peaked and nonpapillose. The papillae on the ventrolateral sectors vary in size, shape and number, but they tend to be short, and the number of distinct fingers per sector varies from three to six. The dorsal papilla consists of two conules. The urethral process has curved lateral lobes (Fig. 6), each frequently assymetrical and carrying a large accessory tubercle. The medial lobe is as long as the lateral lobes, and in two of three specimens it is split distally.

In ventral view, the base of the baculum forms an isosceles triangle set

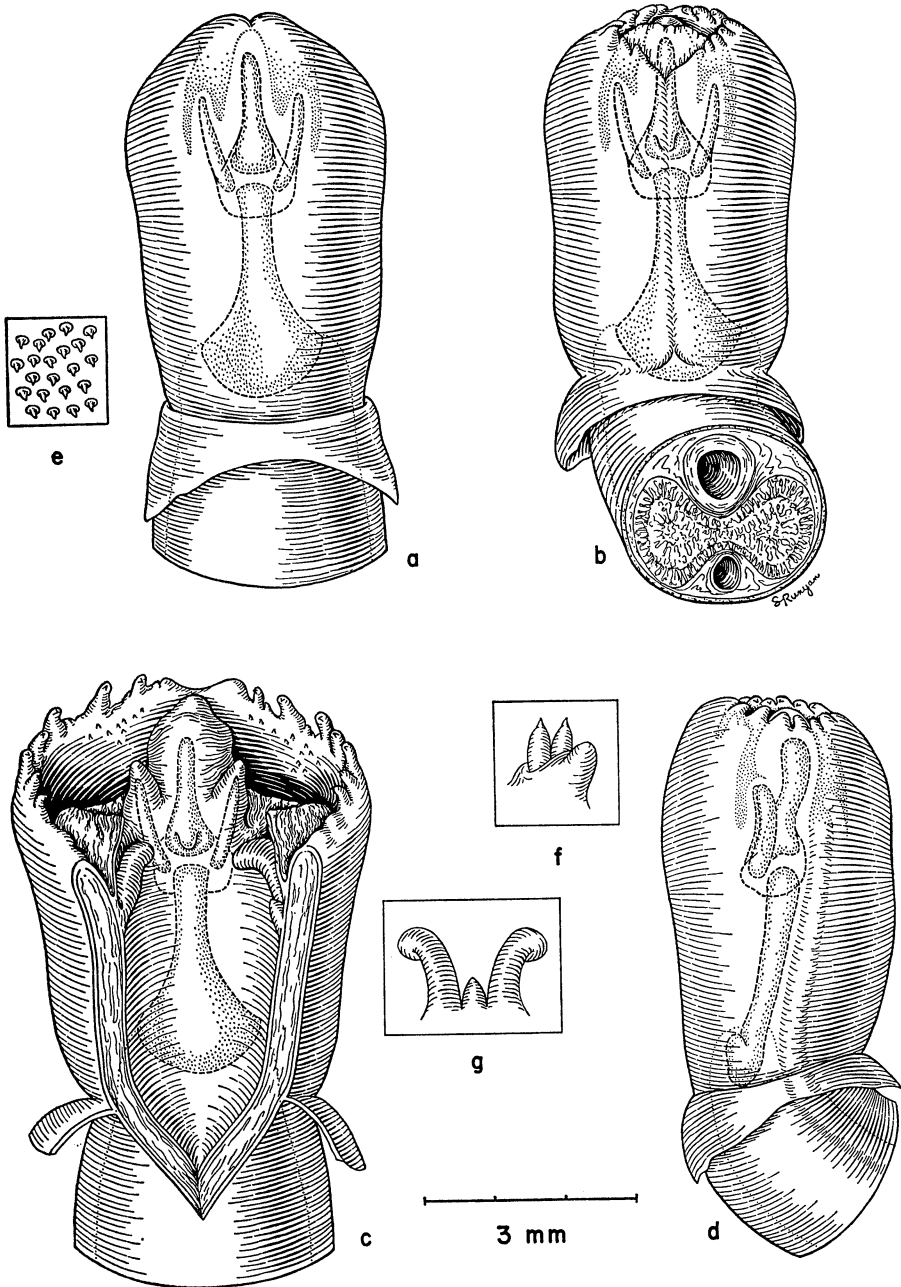


FIG. 7. Views of glans of *Microtus pennsylvanicus*: a, dorsal; b, ventral; c, incised midventrally exposing urethra; d, lateral; e, epidermal spines; f, dorsal papilla, enlarged, lateral aspect; g, urethral process, enlarged, ventral aspect (59461), Michigan.

off by a sharp incurve as it joins the shaft; however, in some specimens it is flattened proximally so that the shape takes on an angular squareness. The shaft is slightly constricted midway between base and head, and in lateral view faintly suggests an S by reason of some proximal curvature. As seen from the side, the head of the bone is not distinguishable, but in ventral view it is a well-formed globe. The medial rod, slightly bowed and blunt at both ends, resembles a cucumber. The lateral processes are straight and slender in ventral aspect and somewhat thicker and curved dorsad as seen in lateral view.

For comparisons, see accounts of *Microtus townsendi* and other species.

Microtus townsendi.—The dorsal lobe carries one or two papillae on the outer edge of each peak, and each ventrolateral sector of the jagged rim bears six to nine fingers of different lengths. Two of three specimens at hand have a double-conule dorsal papilla, but in the third the papilla bears four conules arranged in a transverse row. The urethral process (Fig. 6) consists of two large lateral arms, which curve to the side but apparently are without accessory tubercles, and a medial lobe of similar length which is split distally.

The base of the baculum is wider than long and usually comes proximally to a wide triangular point; however, the point may be reduced and in ventral aspect the outline of the basal face of the bone is crescentic. In the three specimens the shaft is constricted medially and parallel-sided distal to the constriction; it is truncate terminally and there is no distinction between shaft and head. The straight medial rod is untapered in lateral view and tapers only slightly in ventral view. The lateral rods arch laterad and ventrad in the shape of cowhorns.

Microtus pennsylvanicus, *M. montanus*, and *M. townsendi* are similar in regard to dorsal papilla, number of rim papillae, shape of the main bone of the baculum, and in overall external contours.

M. pennsylvanicus differs from both *townsendi* and *montanus* in characters of the urethral process and digits of the baculum. In *pennsylvanicus* the medial lobe of the urethral process is short and in some specimens is wholly divided so that the whole process resembles that seen in *M. longicaudus* and *M. oregoni*. In *townsendi* and *montanus* the medial lobe is as long as the hooked lateral arms and the entire process is rather like that in *Clethrionomys* or, even, *Lagurus*. In regard to digits of the baculum, those of *pennsylvanicus* are long and well ossified and the medial one usually is keeled, in which respects the species is similar to *Clethrionomys*; the keel also occurs in *Lagurus*, *M. longicaudus*, and *M. oregoni*. The digits are less ossified in *townsendi* and *montanus*.

Compared with *montanus*, *townsendi* has a papillose dorsal lobe, more fingers on the dorsolateral sectors of the rim (in which respects it and *pennsylvanicus* are much alike), and larger areas of spines on the crater walls and floor.

Microtus oeconomus.—The dorsal lobe is double-peaked and nonpapillose, and each ventrolateral sector of the rim bears seven to nine fingers (Fig. 8). The dorsal papilla is a single conule which carries a tubercle on its hind side; the urethral process has three lobes, a short medial one and a longer lateral pair which curve slightly to the sides.

The baculum equals the glans in length (Table 1). Its base is as long as wide; its medial point is in evidence on the proximal edge and the basal outline decurves from that point to the lateral prominences. The base-shaft junction is not sharply incurved; the outline formed by the distal and lateral faces of the base often runs a slight distance straight distad before initiating the inward sweep to join the slightly arched shaft. The head of the bone is swollen in ventral view, but it is scarcely distinguishable from the shaft in lateral aspect. The medial rod has an unusually wide base which tapers off to a sharp point. The lateral rods curve dorsad and are exceptionally thick distally in both lateral and ventral aspects.

The unique assemblage of characteristics of *M. oeconomus* has made it difficult to fit the species in any sort of two-dimensional morphological scale. In most respects *oeconomus* may fit in Group II, but in other features it is to be aligned with species of other groups, with those of III especially. It agrees with species of Group II in external proportions (like *Clethrionomys* or *M. montanus*, for example), number and site of rim fingers (like *M. longicaudus* and *M. miurus*), trilobed urethral process, and form and amount of ossification of the medial distal unit of the baculum (like *M. montanus*). In ratio of baculum to glans it resembles *miurus* (of Group II) or *mexicanus*, *californicus*, and *richardsoni*. It also compares favorably with those Group III species in the incomplete ossification of the lateral digits, the lateral profile of the main bone, and the single-cone dorsal papilla.

Microtus longicaudus.—The dorsal lobe is scarcely elevated above the ventral rim of the crater and is nonpapillose, although spines are present on its distal border. The remaining parts of the rim carry between five and eight spine-tipped fingers per side (Fig. 6). The dorsal papilla has two conules, the dorsal one spinous dorsally and laterally as well as distally. The urethral process consists simply of two laterally curved lobes, each bearing a tubercle well down on its medial edge; its form in one specimen suggests a wide flap with four lobes along the distal edge. The lateral lobes

are unmistakable, but the median tubercles may represent a weakly developed bilobed medial process.

The proximal bone of the baculum is broad, straight, and in ventral view parallel-sided. Its proximally rounded base enters the shaft with an abrupt incurve or a gradual slope, and the distally flattened head appears in lateral view simply as the climax to a gradual swelling of the shaft. In some specimens the medial rod is tapered from a wide base, while in others it is of essentially one width from end to end; when it is sufficiently developed to evidence a "base" it may also be keeled midventrally. The compressed lateral segments, which curve laterad and dorsad from the cartilage junction, are set at a greater distance from the sides of the medial rod than is usual in this Group.

For comparisons, see accounts of *Microtus miurus* and other species.

Microtus oregoni.—In relation to hind foot the glans is smaller than usual in the Group (Tables 1, 2). Its smooth-edged dorsal lobe forms a single peak, the middorsal groove being evident only in basal portions of the glans. Bordering it on each lateral sector of the rim are three or four spine-tipped fingers (Fig. 8). The dorsal papilla has two conules, the dorsal one bearing spines both on its sides and tip. In old specimens the lateral arms of the urethral process are longer than usual in the Group; they are hooked outward and each has a tubercle on its medial edge. There is no medial lobe in the urethral process.

The baculum is reasonably sturdy but not gross. The base of the main bone is slightly wider than long; in ventral view its proximal edge forms a smooth curve from one lateral apex to the other—in only one specimen of five is the triangle point apparent in the middle of the curve—and the gradient from the lateral apices into the shaft is almost a smooth 60-degree slope. The sides of the shaft are nearly parallel while the slightly swollen head occasionally has small lateral protuberances at its base; in lateral view the shaft swells into the head like a club. The amount of cartilage at the digital junction is negligible. The medial rod, closely appressed to the head of the proximal bone, is thick and heavy, wide basally, and tapered to a blunt tip as it curves dorsad; an occasional specimen evidences a ventral keel. The thick lateral digits sometimes are arched ventrad, but more often they are straight.

For comparisons, see accounts of *Microtus miurus* and other species.

Microtus miurus.—The dorsal lobe is double-peaked and smooth-edged while the remainder of the rim is papillose, each ventrolateral sector bearing six to nine indistinct fingers (Fig. 8). The dorsal papilla has two conules with extra spines on its dorsal flank. The urethral process carries two long

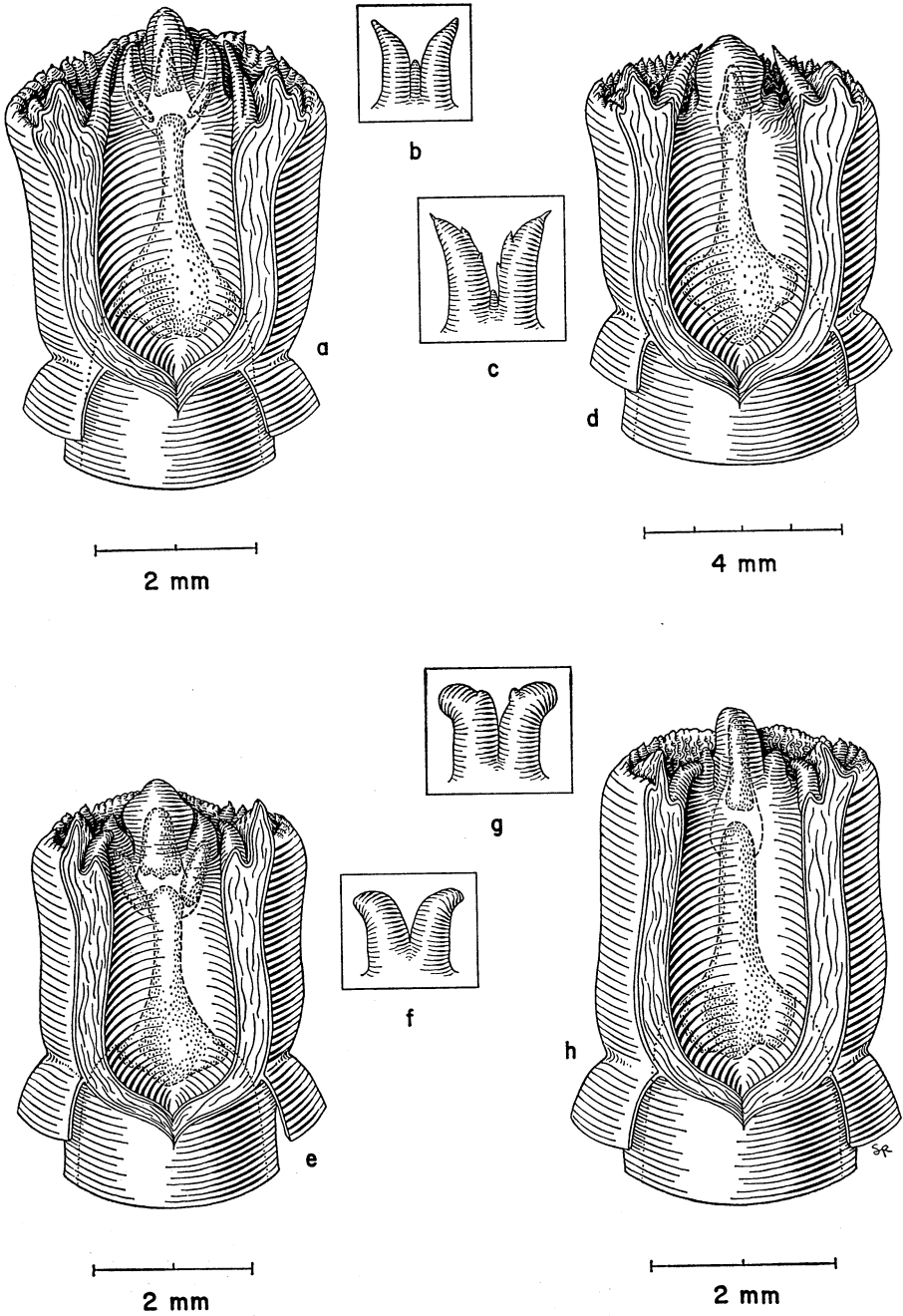


FIG. 8. Ventral views of glans (incised midventrally) and urethral process (enlarged) of: a, b, *Microtus oeconomus* (109254), Alaska; c, d, *M. richardsoni* (110305), Montana; e, f, *M. oregoni* (P-3977), California; g, h, *M. miurus* (P-3998), Alaska.

arms, each bearing a tubercle on the medial side and each hooked outward; there is no medial lobe.

The rather gross and smoothly contoured baculum exceeds the glans in length (Table 1). In ventral view the proximal border of the base is seen as a semicircle extending from one lateral prominence to the other—in one specimen there is a pair of notches in the curve setting off a median point—and the line from base into shaft is a gentle bend. In lateral view the shaft is fairly club-like and is ventrally arched in its distal portion. The medial digit is not keeled; it is slightly wider at its base, and the remainder is almost straight-sided, not forming a point until the very tip. As seen laterally it lacks the usual tapering, but it is slightly arched ventrally. Lateral digits are absent, but vascular cords are present as usual.

Microtus longicaudus, *M. oregoni*, and *M. miurus* are similar and unique in having a double-coned dorsal papilla with spines on its dorsal flank and a bilobed urethral process with lateral curvature to the arms. The baculum-to-glans ratios of the three kinds are also similar and are more appropriate to Group III than to Group II.

M. longicaudus and *M. oregoni* fit together in diameter-length ratios, in degree of ossification of the lateral digits, and in the occasional presence of a keel on the medial segment. Also the single-peaked dorsal lobe of *M. oregoni* is perhaps more like the poorly defined lobe of *M. longicaudus* than that of any other species. The size ratio of both species is close to that of *Clethrionomys* and *Ondatra*; *M. oregoni* further resembles those forms, and also *Lagurus*, in having three or four rim papillae. On the other hand, their size ratios also compare favorably with that of *M. oeconomus*, and the number of rim papillae of *M. longicaudus* reinforces such a comparison.

M. miurus and *M. longicaudus* have a similar number of rim papillae and together they compare favorably not only with *M. oeconomus* but also with *Lemmus* of Group I and *M. californicus* of Group III. *M. miurus* contrasts with *longicaudus* and especially with *oregoni* in the absence of lateral digits and in its diameter-length ratio. *M. oregoni* differs from both *longicaudus* and *miurus* in several characters, the more impressive of which are indicated in the glans-to-foot ratio and degree of ossification of the lateral digits of the baculum.

GROUP III

The following species of *Microtus* are included: *richardsoni*, *californicus*, *guatemalensis*, *ochrogaster*, *pinetorum*, *mexicanus*, and *fulviventer*.

The glans is approximately one-fifth the length of the hind foot, but it is smaller in some species (Tables 1, 2). In general appearance it is short

and squat, with a diameter-length ratio ranging between 70 and 80 per cent. The dorsal lobe is distinguished by its distension distally, but its boundaries are indistinct both on the crater rim and on the dorsal side of the glans where there are but slight swellings, ill-defined by lateral troughs. Rim fingers are present in some species and absent in others. The dorsal papilla is a single short cone bearing a spine on its hind slope in addition to one on its crest. The lateral bacular mounds are short and frequently buried in the tissue folds of the medial mound. The urethral process varies with the species, but the tendency is to be short, compact, and relatively wide; typically it is a lobate flap.

The baculum is always over 90 per cent of the glans in length and may exceed 100 per cent. The shaft of the proximal bone is S-shaped or arched ventrad, and the base is biconcave with the ventral surface curved more deeply than the dorsal one. The head of the bone is enlarged, particularly on the dorsal facet; it bears a small protuberance on each side where the lateral digits should or do attach. Lateral units apparently are absent in some species. When present they are small and mostly or completely cartilaginous; they leave the head of the main bone at right angles, then curl gradually distad. The medial rod usually has some osseous tissue, but the bone is small and simple.

Microtus richardsoni.—The indistinct dorsal lobe, not well set off either by height or by deep lateral rim nicks, is rimmed with papillae. The ventrolateral sectors are also strongly papillose and the entire circumference of the rim may bear anywhere from 34 to 42 fingers, all roughly equal in height (Fig. 8). The dorsal papilla consists of two spine-tipped conules. The lateral bacular mounds are small and scarcely discernible, engulfed as they are in folds of tissue from the large medial mound. The urethral process is made up of two large pointed lobes, each with two spines on its medial edge as well as one on its distal tip; these lateral lobes are separated by a minute medial knob which scarcely qualifies as a lobe.

The base of the main bone is large and usually triangular with a pronounced proximomedial point. As seen ventrally its proximal outline decurves between that point and the lateral prominences; generally there is a moderately sharp incurve as the base joins the shaft, but in one specimen the outline of the base runs slightly distad before curving inward toward the shaft. The shaft tapers gradually distad then enlarges to a rounded head. The medial rod is a small cone closely appressed to the head of the proximal bone; it arches ventrad, and in one specimen it carries a small keel medioproximally. There are no lateral digits in any of the four specimens at hand; only vascular tissue marks their hypothetical location.

Microtus richardsoni is unlike any other North American microtine in

that there is scarcely a trace of a dorsal lobe, the entire rim of the crater is lined with numerous (as many as 42) symmetrical and evenly spaced papillae, and the urethral process has two pointed lobes. Its other characters are approached or matched in species of Groups II or III. The double-cone dorsal papilla is like that of most Group II species and there is fair resemblance in regard to the urethral process; the long pointed urethral arms are similar to those of *oeconomus*, although in that species there is a median lobe in addition; *longicaudus*, *oregoni*, and *miurus* also have bilobed processes, but the arms are curved laterad. The diameter-length ratio is matched by several species of Group II and by *M. californicus* of Group III. Characters of its baculum (for example, baculum-to-glans ratio, absence of lateral digits, and conformation of the main bone in lateral aspect) bear close comparison with species of Group III and to slightly less extent with *M. miurus* of Group II.

Microtus californicus.—The dorsal lobe is well differentiated by height and bears four to six papillae on its rim; the remainder of the rim carries eight or nine fingers per side. The stubby dorsal papilla bears a distal spine only, the long lateral bacular mounds are clearly separated from the medial mound, and the urethral process is broader than long and consists of three subequal lobes (Fig. 9).

The base of the baculum tends to be slightly longer than wide. Unlike Anderson's (1960) specimens, in those at hand the ventral concavity is deeper than the dorsal one. In ventral aspect the proximal edge comes close to a smooth semicircle, the median proximal point only slightly in evidence, and the curve from base into shaft is smooth and gradual. The shaft, straight-sided in ventral aspect and club-shaped in lateral view, gradually enlarges distad to its truncate limits. The medial digit is delicately heart-shaped in ventral aspect, fitting rather like a cap on the head of the proximal bone; laterally it is somewhat rectangular, with its body arched ventrad. There is no lateral ossification in either of the two specimens at hand, but there are fairly long, slim, cartilaginous rods which curve out gently from the head of the proximal bone.

For comparisons, see accounts of *M. guatemalensis* and other species.

Microtus guatemalensis.—Because all of the glandes of this species are refurbished examples from dry study skins (see Materials and Methods), their soft parts are contorted and obscure and, therefore, are definable only in general terms.

The dorsal lobe is papillose, as are other parts of the crater's edge. Papillae on the ventrolateral rim sectors appear typically to number eight, though on some specimens only two show clearly. The lateral bacular mounds are long, perhaps even equaling the medial mound in height

(Fig. 9). The urethral process is a flap terminating in three pointed lobes, of which the lateral pair is distinctly longer than the medial one.

The proximal bone of the baculum is heavy and blunt. Its base is longer than wide, and much of its length lies proximal to a horizontal plane connecting the lateral prominences; in ventral view the proximal border makes a deep smooth curve, but in one specimen of the five the medial part of the border is squared off and the outlines from it decurve before reaching the lateral points; The dorsal face is more deeply concave than the ventral one. The thick shaft is slightly constricted medially and bears a terminal head which is very slightly bulged at the sides and is flat across the top. In lateral view the whole bone is slightly, but distinctly, S-shaped. The cartilage of the digital junction is in some cases sharply squared, in others gently curved. The medial rod is triangular as seen ventrally and sausage-shaped in lateral view. The lateral processes are long, though infrequently ossified; the ossification centers occur either distally or medially and they are ovoid or triangular.

Microtus californicus and *M. guatemalensis* are similar in regard to the presence of papillae on the dorsal lobe, number of papillae on the ventrolateral rim sectors, and the conelike ossicle of the medial digit of the baculum. Both species have a single wide-coned dorsal papilla and a trilobed urethral process which has no lateral hooking. In these latter features they are also basically similar to *pinetorum*, *ochrogaster*, *mexicanus*, and *fulviventer*. In regard to rim papillae, a like number is also seen in *Lemmus*, *M. miurus*, *M. longicaudus*, *M. oeconomus*, and in some specimens of *M. pennsylvanicus*. Further, the aforementioned conelike ossicle also has a similar counterpart in *richardsoni*, *ochrogaster*, and *pinetorum*.

M. californicus shows further resemblance to *ochrogaster*, *pinetorum*, *mexicanus*, and *fulviventer* in that the base of the main bone has a deep concavity on the ventral surface (rather than dorsal one, as in *guatemalensis*). In having no or minute ossifications in the lateral digits, *californicus* also resembles *pinetorum*, *mexicanus*, and *fulviventer* and, in addition, *miurus* and *richardsoni*. Its resemblance to *miurus* is continued in the club-like lateral profile of the baculum, in which respect *oregoni* also fits. Its diameter-length ratio, which is small for most species of Group III, compares favorably with *richardsoni* and with several kinds in Group II.

M. guatemalensis is unlike *M. californicus* in shape of the main bone of the baculum, ossification of the lateral units, and probably in diameter-length ratio (Table 2). Its main bone differs from all other species of Group III in having a deeper concavity on the dorsal side of its base and an S-shaped (rather than ventrally bowed) profile in lateral aspect.

Microtus ochrogaster.—The dorsal lobe is fairly distinct, and in one of

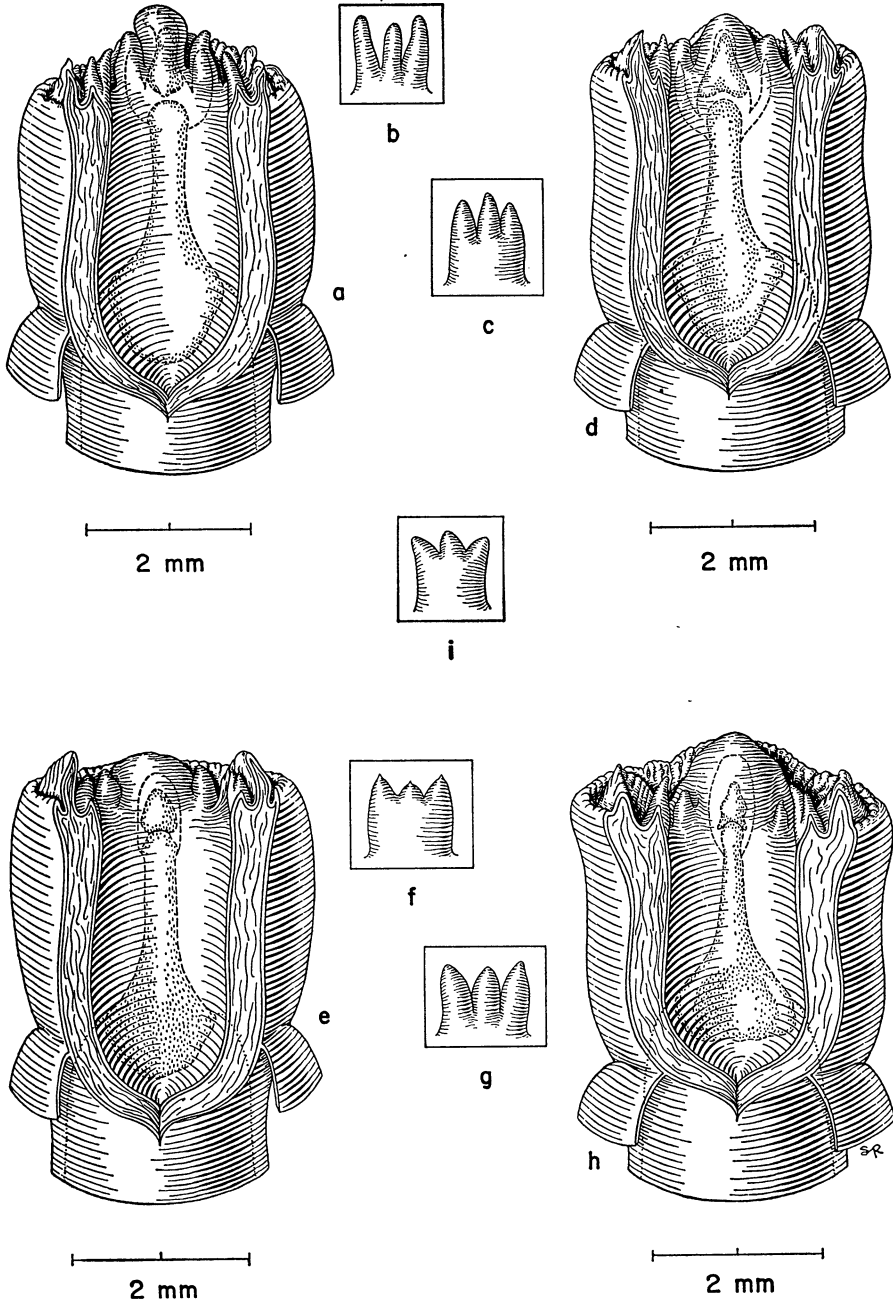


FIG. 9. Ventral views of glans (incised midventrally) and urethral process (enlarged) of *Microtus*: a, b, *guatemalensis* (USNM 76775), Guatemala; c, d, *californicus* (P-3989), California; e, f, *pinetorum* (P-3982), North Carolina; g, h, *ochrogaster* (110307), Montana; i, *mexicanus* (P-3954), Veracruz.

four specimens it is flanked on either side by two short papillae; in the other specimens, however, there are no rim papillae. The dorsal papilla is a single cone, spined distally and dorsally. The urethral process is wider than long and divided into three blunt cones of approximately equal size (Fig. 9). Spines within the crater are centralized in the same locations as in other species, but they are spread over a wider area. The ventral shield is unusually large.

The baculum is variable, sometimes slender but usually thick. The base of the main bone is typically wider than long with a definite tendency for flattening along the proximal edge; the point of the triangle can always be distinguished, but it is usually set back into the plane of the surface. Base tapers into shaft with a smooth slope of about 60 degrees. The shaft itself, generally straight-sided but occasionally bowed ventrad, terminates in a slight head, the enlargement greater in the dorsoventral plane than in the transverse one. The medial ossicle is highly irregular, but it tends to be a small cone which in some specimens is basally concave and fits like a cap over the head of the proximal bone; in one example there are two ossicles side by side within the cartilage of the unit while in the other five fluid-preserved bacula the ossicle is single and ovoid. The lateral digits are extremely short and possibly in some individuals, even old ones, they may be absent. In two of six bacula (all bearing an ossicle in the medial segment) lateral digits appear to be absent; while in four examples they occur as slender cartilaginous rods, three pairs of which contain a slight ossicle near the tip of each.

For comparisons, see accounts of *Microtus fulviventer* and other species.

Microtus pinetorum.—The crater rim has no papillae (Fig. 9). One of four specimens bears two conules as the dorsal papilla. The lateral bacular mounds are small in diameter, but they are moderately long and unobscured by tissue folds. The urethral process is a rectangular flap which is wider than long and serrate along the distal edge; in two specimens it is divided by a slight medial cleft, and in another two it has a slightly larger medial lobule. The ventral shield is large.

The simple but sturdy baculum equals 115 per cent of the glans in length. The proximal border of the main bone is smoothly rounded, and the gradation of base into shaft occurs as a gentle curve. The shaft is bowed ventrad, and as a result the dorsal enlargement of the head may appear quite pronounced; the head bears moderate subterminal lateral prominences. The medial ossicle is ovoid and set close to the head of the proximal bone; in one specimen it has coalesced with that bone. The lateral digits are indistinct or absent. In one specimen they are seen as fine rods of cartilage which leave the proximal bone at right angles and curve

smoothly upward. In the other specimens they are distinguishable only as small fusiform bits of soft cartilage within the bacular mounds, or they are altogether absent. Hamilton (1946) and Burt (1960) indicate the presence of small lateral ossicles in their specimens.

For comparisons, see accounts of *Microtus fulviventer* and other species.

Microtus mexicanus.—The dorsal lobe is distended distally, but it is not well delineated at its lateral margins, and the entire crater edge is smooth and nonpapillose. The single cone of the dorsal papilla is spined not only at the tip and on its dorsal surface but also laterally. The lateral bacular mounds are short and enmassed in the tissue of the medial mound. The urethral process is widely rectangular and distally serrate, the serrations forming three small lobules, the medial one shortest (Fig. 9).

The slender baculum tends to be rounded on the basal edge, though occasionally the medial point is projected proximad. Base and shaft merge in a gentle curve; in one specimen the outline moves distad from the lateral prominences before turning in toward the shaft. The shaft, straight-sided in ventral view and arched ventrad as seen laterally, bears lateral subterminal protuberances which are prominent knobs in adults. The medial distal segment consists of a small rounded ossicle embedded in a mass of cartilage, while each lateral unit is a short slender rod of cartilage. In a few of the old specimens at hand each lateral segment bears a minute ossicle; this is situated in the basal part of the segment, and in some instances it is coalesced with the lateral prominence of the main bone. Following is a summary of the distal segments in 42 fluid-preserved bacula from various parts of Mexico: in 10 specimens the three segments are entirely cartilaginous; in 23, all digits are principally cartilaginous, but the medial one bears an ossicle; in two, the medial unit is cartilaginous and the lateral pair contain small amounts of osseous tissue which is situated near the lateral prominences of the main bone; and in seven, each segment contains an ossicle, the lateral ones always near the prominences and sometimes fused with them.

Microtus fulviventer.—The dorsal lobe is typical of Group III and the crater rim is nonpapillose (Fig. 10). The dorsal papilla is one stubby conule with a spine on its tip and another on its dorsal flank. The lateral bacular mounds are small, in some specimens so slight that they were seen only after the skin was inverted. The urethral process is a longer than wide flap which is distally divided into two or three lobes.

The base of the baculum is comparatively gross with pronounced lateral prominences; in ventral view the medial part of the proximal face is squared-off and bordered on each side by angular indentations. The base curves gently into the shaft which is heavily bowed ventrad and bears

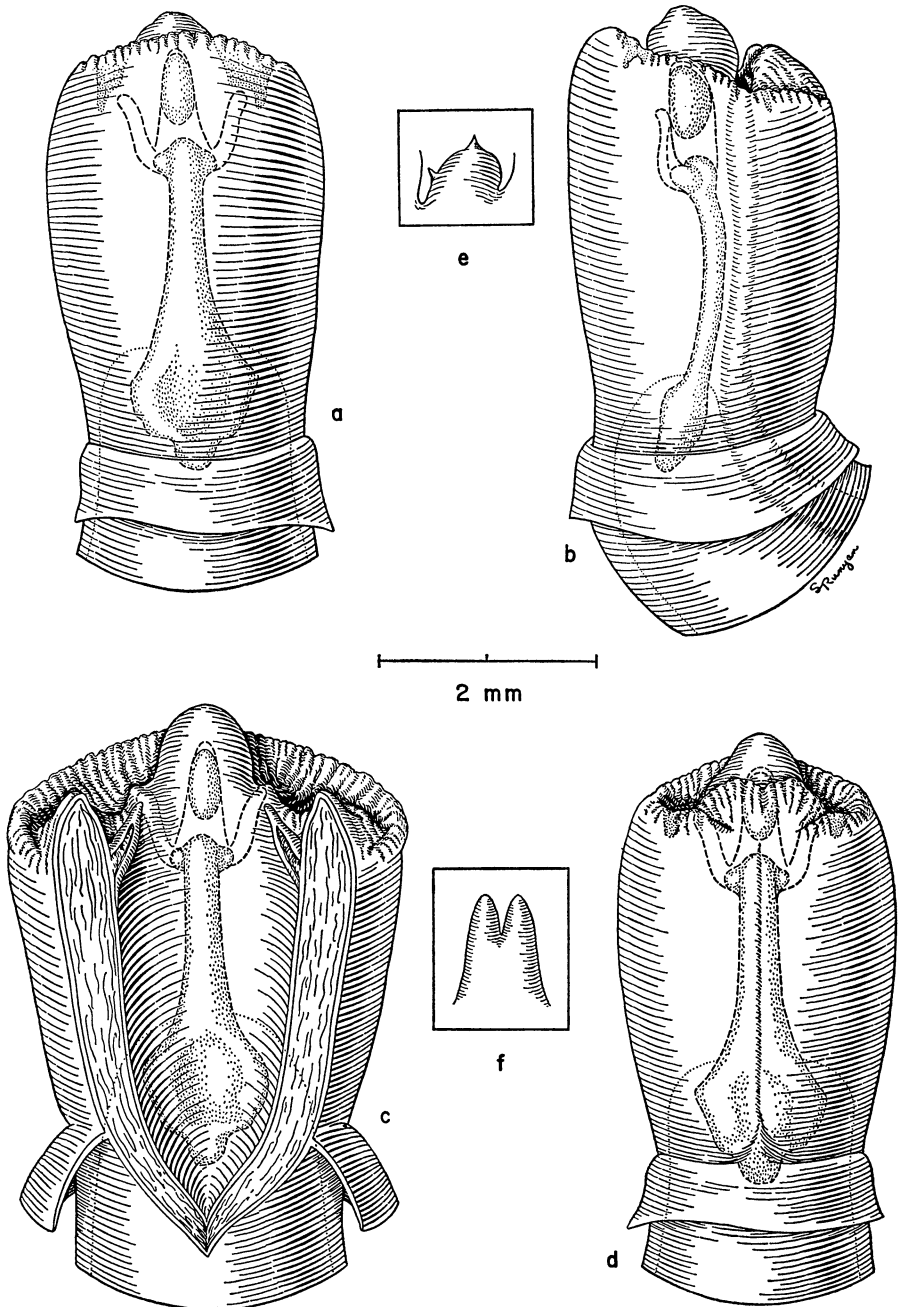


FIG. 10. Views of glans of *Microtus fulviventris*: a, dorsal; b, lateral; c, incised mid-ventrally exposing urethra; d, ventral; e, dorsal papilla, enlarged, lateral aspect; f, urethral process, enlarged, ventral aspect (108805), Oaxaca.

pronounced subterminal lateral protuberances. The medial ossicle, straight-sided and blunt at each end, curves slightly dorsad from the proximal bone; it is imbedded in cartilage. The lateral units are slender cartilaginous rods which curve sharply distad from the lateral protuberances of the proximal bone; they contain no osseous tissue in the four specimens at hand.

In morphology of glans *Microtus ochrogaster*, *M. pinetorum*, *M. mexicanus*, and *M. fulviventris* constitute a comparatively tight assemblage. Among characters common to them are: a nonpapillose crater rim; large diameter-length ratio; single, short-coned and spinous dorsal papilla; short wide urethral process; and a ventrally bowed baculum which has a deep ventral concavity in the base. The main bone is long, relative to foot length, but the distal segments are short and incomplete; the medial digit bears a small ossicle in addition to cartilage, while the lateral segments are mere slips of cartilage with or without a minute ossicle, or they may be absent.

M. ochrogaster differs from the three species (and at the same time shows more resemblance to *guatemalensis*, *californicus*, and species of Group II) in that it occasionally carries one or two minute rim papillae, may have ossicles in the lateral digits, and has smaller or no lateral protuberances on the head of the proximal bone (present in the other species). It is also unlike the three species (but like *californicus*) in the more complete separation of the three lobes of the urethral process.

M. mexicanus and *M. fulviventris* are similar. They differ slightly from *pinetorum* in glans-foot and baculum-glans ratios, number of spines on the dorsal papilla (fewer in *pinetorum*), and size of lateral bacular mounds (larger in *pinetorum*). There are also slight differences between the species in shape of the baculum.

OLD WORLD SPECIES

Although Old World species are placed together here both for convenience and because they were less extensively studied than North American microtines, most of them fit in one or another of the preceding three groups. Some are closely similar to North American kinds. The species examined are as follows: *Antelionomys smithi*, *Arvicola terrestris*, *Ellobius talpinus*, *Eothenomys melanogaster*, *Lemmus lemmus*, *Microtus arvalis*, *Microtus oeconomus*, and *Prometheomys schaposchnikowi*.

Antelionomys smithi.—This species fits in Group II. The glans has an unmistakable resemblance to that of *Clethrionomys*. The ratio of length to hind foot is 25 per cent, of diameter-to-length, 60 per cent. The double-peaked and elongate dorsal lobe is well set off from the remainder of the rim, and each ventro-lateral rim sector carries two to four spine-tipped

papillae. In one specimen the dorsal papilla has two conules, in the other it has three. The lateral bacular mounds in one specimen are lobulate along the distal edge. The urethral process is trilobed with distinct curvature of the lateral arms. The medial lobe is equal to the lateral pair in height, and is distally split into a hammerhead; between it and the lateral lobes there is a pair of shorter assymetrical processes.

The baculum is 84 per cent of the glans in length. The proximal bone is slender and straight, its base widely triangular and the head a small flattened globe. All three digits are well developed; the medial one is wide basally and carries a distinct ventral keel, while the lateral rods arch ventrad and are laterally compressed in their distal half.

Arvicola terrestris.—The glans more closely resembles that of *Microtus richardsoni* than any other species examined; accordingly *A. terrestris* belongs near *M. richardsoni* in our rankings (top of Group III or lower part of Group II). The ratio of glans to hind foot length is 21 per cent and of diameter to glans, 83 per cent. The dorsal lobe is not set off by height; like the rest of the rim it is papillose; fingers of the entire rim total between 22 and 26. The dorsal papilla has three conules. The lateral bacular mounds are lobulate along the distal edge. The urethral process is bilobed, and each lobe carries not only a spine at its distal tip but one or two tubercles (assymetrical in size and location in the two specimens at hand) on its medial edge; there is no lateral curvature of the lobes.

The baculum of the older specimen is 106 per cent of the glans in length. The base of the main bone is triangular, somewhat wider than long; as seen ventrally there is a slight decurving between the median proximal point and the lateral prominences, and the outline moves slightly distad from the lateral points before turning in to meet the sides of the shaft. The shaft is straight in lateral view, but swells gradually toward the distal end; in ventral view there is a small amount of medial constriction; the head of the bone carries pronounced lateral protuberances. The well ossified medial digit forms 28 per cent of the total baculum instead of 16 per cent as observed in our specimens of *M. richardsoni*; it is tapered in ventral view and of the same thickness throughout in lateral view. The small lateral digits are incompletely ossified, the ossifications occurring as short fusiform slivers.

Ellobius talpinus.—This species is set well apart from all others studied; it fits in none of the three groups. The glans is a minute conical mound occupying only about one-third of the distal tract of the penis (Fig. 11). Its width is 95 per cent of its length and the length is 10 per cent of that of the hind foot. There are no spines anywhere on the exterior surface, but the skin is gathered into thick wrinkles which generally run longitudinally.

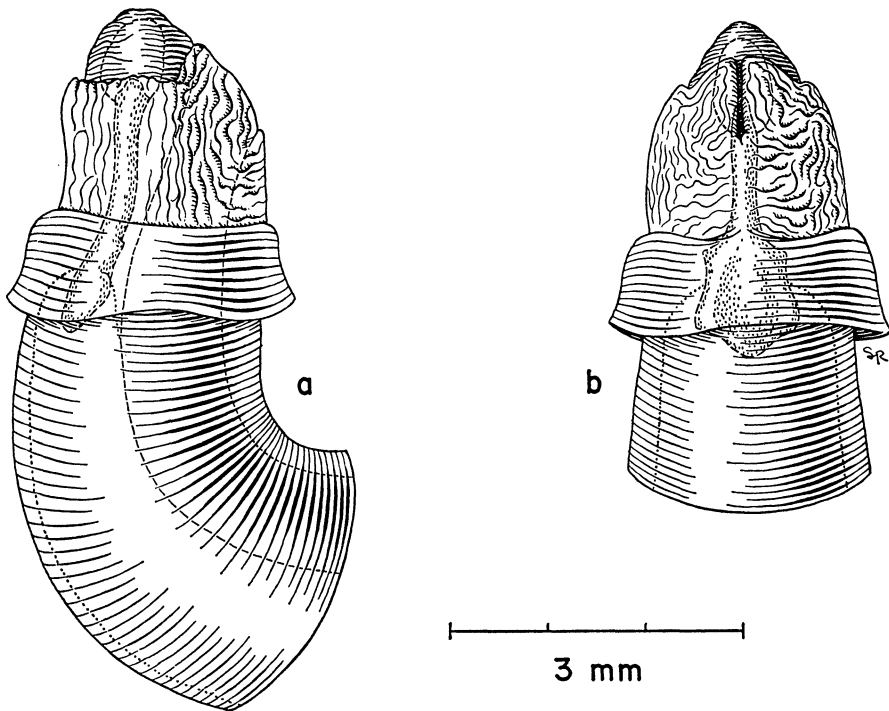


FIG. 11. Glans of *Ellobius talpinus* as seen: a, laterally and b, ventrally (108473), U.S.S.R.

The dorsal lobe is demarcated only by a medial cleft in the rim and by smaller more tightly collected lateral wrinkles. The ventral part of the rim rises distad as a prominence which equals the bacular mound in height. This prominence may be homologous either to the ventral shield or to the urethral process of other microtines, but it is not set apart from the rim by any horizontal infolding of the exterior skin. It is divided by a deep medial cleft which is so extensive that the glans appears to be split for about one-half its length; thus, it consists of two long ventral lips which guard the meatus urinarius. The crater, which is scarcely more than a deep wrinkle, contains no spines, no urethral process, no dorsal papilla, and no lateral bacular mounds. A shallow fold of tissue extends from each side of the large medial mound to the crater edge, joining the rim at the sides of the ventral prominence to form a wall around the urogenital opening.

The baculum is one and one-half times the glans length and 15 per cent of the hind foot length. It has no lateral digits and no appropriately placed vascular rods which are present in other microtine species, even those

without lateral segments of the baculum. The proximal bone is guitar-shaped; its pointed head is enclosed in a wide triangular mass of cartilage which tapers to a blunt end.

Eothenomys melanogaster.—This species fits in Group II. Its glans more closely resembles that of *Clethrionomys* than any other New World microtine examined, though it does not appear to have as many similarities with that genus as does the Old World *Antelionomys*. The glans-to-hind foot ratio is 23 per cent and diameter-to-length ratio 52 and 61 per cent in the two specimens. The elongate dorsal lobe is not medially cleft and bears no papillae, but each ventrolateral sector of the rim carries four to eight spine-tipped fingers. The dorsal papilla has two conules in one specimen and three in the other. The urethral process is trilobed, the lateral arms curved and about twice the length of the medial lobe; in one specimen each lateral arm carries a tubercle on its medial edge.

The baculum is about 85 per cent of the glans in length. The base of the main bone has the shape of an inverted trapezoid, which in one specimen has a medial notch in the proximal edge. The straight and slender shaft ends in a small head no wider than the shaft itself. The long and tapered medial digit bears a pronounced ventral keel which projects proximad, overlapping the head of the main bone. The long straight lateral digits are angular basally.

Lemmus lemmus.—There seems to be virtually no difference in glandes between this species and the New World *Lemmus sibiricus*. In the largest specimen at hand the glans measures 23 per cent of the hind foot length and its diameter is 60 per cent of the length. The rim processes are similar, perhaps shorter and less distinct in this specimen; the urethral process carries a short medial lobe; the baculum equals 88 per cent of the length, and its base is very slightly longer than wide. All of these items, however, fall within or barely without the range of variation observed in *L. sibiricus*.

Microtus arvalis.—The glans is 22 per cent of the hind foot in length and its diameter is 65 per cent of its length. The elongate dorsal lobe is double-peaked and smooth-edged. Between six and eight papillae rise from each ventrolateral sector of the rim. The dorsal papilla has two conules and carries excess spines on its rear flank. The urethral process is bilobed with very slight lateral curvature; the lobes are pointed, however, and the process as a whole is longer than wide.

In the specimens at hand the baculum averages 93 per cent of the glans in length. The base is wider than long and proximally flattened to produce a rectangular shape. In one specimen the shaft is slender and slightly S-shaped in side view; in the other it is thick and club-like; in both, the

ventral view presents parallel sides and virtually no distinction of a head. The medial distal ossicle, constituting 36 per cent of the entire baculum, is well formed, with a wide base and distinct ventral keel; laterally it is of the same thickness from end to end, and its medial portion is arched ventrad. Each lateral ossicle is angular basally but generally fusiform.

The two specimens, both poorly preserved, provide few data for assessing characters of the species. They clearly fit in Group II, and somewhere in the middle of it, but precisely where is questionable. Their structures are variously matched in specimens of *townsendi*, *pennsylvanicus*, *montanus*, *longicaudus*, and *oregoni*, but considering all traits there are more resemblances with specimens of *townsendi*, *longicaudus*, and *oregoni* than with those of other North American species.

Microtus oeconomus.—The glans of this European specimen resembles that of *M. oeconomus* of the New World, but there are a few pronounced differences between the two samples (see description of the North American specimens). The glans-to-hind foot ratio is 20 per cent, the diameter-to-length, 70 per cent. The overall appearance of the glans is short and squat. The dorsal lobe is flattened, and the short and indistinct rim processes number twelve on each ventrolateral rim sector. The dorsal papilla and the urethral process are like counterparts in the New World specimens, but the urethral process is less elongate in the European example.

The baculum is longer than the glans (119 per cent). Its form is essentially like that in the New World specimens, but the head of the proximal bone has pronounced lateral swellings; the medial ossification, 24 per cent of the entire baculum, tapers from a wider base; and the lateral ossicles are larger, 18 per cent of the baculum in length, each angular basally and pointed distally.

Prometheomys schaposchnikowi.—The one specimen at hand is subadult; the lateral digits of the baculum, which are ossified in adults (Ognev, 1948:552), are cartilaginous in this specimen. The soft anatomy distinctly indicates affinities with species of Group I. The glans length is 16 per cent of the hind foot measurement and the diameter equals 47 per cent of the length. The external contours also have the characteristic shape of Group I. The dorsal lobe is only slightly elevated from the remainder of the rim and it is not bulged above the rest of the dorsal face of the phallus. The ventrolateral sectors of the rim are crenate and irregular, but they are not papillose. The dorsal papilla is a single conule set high on the inner wall of the crater and partially exposed above the crater edge. No spines were seen inside the crater. The urethral process is longer than wide and is divided in its distal half into three equal blunt lobes.

SYNOPSIS OF CRANIAL AND EXTERNAL CHARACTERS

Listed below are principal cranial and external characters of North American microtines. These are the ones that have been most used by authors in distinguishing the species and particularly in diagnosing supra-specific taxa within the subfamily. Although most of them are described by Miller (1896), Bailey (1900), Hinton (1926) or Ellerman (1941), a few emerged from our studies of skins and skulls of North American species when we found it necessary to assess both the quality and the inter-specific distribution of the various characters, particularly those of the skull. In checking the published descriptions of these characters against specimens, we studied samples of all North American species the glands of which are herein described; the only lack was skulls, but not skins, of *Microtus guatemalensis*. The study was rather cursory, certainly no detailed analysis of variation in each species, nevertheless it was sufficiently rigorous to achieve the stated purpose.

DENTAL CHARACTERS

POSITION OF LOWER INCISOR ROOT.—The species form a graded series in regard to site of the roots of the lower incisors; therefore, to assign each species to one of two groups on the basis of the characters "root entirely lingual to molar row" and "root labial to the row" is strictly an arbitrary tactic. The following categories are equally arbitrary, but they better indicate the observed variation in site of the roots.

Medial to M_2 – M_3 in *Synaptomys borealis*, *S. cooperi*, and *Lemmus sibiricus*.

Medial to M_3 to slightly posterior to M_3 in *Dicrostonyx torquatus*.

Slightly posterior and labial to M_3 in *Phenacomys intermedius*, *P. longicaudus*, *Lagurus curtatus*, and *Neofiber alleni*.

About midway between alveolus of M_3 and condyle of ramus in *Clethrionomys gapperi*, *Ondatra zibethica*, and the following *Microtus*: *mexicanus*, *californicus*, *oeconomus*, and *longicaudus*.

Farther dorsad on condylar process (nearer condyle) in the following *Microtus*: *ochrogaster*, *pinetorum*, *richardsoni*, *oregoni*, *miurus*, *montanus*, *townsendi*, and *pennsylvanicus*.

LONGITUDINAL GROOVE IN UPPER INCISORS.—Depth and position of any longitudinal groove also varies. A shallow groove occurs sporadically in several species, among which are *Lagurus curtatus* and the following *Microtus*: *richardsoni*, *longicaudus*, *ochrogaster*, and *oeconomus*. A deeper one occurs regularly in *Lemmus sibiricus*, *Synaptomys borealis*, and *S. cooperi*. In *sibiricus* and *borealis* the groove occupies a medial position on the in-

cisor, while in *cooperi* the groove is situated laterally. It is shallower in *borealis* than in *sibiricus*.

WIDTH OF CROWNS OF M^1 - M^3 .—Miller (1896) and others following him recognized that this is a minor and variable character of slight taxonomic value since, again, there is no sharp cutoff point in the graded series. The teeth are gross and wide both anteriorly and posteriorly in *Synaptomys*, *Phenacomys*, and *Lemmus*. Relative to skull size the tooth rows are almost as gross and have but slightly more taper in *M. pinetorum*, *M. mexicanus*, *M. richardsoni*, and *Ondatra*. The cheek teeth are relatively small in *Lagurus*, *M. oregoni*, *M. miurus*, and *Clethrionomys*, perhaps smallest relative to cranial size in the latter genus.

ROOTED MOLARS.—In the following groups of species the cheek teeth develop roots with advancing age (Ellerman, 1941: 550): *Ellobius*, *Promethiomys*, *Ondatra*, *Dolomys*, *Phenacomys*, and *Clethrionomys* (including *Neoschizomys*). They are rooted earlier in *Phenacomys* than in *Clethrionomys* or *Ondatra* (Howell, 1926: 10). In other genera of microtines the pulp cavities usually remain open throughout the life of the animal.

DISTRIBUTION OF ENAMEL ON THE UPPER MOLARS.—In all North American microtines the enamel layer which girds each tooth varies in thickness, and the enamel plates tend to be thin or discontinuous at the apices of each salient angle. The size of the gap between the enamel plates at these apices varies among individuals of a given species and also varies as between species. In the series of specimens that we examined the gaps are widest in *Lemmus*, *Synaptomys*, and *Dicrostonyx*. In these the wide gap is situated on the labial and lingual faces of each salient angle of each cheek tooth and also on the posteromost face of each tooth. A gap occurs at those same sites in the teeth of *Ondatra* and *Neofiber*, but the gap is slightly narrower than in the above-listed forms. In all other North American species examined the enamel plates are more continuous; the gaps usually are slight and only on the labial and lingual apices of the anterocone of each molar, the lingual face of the first lingual angle of M^1 and the posteromost face of each tooth.

OCCUSAL PATTERN OF THE CHEEK TEETH.—That the molar patterns of microtines are highly variable is well known (Miller, 1896; Howell, 1924; Hinton, 1926; Prychodko, 1951; Zimmermann, 1952, 1956; and many others). Each species has its own characteristic pattern, of course, but in each kind studied to date the amount of variation is considerable and such to suggest that molar patterns, which necessarily are in close contact with the environment, are evolutionally labile, relatively easily modified to meet changing environmental conditions.

The molar pattern groupings of species by Miller (1896) and Bailey

(1900) are only some of the several possible combinations of species of like dental patterns. In examining a set of diagrams representing average occlusal patterns of the North American species, we see other possible groupings the scope of which depends upon which tooth or teeth we select as the basis for primary or secondary divisions within the subfamily. Following is a summary of occlusal characteristics of the cheek teeth. M^1 is excluded because its pattern rarely has been considered diagnostic.

M^2 : In all species there are four enamel-bordered dentine sections, the posterior three of which are smaller and more angular than the anterior one. These are set apart by one lingual and two labial folds. Presence and size of lingual fold 2 (the second, counting posteriad) and labial 3 (the third, counting posteriad) vary. Lingual 2 is at most a slight indentation except in *Dicrostonyx* wherein it and a long labial 3 cut off a posterior section, the fifth of the tooth. Labial 3 is also typically present in *Lagurus* and the following *Microtus*: *pinetorum*, *ochrogaster*, *oregoni*, and *richardsoni*; in *pennsylvanicus*, *californicus*, and to a lesser extent in other species of the subgenus *Microtus*, it tends to pinch off a posterolingual knob, thus, a fifth section of the tooth.

M^3 : In most of the species the pattern consists of four sections—a large one preceding three smaller angular parts (one lingual and two labial)—followed by a posterior cingulum. These are set off by two lingual and three labial enamel folds; there may be additional folds in the posterior cingulum. This pattern is seen in *Dicrostonyx*, *Phenacomys*, *Neofiber*, and the following *Microtus*: *oeconomus*, *miurus*, *pennsylvanicus*, *montanus*, *californicus*, *townsendi*, and *mexicanus*. In *Dicrostonyx*, usually unlike any other of these, the long labial 3 fold cuts off another dentine section and, thus, the tooth has five sections plus the remaining part of the posterior cingulum. In *Phenacomys* the labial sections are smaller, relative to lingual ones, than in others of this group.

A slightly different pattern is seen in *Clethrionomys*, *Ondatra*, and the following *Microtus*: *richardsoni*, *longicaudus*, *oregoni*, and *guatemalensis*. In these the short labial fold 3 usually does not meet lingual 2, and the dentine of the fourth section and of the cingulum are confluent; thus, the tooth bears three closed sections plus a fourth confluent with the cingulum.

Simpler patterns are seen in the remaining species, and this simplicity is achieved in quite different ways. In *Lagurus*, *M. pinetorum*, and *M. ochrogaster* there are typically only two labial and two lingual folds, the posterior pair shallow, and the tooth consists of two closed sections; the indistinct third or fourth sections, if present, are confluent with a slight posterior cingulum.

The configuration in *Lemmus* is distinctive. The tooth consists of four

transverse loops, the posterior three joined labially (short labial folds 2 and 3) and the anterior two joined lingually (short or no lingual fold 1). Although distinctive, this pattern is more like those of *Microtus* than is the following one.

In *Synaptomys borealis* and *S. cooperi* the configuration also consists of four transverse loops, but they are formed differently from those of *Lemmus*. Long labial folds 1 and 2 extend almost to the lingual border while labial 3 and lingual 1 and 2 are negligible. The anterior three sections (each quite angular) thus are joined lingually, only the third and fourth being joined labially by enamel.

M_1 : In most of the species the tooth bears six sections preceded by an anterior appendage—anterocone or trefoil. These seven parts are defined by three labial and four lingual enamel folds, the lingual ones of which are typically longer and, thus, the labial sections usually are smaller than the lingual ones; they are relatively smallest in *Phenacomys*. Principal inter-specific differences are seen in size and degree of isolation of the sections and, particularly, in configuration of the anterior part of the tooth—anterior to the basic six sections. The patterns are arranged below approximately in order of increasing complexity.

The simplest scheme is seen in *Synaptomys borealis* in which there are only three separate sections, each acute lingually and spanning the width of the tooth, plus a shorter fourth one which bears a slight cingulum on its anterior face. Labial folds are indistinct or absent.

The pattern in *S. cooperi* and *Lemmus* is slightly different. Longer labial folds cut off a labial section and, thus, in each of these forms the tooth has four sections, the posterior one widest and least angular, plus a fifth which bears an indistinct cingulum on its anterior face.

In *Clethrionomys*, *Lagurus*, *M. pinetorum*, *M. ochrogaster*, and *M. guatemalensis* there are six posterior sections plus a somewhat lobulate anterior cingulum, but the anterior pair of sections tends to be open, the dentine confluent both between them and the cingulum.

In the other species there are usually at least six posterior sections and the anterocone is more or less constricted by a labial and a lingual fold, tending to form a trefoil. The amount of constriction of the anterocone is highly variable within each species, but appears to be greatest, tending to set off both labial and lingual sections of the cone, in the following species of *Microtus*: *miurus*, *townsendi*, *montanus*, and *pennsylvanicus*.

More complex configurations are seen in *Ondatra* and *Dicrostonyx*. In *Ondatra* the anterocone bears two incompletely isolated sections (one labial, the other lingual) in addition to the lobulate remainder of the cingulum; thus, the tooth bears six closed posterior sections preceded by two

confluent ones and a lobulate anterior appendage. In *Dicrostonyx* the anterior pair is isolated and, thus, the tooth has eight closed sections plus an indented anterior cingulum.

M_2 : The pattern in most species consist of four sections preceded by an anterocone, these delineated by two labial and three lingual enamel folds. The posteromost section, the largest, is a full transverse loop, while the smaller anterior three tend to be more angular and restricted to one or the other side of the tooth; although they vary in size, both intra- and inter-specifically, the labial one usually is smallest. The species are grouped below approximately in order of increasing complexity of occlusal pattern of M_2 .

Synaptomys borealis is simplest. The tooth consists of three transverse units joined labially, labial folds being indistinct or absent. Longer labial folds in *S. cooperi* cut off a labial angle and the pattern thus contains two large transverse posterior sections and a small labial one preceded by a slim transverse one which bears a slight cingulum on its anterior face. Long lingual folds are also seen in *Phenacomys* and the tooth pattern is much like that in *S. cooperi*, except that the small anterocone usually is isolated from the large anterior section.

In the other species the lingual folds are shorter and the anterior cingulum is about the size of the anterolabial section. In the following the tooth has three closed sections plus another anterior section which usually is confluent with the anterior cingulum: *Clethrionomys*, *Ondatra*, and the following *Microtus*: *oregoni*, *ochrogaster*, *pinetorum*, *guatemalensis*, and *miurus*. In the following the cingulum is perhaps more often closed off from the posterior four closed sections: *Neofiber*, *Lemmus*, *Lagurus*, and all other *Microtus*. The pattern in *Dicrostonyx* is perhaps the most complex; there are four closed sections preceded by a trilobed cingulum.

M_3 : Although relative lengths of labial and lingual folds in M_1 and M_2 set *Synaptomys* and *Phenacomys* somewhat apart from other forms, those in M_3 do not do so. In the following forms the tooth usually bears three closed transverse sections delineated by two labial and two lingual folds: *Synaptomys borealis*, *Clethrionomys*, *M. oregoni*, *M. richardsoni*, *M. pinetorum*, and all of the subgenus *Microtus*. In the following the second labial fold tends to divide the middle into two parts, thus giving the pattern four sections: *Synaptomys cooperi*, *Phenacomys*, *Neofiber*, *Lagurus*, *M. ochrogaster*, *M. guatemalensis* and *Ondatra*.

The pattern in *Dicrostonyx* is perhaps the most complex. In it there are five closed sections, four of approximately equal size and a small one anterolabially.

OTHER CRANIAL CHARACTERS

STRUCTURE OF THE POSTERIOR PART OF THE HARD PALATE.—In microtines the posterior part of the hard palate tends to be incomplete, the lateral portions perforated by foramina and more or less excavated as posterolateral pits which also usually are perforated. In some forms—for example *Clethrionomys*, *Dicrostonyx*, and *Lemmus*—the palate terminates posteriorly in a more or less complete transverse shelf which may or may not be furnished with a median process; in these, the posterolateral pits pass forward under, that is dorsal to, the palatal shelf and, thus, their medial borders form no part of the ventral face of the palate. In other species the posterolateral pits continue anteriorly into the ventral part of the palate, leaving an undented medial portion—a spine or inclined septum—the sides of which are the medial borders of the posterolateral pits. This sloping median septum may or may not extend over the mesopterygoid fossa. These and other palatal arrangements are described in detail by Miller (1896) and Hinton (1926), but their variational limits within each species are not yet known. It is clear, however, that between any two architectural types there are essentially all degrees of intermediacy.

The species differ in regard to length of the palatal portion of the palatine bones and the location of the palatine-maxillary junction on the midsagittal plane of the skull. Among North American species the palatal portion of the palatines is smallest in *Lemmus*, wherein only a small posterior segment of the palate consists of palatines; the palato-maxillary midsagittal junction is situated posterior to the middle of M^2 . The palatal portion of the palatines is long in *Ondatra*, *Phenacomys*, *Clethrionomys*, *Neofiber*, *Lagurus*, and *M. richardsoni*; in these the palato-maxillary midsagittal junction is situated anterior to M^2 . The other North American forms fall between these two extremes. *Synaptomys cooperi*, but not *S. borealis*, seems to be peculiar in that the palatines and maxillaries fuse very early in life, soon after birth, and their separate identities thereafter are not evident. In the other species the junction of those two bones on the palate is evident to middle or late age.

SIZE AND SHAPE OF THE BASISPHENOID.—There are obvious differences in the basicranial axis among the species. Although we made no attempt to analyze all of the differences, the following characteristics of the basisphenoid will serve to illustrate one of several basic cranial distinctions seen in the species.

In *Synaptomys borealis* and *S. cooperi* the basisphenoid is long and narrow. Posteriorly it is like an hourglass, strongly constricted beside wide and long posterior sphenoidal fissures. The anterior limit of the basi-

sphenoid (its junction with the presphenoid) is situated anterior to the mesopterygoid fossa and is hidden by the hard palate when the skull is viewed ventrally. In *Lemmus* the basisphenoid is not quite as long and is less constricted posteriorly to conform to relatively smaller fissures on each side of the bone.

In all other North American species examined the basisphenoid is short and wide. The posterior part is scarcely or not at all constricted and it is bordered by small foramina. The anterior limit of the bone is situated within the mesopterygoid fossa and is not hidden by the hard palate when the skull is viewed ventrally. Among these species, however, there are differences in regard to dorsoventral depth of the basisphenoid. The bone is shallow in *Clethrionomys* and *Phenacomys*, intermediate in depth in *M. oregoni* and *Lagurus*, and deep in the other forms (excluding *Synaptomys* and *Lemmus*, in which it is also shallow).

SIZE AND SHAPE OF THE ECTOPTERYGOID FOSSAE.—In *Lemmus*, *Ondatra*, *Neofiber*, and *Synaptomys* the ectopterygoid fossae are small and their almost fully osseous walls bear few foramina and no large fenestrae interconnecting each fossa either with the brain cavity or with the mesopterygoid fossa.

In *Clethrionomys* and *Phenacomys* the ectopterygoid fossae are larger and their walls are less completely ossified, there being foramina into the posterolateral palatine pits and small openings leading directly dorsad into the brain cavity; in some specimens there is a slight perforation to the mesopterygoid fossa but no large connection with it.

In the other North American species examined the fossae are as large or larger than in *Clethrionomys* and *Phenacomys* and, in addition, their walls are highly fenestrated, the openings connecting broadly dorsad with the brain cavity, anteriorly with the posterolateral pits, and medially with the mesopterygoid fossa.

POSITION OF THE DENTAL FORAMINA.—Position of the dental foramen as a taxonomic character has been used principally by paleontologists. Its site on each mandible is individually variable within each species and that variation tends to obscure distinctions between species. Its position is related to site of the roots of the lower incisors.

In *Dicrostonyx*, *Phenacomys*, and *Lagurus* it is situated proximally near the level of the molar row. In *Synaptomys*, *Lemmus*, and *Neofiber* its average position is slightly less proximal than in the aforementioned group, but it is still near the level of the molar row. In the other North American species it is situated distally, nearer the tip of the condylar process.

Site of the foramen with respect to the ridge which extends ventrad from the tip of the condylar process also varies. The foramen is situated posterior

to the ridge in *Dicrostonyx*, *Synaptomys*, *Lemmus*, and *Phenacomys*. It usually lies on the ridge or slightly posterior to it in *Neofiber*, *Clethrionomys*, and *Microtus californicus*; on or slightly anterior to the ridge in *M. mexicanus*; and principally anterior to the ridge in the other species.

AUDITORY BULLAE.—There are interspecific differences in size of the auditory bullae and in architecture of their walls. The following information is from Hinton (1926). In the following forms the bullae are large, and in the first three of them the mastoid portion also is somewhat inflated: *Lagurus*, *Chilotus*, *Pitymys*, *Lasiopodomys*, *Phaiomys*, *Dolomys*, and *Synaptomys*. They are moderate in *Pedomys* (but mastoid portion inflated), *Clethrionomys*, *Eothenomys*, *Anteliomys*, *Alticola*, and *Dicrostonyx*; and they are small in *Lemmus*, *Ondatra*, *Neofiber*, *Arvicola*, *Phenacomys*, *Hyperacrius*, *Promethiomys*, and *Ellobius*. The bullae tend to be small in burrowing and amphibious species and larger in open-terrain terrestrial forms.

In the following forms the walls of the bullae are spongy and threads of bony tissue, lined by mucous membrane, partly fill the cavity of the middle ear: *Lemmus* (cavity almost filled), *Dicrostonyx*, *Synaptomys*, *Phaiomys*, *Chilotus*, *Proedromys*, *Microtus*, *Lagurus*, *Lasiopodomys*, *Pitymys*, *Pedomys*, *Neodon*, *Arvicola*, *Herpetomys*, and *Orthiomys*. In the latter six forms the bony network may be more open, and in *Ellobius* and *Promethiomys* the walls contain stout septa. The walls are usually thin and there is slight or no spongy tissue in *Clethrionomys*, *Aschizomys*, *Eothenomys*, *Anteliomys*, *Alticola*, *Hyperacrius*, *Dolomys*, *Phenacomys*, *Ondatra*, and *Neofiber*.

EXTERNAL CHARACTERS

NUMBER OF MAMMAE.—The number of mammae, as reported in the literature, for the various species are as follows: no more than four in *Phenacomys longicaudus*, *M. pinetorum*, and *M. mexicanus*; typically six in *Ondatra*, *Neofiber*, *M. ochrogaster*, and *M. guatemalensis*; and usually eight in all other North American forms.

NUMBER OF PLANTAR TUBERCLES.—The number of plantar pads of the hind foot, as reported in the literature and supplemented by information from our own specimens, is as follows. There are reported to be no tubercles present, or mere vestiges, in *Dicrostonyx*. There are five present on each hind foot in the following: *Neofiber alleni*, *Ondatra zibethica*, *Lagurus curtatus*, *M. richardsoni*, *M. oregoni*, *M. pinetorum*, and *M. ochrogaster*. *M. miurus* is reported to have six tubercles, but there are only five present on some of our specimens. Six tubercles are present in the other

species of the subgenus *Microtus* and in *M. guatemalensis*, *Clethrionomys*, *Synaptomys*, *Phenacomys*, and *Lemmus*.

DISCUSSION

MORPHOLOGICAL AFFINITIES OF THE SPECIES AS INDICATED BY THE GLANS

The glanses of North American microtines, all constructed around a compound baculum, are remarkably similar in external shape and size. Among them there is not the diversity in form that is seen in some other cricetids in which the baculum is a single rod and the glans is architecturally comparatively simple. In *Neotoma* for example, the glans-to-hind foot ratios span 42 per cent and the diameter-to-length proportions have a spread of 88 per cent (Hooper, 1960); comparable ranges in *Peromyscus* are 35 per cent and 38 per cent, respectively (Hooper, 1958). In contrast, in the microtines the glans-to-foot ratios range within 12 per cent and the diameter-to-length within 30 per cent. External shape is similarly constant in microtines; even the divergent species—*Dicrostonyx torquatus*, *Neofiber alleni*, and *Phenacomys longicaudus*—are not as distinctive as variant species of *Neotoma* or *Peromyscus*. Shape and size of glans appear to be evolutionally less labile in species with a complex architecture centered on a four-part baculum. Seemingly the compound baculum has been an evolutionary deterrent to diversity in form of glans.

Nevertheless, microtine species do differ in regard to gross form and size of glans (Tables 1, 2) and there are pronounced interspecific differences in various particular parts of the glans. For example, the rim of the glans' terminal crater may be even in contour, without lobes, as in *M. pinetorum* and *M. mexicanus*, or be divided by grooves into a pair of lateral sectors and a prominent dorsal lobe which extends beyond and overhangs the crater, as in *Clethrionomys*; there are all stages of intermediacy among the species. The surface of the rim is smooth or crenate in some forms (e.g., *Neofiber*, *M. ochrogaster*) and studded with spine-tipped papillae of various sizes in others; the number of rim papillae varies from two (*Phenacomys longicaudus*, *Dicrostonyx torquatus*) to 42 (*Microtus richardsoni*).

There are a number of variable structures within the crater. All forms except *Dicrostonyx* have a dorsal papilla. It consists of a single cone in most species of Group III, two conules in most Group II kinds, and as many as four conules in *Ondatra* and *Neofiber*. Usually each bears a spine or tubercle only on the crest of each cone, but in *M. oregoni*, *longicaudus*, *oeconomus*, *miurus*, *mexicanus*, *fulviventer*, *ochrogaster*, and *pinetorum* the papilla is studded with several tubercles. The bacular mounds vary in size and shape. The medial one is always largest; it is a prominent structure within the crater even in species with small bacular digits. The lateral pair

roughly approximate the lateral digits in size—large in long-digit forms like *Clethrionomys* and small in *Phenacomys longicaudus*, *M. pinetorum*, and other species that have small or no lateral digits, but however small, they are present and discrete in all forms save possibly *Dicrostonyx*.

The urethral process varies in size and shape, ranging from a single short flap with a serrate or lightly lobulate distal border (as in the species listed low in Group III and Table 1), or a long narrow tongue-like structure with accessory lobules (*Neofiber*), to a deeply branched multilobate device with pronounced curvature in its lateral arms (e.g., most species of Group II).

The baculum provides numerous additional characters among which are: size and shape of the proximal segment, which in adults is entirely osseous in all species; shape of the cartilage around the head of the bone (the digital junction) wherein the digits join the main bone; and shape, size and degree of ossification of each of the distal segments. The baculum is as long or longer than the glans in *Lagurus curtatus*, *M. miurus*, and most species listed in Group III; it is shorter than the glans in the other kinds. In most of the long-baculum forms the digital segments are short and the lateral ones tend to be solely cartilaginous or to be absent (Group III), but in *Lagurus* and *M. miurus* the distal segments as well as the proximal bone are long (Tables 1, 2). In these characters, as in others, various degrees of intermediacy are demonstrated by the species.

The phallic characters are distributed among the species in a reticulate pattern, in a manner much like that for cranial or any other systematic traits. Any given character or characters may occur in one or in several species and they may or may not be linked in their distribution. In analyzing this reticulate pattern we find no logical basis for weighting the characters, for considering any one structure in itself—the dorsal papilla, urethral process or baculum, for example—to be taxonomically more important or evolutionally more significant than any other. Therefore, in arranging the species according to similarities of glans we recognize no “key” characters for various taxonomic levels. Rather, we infer that the reticulate character-pattern reflects a similarly branched pattern of relationships. Morphologic affinities of the species, as judged from structure of the glans, are approximately as indicated below.

Dicrostonyx torquatus, *Neofiber alleni*, and *Phenacomys longicaudus* are highly distinctive. Each is well differentiated from the other and set apart from other North American microtines. *Dicrostonyx* is unique in external shape, length of ventral frenum, absence of a dorsal papilla, peculiar configuration of the urethral process and lateral bacular “mounds,” and entire configuration of the baculum. It is second to *Ellobius talpinus* in regard to divergence from the mass of the species studied. If a stubby com-

paratively simple glans (bearing a large frenum, plain crater rim, large ventral shield, shallow spineless crater, no dorsal papilla, simple two-lobed urethral process, and gross basal bone with small, scarcely discrete, distal units and covering mounds) represents the generalized microtine condition, then *Dicrostonyx* is perhaps the most generalized of the North American forms. If the complex and ornate type of glans is basic, then that of *Dicrostonyx* is the most specialized; it clearly fits at one end of the scale. Considering all species here reported on, it is as close to *Synaptomys* or *Phenacomys* as any and may be closer to *Prometheomys*, which we know only from an immature specimen. Similarities with *Synaptomys* have already been pointed out by Hamilton (1946) and Dearden (1958).

Neofiber belongs at the same end of the generalized-specialized scale, but removed from *Dicrostonyx*. In it, too, the glans is stubby and comparatively simple with a shallow crater bordered by a simple rim; but the equally large frenum is differently shaped, the crater is partly spinous and usually has a peculiar inner rim, and the urethral process, bacular mounds, and baculum are different, each in several respects. *Neofiber* resembles *Phenacomys longicaudus* or *P. intermedius* more than any other, but the resemblance is not especially close.

Phenacomys longicaudus also is unique in several features of the baculum, as indicated by Hamilton (*op. cit.*) and Dearden (*op. cit.*), and in other parts of the glans. It is morphologically set apart from other species, but several of its characteristics (form of crater rim, dorsal papilla, and urethral process, for example) approach those of *Neofiber* on the one hand and *Synaptomys* and *Phenacomys intermedius* on the other. Both *Neofiber* and *P. longicaudus* may have stemmed from *P. intermedius*- or *Clethrionomys*-like stock, a stock which also gave rise to *Synaptomys* and, further removed, possibly *Dicrostonyx*. The phallic data are in harmony with such a hypothesis.

Synaptomys borealis and *S. cooperi* differ in number of rim papillae, shape, size, and amount of ossification of parts of the baculum, and in other respects; but the two are morphologically closer than either is to any other species. The characters of both, particularly of *S. borealis*, suggest a fairly close connection with *Phenacomys intermedius* and, as suggested above, the three species may well be part of the same phyletic network which also includes *P. longicaudus*, *Neofiber*, *Dicrostonyx*, and possibly *Prometheomys*. Of all of these *P. intermedius* is clearly nearest the stem that connects them with *Lagurus*, *Clethrionomys*, and other forms with elaborate glandes.

Dearden (1958, 1959) has pointed to the number of meibomian glands in *Lagurus* and to the diversity which is seen in the genus in regard to structure of the baculum; both he and Hinton (1926) believe that *Lagurus*

is primitive and perhaps is derived from some *Phenacomys*-like ancestor. Our data support the hypothesis that *Lagurus* and *P. intermedius* are fairly closely related and they further suggest that the interconnection of *Phenacomys* and *Synaptomys* on the one hand and of *Microtus pennsylvanicus* and allies on the other is through *Clethrionomys*- or *Lagurus*-like stock. In morphology of glans the *Synaptomys-Phenacomys* complex, *Lemmus*, *M. pennsylvanicus*, the *M. pinetorum-ochrogaster* group of species (see below), and possibly also *M. richardsoni*, *M. oregoni*, and *Ondatra* all appear to connect individually with *Clethrionomys*- or *Lagurus*-like stock.

Affinities of *Lemmus* are much as indicated by Hamilton (*op. cit.*) and Dearden (*op. cit.*). In regard to the phallus *Lemmus* differs greatly from *Dicrostonyx* and *Synaptomys*, genera with which it is customarily aligned in classifications, and is closer to *Lagurus*, *Clethrionomys*, and *Microtus*. Its relatively large glans (with differentiated dorsal lobe, papillose rim, large crater, double-coned dorsal papilla, trilobed urethral process, and complete long-digit baculum) compares favorably with the glandes in those forms and suggests that the three are derived from a common ancestral stock. *Lemmus* shows some resemblance to the *Synaptomys-Phenacomys* group, particularly *P. intermedius*, but this is overshadowed by the similarities with *Lagurus curtatus*, *Clethrionomys gapperi*, and *Microtus pennsylvanicus*.

The two species of *Clethrionomys* studied, *gapperi* and *rutilus*, apparently are distinguishable in structure of the glans, and a specimen supposedly of *rutilus* from St. Lawrence Island, Alaska, agrees closely with Tokuda's description (1941) of *rufocanus*. These species are morphologically close to each other, however, and are not far removed from *Lagurus*, *Lemmus*, and three species of *Microtus* (*pennsylvanicus*, *montanus*, and *townsendi*).

Ondatra also fits within that radiating network of forms. It shows several resemblances to those species, particularly in the baculum, and may have closest affinities with one of them, with *C. gapperi* or *C. rutilus* in particular. However its combination of characters—for example, size of glans (the largest, yet relative to hind foot perhaps the smallest), multilobed dorsal papilla, spinous dorsal wall, and ornate urethral process—set it somewhat apart from those and other microtines.

Microtus pennsylvanicus, *M. montanus*, and *M. townsendi* are approximately each equally differentiated from the other, *townsendi* and *pennsylvanicus* being more similar in some features and the additional pairs of this trio matching better in other characteristics. Although each is slightly different, the three form a rather tight group which, like *Lemmus* and *Clethrionomys*, is characterized by a large and elaborate glans and baculum,

the latter equipped with large osseous digits. Their affinities are with *Lagurus*, *Clethrionomys*, and *Lemmus* on the one hand and, perhaps more closely, with *M. longicaudus* and *M. oregoni*.

Some other North American species of *Microtus* form no such compact morphological groups. By reason of unique traits or of peculiar combinations of characters each is distinctive and not easily placed with respect to these and other microtine species; some have no close morphological connection with *M. pennsylvanicus* and allies. The species *longicaudus*, *oeconomus*, *miurus*, and *oregoni* all have similarly proportioned and (excepting *oregoni*) comparatively large glandes, a smooth dorsal lobe, several rim fingers, a dorsal papilla that is spinous on the sides in addition to the tip, and a moderately long baculum equipped with a long and mostly osseous medial digit. In these and other characters these four species variously resemble each other as well as *pennsylvanicus*, *montanus* and, particularly, *townsendi*, but in some respects each is dissimilar. *M. miurus* and *M. townsendi* each has the same number of rim fingers (5-9 per side), a two-coned dorsal papilla and an urethral process of two long hooked lobes, each with a median tubercle; but *miurus* has no lateral bacular ossicles and about one-third of the medial digit is unossified. *M. oeconomus* has the same number of rim fingers, but it has a single-cone dorsal papilla and a three-lobed urethral process. In *M. oregoni* there are three or four fingers per side of rim, two dorsal papilla cones, two long hooked urethral arms, and large ossicles in all bacular digits. To judge from the entire glans, affinities of both *miurus* and *oeconomus* possibly (but questionably) are with *longicaudus* and, slightly more distantly, with *townsendi*; *oregoni* may also tie in there, but it fits almost as well near *Lagurus*.

M. richardsoni is a strongly differentiated species which in morphology of glans is more similar to the Old World *Arvicola terrestris* than to any North American species. The ornately papillose rim, double-coned dorsal papilla, and two large urethral arms (disregarding its spines) suggest affinity with *Clethrionomys* or *M. pennsylvanicus*, but the entire baculum and its crater mounds do not conform, rather they point to possible kinship with some long-base incomplete digit forms such as *pinetorum* or *ochrogaster*. Its closest affinities may lie with Old World species.

As already delineated on preceding pages the characters of *M. californicus* are in most respects between those of *M. guatemalensis* and the *M. ochrogaster-pinetorum* group on the one hand and species with more ornate glandes (e.g., *M. townsendi* and *M. pennsylvanicus*) on the other. Resemblances of *californicus* with *guatemalensis* and *ochrogaster* are fairly close, perhaps as close as with *townsendi*, *pennsylvanicus*, or *oeconomus*, and to

judge from the glans the first three could be offshoots of the same minor phyletic branch.

Microtus ochrogaster, *M. mexicanus*, *M. fulviventer*, and *M. pinetorum* constitute a compact morphological assemblage. *M. mexicanus* and *M. fulviventer* are similar, perhaps identical, and both are close to *M. pinetorum* such that the three make up one of the tightest morphological groups of North American microtines; the distinctions between the three are perhaps less than between *pennsylvanicus*, *montanus* and *townsendi*. *M. ochrogaster* is slightly farther removed from *pinetorum* and *mexicanus* (the differential characters pointing toward *californicus* and its southern ally, *guatemalensis*), but the resemblances overshadow the differences and suggest close relationship of those three species, *ochrogaster* linking *pinetorum* and *mexicanus* with *californicus*.

It is clear that those species are morphologically similar, and they may be closely interrelated, but it is less certain as to where they fit in a scale of specialization. On the basis of general simplicity of glans and its parts they might be aligned near other simple-glans species, *Phenacomys longicaudus* and *Synaptomys cooperi* for example. And perhaps that is where they naturally belong, for in *P. longicaudus* and *S. cooperi* as well as in *M. mexicanus*, *M. fulviventer*, *M. ochrogaster*, and *M. pinetorum*, the glans is comparatively small and simple, with an indistinct or no dorsal lobe, plain nonpapillose rim (one papilla per side in *longicaudus*), single-cone dorsal papilla, flaplike urethral process, small lateral bacular mounds, short partly osseous medial digit, and small or no lateral digits. These similarities are impressive, but on the other hand these two groups of glanses are dissimilar in total aspect; they "look different." This is strictly a subjective quality, but it is bolstered by a few quantities. In contrast to the glanses of *P. longicaudus* and *S. cooperi*, those of the *M. mexicanus-pinetorum* assemblage are stubby rather than elongate (see diameter-length ratios, Table 2), the ventral shield is larger, and the baculum is not only longer with respect to both glans and hind foot, but it is also different in shape. Because of these and other distinctions we view the glans of the *mexicanus-pinetorum* group as a different morphologic type (possibly representing an evolutionary line quite apart) from that leading to *P. longicaudus* and *S. cooperi*. The latter species appear to tie through *Phenacomys intermedius* to *Clethrionomys* and *Lagurus* while the *mexicanus-pinetorum* assemblage seems to connect through *californicus* to *townsendi* and *pennsylvanicus*. Both the *S. cooperi* and *M. mexicanus* assemblages may belong at the same end of a scale of specialization, but they appear to represent quite different parts of the reticulate evolutionary pattern of North American microtines.

In summary, the following species cluster closely in regard to structure

of the glans: *M. mexicanus*, *fulviventer*, *pinetorum*, and *ochrogaster*, the latter, however, slightly set apart from the other three; *pennsylvanicus*, *montanus* and *townsendi*, the latter two most similar; *C. gapperi* and *C. rutilus*; *S. cooperi* and *S. borealis*. The other species are more discrete, but in various degrees they may fit best as follows: *M. guatemalensis* with *californicus*, the latter between *ochrogaster* and *townsendi*; *M. longicaudus* with the *montanus-townsendi* group; and the more distinctive *miurus*, *oeconomus*, and *oregoni* each may (through *longicaudus*) tie in to *montanus-townsendi* or to *Lagurus*. *M. richardsoni* fits well with no other North American species. The species of the *pennsylvanicus-townsendi* group together with *Lagurus* and *Lemmus* tie to *Clethrionomys*; *O. zibethica* and *P. intermedius* individually also to *Clethrionomys*; and *Synaptomys* to *P. intermedius*. The most divergent species are *P. longicaudus*, *N. alleni*, and *D. torquatus*.

A glans equipped with a deep terminal crater, papillose rim, multiconed dorsal papilla, multilobed urethral process, three large bacular mounds and three large osseous distal segments (as seen in *Clethrionomys* for example) is comparatively elaborate. Because it is ornate it may be considered to be specialized, although the special functions or conditions to which its parts are particularly fitted are unknown. Possibly it is a specialization of the Muroidea, in contrast to the Gliroidea or Dipodoidea for example. But at the same time it may represent the primitive microtine condition. Three observations suggest the hypothesis that an ornate glans may be primitive in the Microtinae. (1) The complex glans constructed around a four-part baculum is the usual and widespread type in the Muridae and Cricetidae. If, as generally believed, the Microtinae and Murinae, or Microtinae and Cricetinae are derived from a common ancestral stock characterized by a simple glans and baculum, then the complex type complete with appurtenances would subsequently have to be acquired independently in each subfamily (unless, of course, the subfamilies as now understood are erroneously constituted). It seems unlikely that the four-part baculum and associated structures were acquired independently in each of the three subfamilies. (2) The small lateral bacular mounds that apparently contain no cartilage or bone (as in *M. richardsoni*, *M. miurus*, and some other species) have the aspect of vestiges. The mounds for the lateral digits are present but digits are absent. To be sure, these small mounds with small or no digits may represent incipient stages in phyletic development, but with equal or more reason they may be taken as remnants of a former more complete state. (3) A complex glans, such as in *Clethrionomys* or *Phenacomys intermedius* for example, qualifies well as a morphotype from which the microtine species are derivable in a manner that is in harmony with cranial

data and with current thinking in regard to interrelationships and classification of the species. This hypothesis—that in the Microtinae there are trends toward simplification of glans—is reasonable, but at present there are no precise data either in support of it or contrary to it.

CLASSIFICATION

Modern classifications of the Microtinae are based upon Miller's review of the genera and subgenera of voles and lemmings published in 1896. Since then new species have been described and there have been numerous differences of opinion as to the number and content of various microtine taxa, but the morphological range of the subfamily remains much as when defined by Miller (1896). The only significant increases in scope have been the addition of *Promethiomys* by Satunin (1901), *Ellobius* (to Arvicolidae) by Tullberg (1899), and *Brachytarsomys* by Ellerman (1941) following Hinton's (1926) suggestion. There is reasonably good basis for accepting *Promethiomys* and *Ellobius* within the subfamily, but on both zoogeographic and morphologic grounds it remains doubtful that *Brachytarsomys* should be included (see Vorontsov, 1959); it is omitted from the present discussion.

While the morphological span of the subfamily has remained much the same, viewpoints as to interrelationships of the species have varied considerably. Following is a summary of several principal opinions, expressed in terms of number of subgeneric, generic, and supergeneric groups within the subfamily.

Miller (1896) grouped all of the Recent species known to him in 14 subgenera, seven genera, and two supergeneric groups. Later (1912: 610) he estimated that the subfamily "contains about 30 groups, genera or subgenera, the status of which is still imperfectly understood. These fall naturally into three main subdivisions the *Lemmi* . . . , the *Microti* . . . , and the *Ellobii*."

Hinton (1926) raised several of the subgenera of Miller to generic rank and in addition he recognized others which had been described since Miller's initial synopsis. He grouped all of the known species into eight subgenera, 28 genera, and two supergeneric groups, *Lemmi* and *Microti*.

Simpson (1945) listed 21 valid genera contained in three tribes, namely the *Lemmini*, *Microtini*, and *Ellobiini*. Ognev (1948: 390–397) recognized 13 subgenera and 22 genera which he grouped in four "supergenera," the *Lemmi*, *Microti*, *Ellobii*, and *Fibrini*, the latter composed of the genera *Phenacomys*, *Ondatra*, *Clethrionomys*, *Dolomys*, and *Prometheomys*.

Ellerman (1941) listed all microtine species in 12 subgenera, 29 genera, and three supergeneric groups which excluded Ognev's heading, *Fibrini*.

Later (1949: 111-115) he concluded that several of his genera should be reduced to a lower level and, if we understand him correctly, he would recognize 20 subgenera, 22 genera, and three supergeneric groups, namely the *Brachytarsomyes*, *Lemmi*, and *Microti*; *Ellobius* is included within the *Microti*.

There are similar differences of opinion with respect to the microtines of North America. According to Miller (1896) the North American species then known should be grouped in nine subgenera of seven genera and two supergeneric groups. Hinton (1926), working with a larger number of species than was known to Miller, concluded that there were five subgenera and 15 genera contained in two supergeneric groups. Miller and Kellogg (1955) considered valid nine subgenera, 13 genera, and two tribes, while Hall and Kelson (1959), writing of the same fauna, recognized ten subgenera and nine genera.

These inconsistencies and fluctuations in classification are to be expected for it is particularly within subfamilies that phyletic relationships are stressed, and in the absence of an adequate fossil record phyletic estimates are likely to be as diverse as sentiments of the classifiers. All classifications of the subfamily have been typological. Emphasis has been on morphological types or kinds, and all reflect both the usual taxonomic practice of weighting characters and the procedure of assigning particular significance to some traits. For example, in 1833 Lataste (*vide* Miller, 1896: 23) considered the characters derived from the teeth of voles to be of no value except in distinguishing between genera. He arranged the subgenera on the basis of number of mammae and plantar tubercles. Miller (1896), holding a different view, based his classification on the following characters which, to him, were the more important ones and ". . . the ones least adapted to the special needs of the different animals, and hence less likely to vary . . .": form of skull, structure of bony palate, pattern of enamel folding, number of mammae, number of plantar tubercles, and presence or absence of musk glands on the sides. On the basis of these characters, he concluded that: "The members of the subfamily *Microtinae* fall naturally into two supergeneric groups, the *Lemmi* and *Microti*, or lemmings and voles. The former includes the genera *Synaptomys*, *Lemmus*, and *Dicrostonyx*, the latter the genera *Phenacomys*, *Evotomys*, *Microtus*, and *Fiber*." These two groups are defined by a number of characters, but of these, only dental characters are truly restrictive, and it is clear that Miller, in contrast to Lataste, considered the teeth to be paramount in classifying the *Microtinae*. Most other students of the subfamily have shared this opinion.

Howell (1924: 1015; 1926: 11), however, in discussing growth and variation of microtine teeth, pointed out that there is no radical difference in

the development of the rooted and rootless teeth, that occlusal patterns (*especially* of M^3 and M_1) are exceedingly variable within populations, and that these and other conditions of the root and crown apparently represent specializations for certain foods or manner of feeding. He (Howell, 1926) questioned that the evidence gave adequate support for "taking the teeth as a criterion of the greatest importance in judging the systematic position of the genus [*Phenacomys*], as is usually done." Subsequent variational studies of microtine teeth have served to bolster this viewpoint and to give additional force to the opinion that teeth constitute no panacea in classification of microtines. Neither does the glans penis; it merely adds additional data to the total available for estimates of microtine interrelationships.

In the present review of principal characters of skull, skin, and glans we think that the total evidence points to the following conclusions.

1. Assuming that the primitive microtines were scampering, terrestrial or slightly scansorial herbivores, then adaptive radiation of the group has proceeded in two principal directions, namely toward fossorial and toward aquatic life, and in each there were accompanying trends toward hypsodonty and the development of massive zygomata and skulls. Of present day forms *Clethrionomys* or *Eothenomys* approximates the morphotype from which the others may be derived. It is characterized by moderate size of eyes, ears, tail, and feet, the latter with six planter pads; low, comparatively smooth skull with slight zygomata; short, wide, shallow basisphenoid; moderate-sized ectopterygoid fossae with slight fenestration dorsally and anteriorly; complete hard palate containing long palatal portions of the palatines and without lateral palatal pits; thin-walled (non-spongy) auditory bullae; slight, brachyodont, rooted molars with a simple occlusal pattern; moderately long lower incisors, the roots situated in the ascending arm of the ramus; ungrooved upper incisors; and an ornate glans penis containing an osseous four-part baculum.

2. In regard to suprageneric groups, the highly reticulate evolutionary pattern in the Microtinae is disguised, rather than revealed, by the recognition of either the two groups *Lemmi* and *Microti* (Miller, 1896; Hinton, 1926; Ellerman, 1941) or the three groups *Lemmini*, *Microtini* and *Ellobiini* (Simpson, 1945). *Ellobius* is the most distinctive and a case could be made for excluding it from the Microtinae. If it is retained it best qualifies for tribal separation from the remainder of microtines. However, if there is sound basis for recognition of *Lemmini* in addition to *Ellobiini* and *Microtini*, then there is equal reason for recognizing eight tribes, not merely three or four. These should be constituted as follows but not necessarily in this order: (a) *Ellobius*; (b) *Promethiomys*; (c) *Dicrostonyx*; (d) *Synaptomys*, *Myopus*, and *Lemmus*; (e) *Clethrionomys*, *Eothenomys*, *Antelionomys*,

Aschizomys (the latter three possibly no more than subgenera of *Clethrionomys*), *Alticola*, *Hyperacrius*, *Dolomys*, and *Phenacomys*; (f) *Neofiber*; (g) *Ondatra*; (h) *Lagurus*, *Arvicola*, and *Microtus* (including *Blandfordimys*, *Neodon*, *Pitymys*, *Pedomys*, *Herpetomys*, *Orthriomys*, *Phaiomys*, *Proedromys*, *Lasiopodomys*, *Chilotus* and *Microtus* of authors). Thus, we think the evidence is best served by recognizing no tribes, two tribes (*Ellobiini* and *Microtini*), or eight tribes, namely *Ellobiini*, *Prometheomyini*, *Dicrostonychini*, *Lemmini*, *Clethrionomyini*, *Neofibrini*, *Ondatrini* and *Microtini*. From the standpoint of morphology of Recent species the third alternative is preferred, but in the absence of an adequate fossil record the second choice (two tribes, *Ellobiini* and *Microtini*) may be called for. Kretzoi (1955), however, believes that the known record evidences a number of independent lines and he recognizes 12 suprageneric groups of fossil and Recent microtines or microtine-like forms.

3. In regard to North American Recent species the data suggest the following:

Cranially, externally, and phallically, *Dicrostonyx* stands well apart from all other forms and more than any other it qualifies for tribal separation. There are more reasons for a wider taxonomic gap between it and *Microtus* than between *Lemmus* and *Microtus*. It does not belong with *Lemmus* since it is no more similar to that form or to *Synaptomys* than to *Neofiber* or, even, *Lagurus*. Among its unique characters, in addition to those of the glans, are: small ears; plain soles, with slight or no plantar and palmar pads; white winter pelage; large winter foreclaws; prominent peg-like postorbital processes; and complex enamel pattern, the most complicated among voles. Other characteristics are listed by Hinton (1926). *Dicrostonyx* is highly distinctive and Kretzoi's estimate that it "will yet be classed with the most ancient independent branches" of microtine-like forms well may prove to be correct.

Synaptomys and *Lemmus* are each strongly characterized genera. Characters of the glans suggest close affinities of *Lemmus* and *Clethrionomys* and the two are similar in some cranial characters (for example depth of basisphenoid and shape of hard palate), but for the most part *Lemmus* is nearer *Synaptomys*. Among the characteristics of both are: long, narrow, shallow basisphenoid; short palatal portions of palatines, small ectopterygoid fossae; spongy auditory bullae; hypsodont cheek teeth with simple patterns; grooved upper incisors and comparatively short lower incisors. Excepting the lengths of basisphenoid and palatines these characters are also seen in various other microtine genera. *S. cooperi* and *S. borealis* are distinct cranially, externally, and in phallic characters, and there is sound but perhaps inadequate basis for the subgenera *Synaptomys* and *Mictomys*.

Phenacomys intermedius and *P. longicaudus* have quite different habits, mammary count, glandes, and external appearance, but they are similar cranially. There is insufficient basis for subgenerically separating the two species. Some of their characters suggest a fairly close relationship of *Phenacomys* and *Clethrionomys*.

The distinctive morphology and habits of *Neofiber alleni* warrant at least generic recognition. Its affinities are unclear, but it appears to be well removed from *Microtus* as evidenced, for example, by the structure of the auditory bullae, position of lower incisor root, and of dental foramina, length of palatines, nature of ectopterygoid fossae, number of meibomian glands (Quay, 1954), and structure of the glans penis. Characters of the glans suggest that *Neofiber* represents an independent line stemming directly from stock which also gave rise to *Phenacomys* and *Clethrionomys*.

The strongly differentiated *Ondatra zibethica* also warrants at least generic recognition. Its small and mostly enclosed ectopterygoid fossae, non-spongy auditory bullae, long palatines, rooted molars, and characters of the glans suggest closer connection with *Clethrionomys* than with *Microtus* or *Arvicola*, but long independence from any of these.

Although unique in several characters (e.g., inflation of audital region of skull), *Lagurus curtatus* is morphologically somewhat between *Phenacomys intermedius*, *Clethrionomys gapperi*, and species of *Microtus*. Authors generally agree that *Lagurus* is generalized and primitive in most respects, and our data are in harmony with that viewpoint.

The species *M. (Aulacomys) richardsoni* should be transferred from *Microtus* to *Arvicola*. Its glans resembles that of *Arvicola terrestris*, and both Miller (1896) and Zimmermann (1955) contend that both species belong in the same supraspecific taxon. If their appraisals are correct, and present evidence indicates that they are, *Aulacomys* becomes, at most, a subgenus of *Arvicola* and the name of the American water vole is *Arvicola richardsoni*. We have studied no skulls and skins of Old World *Arvicola*.

M. miurus is sufficiently differentiated cranially, phallically, and in regard to meibomian glands (Quay, 1954) to warrant subgeneric separation from other species of *Microtus*. However, *M. oregoni* is not, although Matthey (1957) indicates a peculiar chromosome count for *oregoni*. In our view if *Chilotus (M. oregoni)* is recognized, there is as much reason for assigning *M. oeconomus* and *M. arvalis* each to a separate subgenus; to do so, however, would overemphasize the distinctness of each of those species.

Miller (1896) and others following him have pointed out the many similarities of species of *Pitymys* and *Pedomys*. We think that the two forms are so close that they should be arranged as subgenera of the one genus, *Pitymys*, or that *Pitymys (sensu lato)* be considered a subgenus of *Microtus*.

Furthermore, that taxon should also include *Microtus mexicanus* and the similar and probably conspecific *M. fulviventer*; those two forms are more similar to *Pitymys pinetorum* than to *Pedomys ochrogaster*. There is no question that *pinetorum* (with *quasiater*), *mexicanus* (with *fulviventer*), and *ochrogaster* are distinct species, but to list each in a different genus is to mask their general likeness and to misrepresent their apparent relationships both with each other and with other species of *Microtus*. We think the data are best served by arranging each as a species group of the one subgenus, *Pitymys*, of the genus *Microtus*.

It is definitely questionable that *M. (Herpetomys) guatemalensis* warrants subgeneric status, and *M. (Orthriomys) umbrosus* likewise seems unworthy of supraspecific segregation, but we have insufficient data on those species to form a firm opinion.

The remainder of the species studied, namely *pennsylvanicus*, *montanus*, *townsendi*, *longicaudus*, and *californicus* fit along with *oeconomus* and *oregoni* in the one subgenus *Microtus*.

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Accepted for publication November 9, 1961

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