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MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 82

The Meibomian Glands of Voles and Lemmings (Microtinae)

BY

WILBUR B. QUAY

ANN ARBOR
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CONTENTS

ILLUSTRATIONS

Plates

(Plates I-III follow page 17)

Figures in the Text

THE MEIBOMIAN GLANDS OF VOLES AND LEMMINGS (MICROTINAE) *

INTRODUCTION

IN the eyelids of mammals there are enlarged, sebaceous-type glands not associated with hairs during any stage of their development. These are the Meibomian (glands of Meibom) or tarsal glands. They are situated in the dense connective tissue plate or tarsus that supports the free edge of each eyelid. In microtines the glands may be clearly seen from the conjunctival side of the eyelids, in either fresh or preserved specimens, as small white lobules extending from the tarsi in which their ducts are embedded. Owing to the flat, platelike nature of the eyelids, the enclosed Meibomian glands branch and expand primarily in one plane. This makes their structure easier to visualize and to interpret.

The embryological development of the Meibomian glands in various mammals has been described in detail for the white mouse by Klee (1921) and for the white rat by Addison and How (1921). The primordia of the glands were first seen in the 15-day-old mouse embryo and in the 21-day-old rat embryo. Thus, their appearance is early. The full complement of glands is present at birth.

The morphology of the tarsal glands in domesticated, laboratory, and common European species of mammals has been described in a number of short articles by European anatomists and histologists. The articles containing information on the tarsal glands of microtines are those by the following authors: Loewenthal (1931a, b, c, and 1932a, b) on the field vole and several rodents of other groups; Vesely (1923) on *Microtus arvalis*; Vrtis (1929) on *Microtus arvalis, Arvicola amphibius* [= *Arvicola schermani*?], *Fiber* [= *Ondatra*] *zibethica*, and rodents of other groups; and Sulc (1929) on *Evotomys* [= *Clethrionomys*] *glareolus* (Schreber), *Arvicola schermani* (Shaw), *Microtus arvalis* (Pallas), and *Fiber* [= *Ondatra*] *zibethica* L. These authors discovered that there is much variation in the number and morphology of the glands in rodents and that this variation has taxonomic and evolutionary significance. Vrtis (1929) found that some squirrels, *Spermophilus citellus* and *Sciurus vulgaris*, have small, evenly spaced, and similar glands, numbering about 40 in the upper and lower eyelids. In certain other rodents the number of glands is reduced, and the glands present are increased in size. For species of microtines the most extensive information on tarsal glands is provided by Sulc (1929), who described the variations in detail and recognized a phylogenetic reduction in the number of tarsal glands in his series of four species, *Clethrionomys glareolus* having the greatest number of glands of least modification and *Ondatra zibethica* having the least number of glands.

These earlier studies indicated that a further study of the number and morphology of tarsal glands in microtines would be worth while. The subfamily contains 25 genera, according to the classification

* Accepted for publication July 21, 1953.

followed here, and a large number of species arranged in subgeneric or species groups that are poorly understood. Further investigation of the variation of the tarsal glands in the subfamily was thought desirable in order to demonstrate the trend of gland reduction within the subfamily. The variation and trends in the Meibomian glands, if sufficiently well analyzed, should aid in understanding the morphological relationships of the groups within the subfamily.

Taxonomy

The generic and species names used for microtines included in this report follow Ellerman's (1941) usage in most instances. For some North American species, however, the taxonomy used is more recent. The reader is referred to Hall and Cockrum (1953) for the most recent review of North American microtine systematics. The taxonomy which I have followed is one of convenience and of general, although tentative, acceptance.

Materials and Methods

The most satisfactory material for study of variation in tarsal glands was found to be whole mounts of eyelids stained in a supersaturated solution of Oil blue N in 50 per cent isopropanol. In the course of the study 350 whole mounts were made, representing 14 genera and 47 species of microtines. These are listed in Table I. Serial paraffin sections of the eyelids and their glands from various species comprising 10 genera were also made, but were not found to be of as much interest.

Specimens, glands of which are illustrated in Plates I-III, are given their respective collection numbers in the accompanying legends. The collections concerned are abbreviated as follows: AMNH, American Museum of Natural History; CNHM, Chicago Natural History Museum; MCZ, Museum of Comparative Zoology, Harvard University; QC, W. B. Quay collection; UMMZ, University of Michigan Museum of Zoology; USNM, U. S. National Museum.

Acknowledgments

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Division of Mammals I am most grateful for the opportunity of pursuing this work in the Division of Mammals and for timely aid. I wish to thank also the curators of other collections and the collectors who supplied specimens of certain otherwise unavailable microtine species.

MORPHOLOGY AND TERMINOLOGY

For orientation it is wise first to consider the basic morphology of the eyelids, the structures adjacent to the tarsal glands, and the terminology that has been introduced by earlier writers.

At the anterior corner of the eye the eyelids are separated by the lacrimal caruncle, a small mound of skin bearing a tuft of convergent hairs which point posteriorly, and a well-developed plica semilunaris containing a cartilage plate. At the posterior corner of the eye the eyelids appear externally to be continuous, but a division between upper and lower lids can be assigned to the spot where the duct of the exorbital, or preparotid, lacrimal gland opens onto the palpebral rim.

In many microtines the tarsal glands at the posterior corner of the eye become greatly enlarged and extend posteriorly along the duct of the exorbital lacrimal gland. Since the glands no longer lie within the eyelids, they have been called extrapalpebral sebaceous glands by Loewenthal (1931a). In those microtine species with considerable loss of the tarsal glands the reduction in number occurs primarily in the center of the eyelids, so that the glands are clustered at the anterior and posterior ends of both the upper and lower eyelids. Sulc (1929) employed a terminology for the tarsal glands, using a numbering system starting from each corner of both upper and lower eyelids. Thus, the most posterior gland in the upper lid was called glandula tarsalis posterior superior prima, and the next one anteriorly was called secunda; the most anterior gland in the upper lid was called glandula tarsalis anterior superior prima, and the next one posteriorly was called secunda, and so on. This seems to me to be a somewhat laborious procedure and often a confusing one as well, since in many species of microtines and in most other rodents there are no distinct gaps between the anterior and posterior tarsal glands to be used as convenient markers.

INDIVIDUAL VARIATION

The most easily studied aspect of variation in tarsal glands is the number of glands present. This has been the phase emphasized by previous writers. Studies have not been made, however, of the possible correlation between gland number and age, sex, or hormonal condition of the individual. The complete set of glands is said to be obtained before birth, but this statement is based upon embryological evidence, and the subsequent history of the glands has not been well documented.

TABLE I

The Number of Tarsal Glands in Species of Microtinae

For each species the number of glands occurring in the dorsal eyelid, the ventral eyelid, and in both eyelids together is shown. In each microtine specimen examined the eyelids and their glands were studied on only one side of the specimen; therefore, each microtine specimen examined provided one figure each for number of glands in the dorsal eyelid, for number of glands in the ventral eyelid, and for the number of glands in both dorsal and ventral eyelids. In a few specimens, however, either the dorsal or the ventral eyelid and its glands had been damaged in such a way that the number of glands in the damaged eyelid could not be accurately determined. These specimens provided a figure for only the number of glands in the undamaged eyelid.

N= number of specimens, $\bar{x}$ = mean gland number, R = observed range in gland number, s = standard deviation.

Genus and Species	NUMBER OF GLANDS											
	Dorsal Eyelids				Ventral Eyelids				Both Eyelids			
	N	$\bar{x}$	R	s	N	$\bar{x}$	R	s	N	$\bar{x}$	R	s
Dicrostonyx groenlandicus	5	12.8	7-15	. . .	5	11.6	7-15	. . .	5	24.4	14-29	. . .
hudsonius	2	13.5	13-14	. . .	2	10.0	9-11	. . .	2	23.5	22-25	. . .
Synaptomys cooperi	10	11.1	9-13	1.3	10	10.2	9-12	1.2	10	21.3	18-25	1.9
Lemmus lemmus	3	11.6	11-13	. . .	3	11.3	10-13	. . .	3	23.0	22-24	. . .
trimucronatus	8	11.7	8-16	. . .	8	10.7	9-13	. . .	8	22.5	18-27	. . .
Clethrionomys glareolus	16	9.6	6-12	1.8	16	10.1	7-13	1.9	16	19.8	14-25	3.2
rufocanus	3	10.3	9-12	. . .	3	10.0	10-10	. . .	3	19.5	19-20	. . .
mikado	1	9.0	9	. . .	1	8.0	8	. . .	1	17.0	17	. . .
gapperi	73	8.9	3-13	1.6	70	8.3	3-12	1.8	70	17.2	6-24	3.0
brevicaudus	3	11.6	11-13	. . .	3	10.3	10-11	. . .	3	22.0	21-23	. . .
californicus	1	11.0	11	. . .	1	9.0	9	. . .	1	20.0	20	. . .
Phenacomys intermedius	4	12.7	12-13	. . .	4	11.0	9-13	. . .	4	23.7	22-25	. . .
longicaudus	4	8.7	8-9	. . .	4	8.2	7-10	. . .	4	17.0	15-19	. . .
Eothenomys melanogaster	1	7.0	7	. . .	1	8.0	8	. . .	1	15.0	15	. . .
fidelis	2	10.5	9-12	. . .	2	9.0	9-9	. . .	2	19.5	18-21	. . .
proditor	2	8.5	8-9	. . .	2	8.0	8-8	. . .	2	16.5	16-17	. . .
olitor	1	6.0	6		1	4.0	4		1	10.0	10	

Anteliomys custos	1	9.0	9	. . .	1	8.0	8	. . .	1	17.0	17	. . .
Arvicola terrestris	5	2.6	2-3	. . .	5	1.4	1-2	. . .	5	4.0	3-5	. . .
amphibius	2	5.0	3-7	. . .	2	3.0	2-4	. . .	2	8.0	5-11	. . .
Microtus oregoni	4	3.2	2-5	. . .	4	1.2	0-3	. . .	4	4.5	2-8	. . .
richardsoni	9	4.1	2-7	. . .	9	2.3	0-5	. . .	9	6.4	3-12	. . .
pennsylvanicus	51	2.8	1-9	1.4	53	0.1	0-2	0.4	51	2.9	1-11	1.6
montanus	3	3.3	2-4	. . .	3	0.3	0-1	. . .	3	3.6	3-4	. . .
longicaudus	48	3.2	2-9	1.5	48	1.3	0-5	1.2	48	4.5	2-14	2.5
townsendi	1	5.0	5	. . .	1	0.0	0	. . .	1	5.0	5	. . .
californicus	10	4.2	3-6	0.9	10	1.9	1-3	0.9	10	6.1	4-9	1.4
mexicanus	6	3.8	2-7	. . .	6	1.5	0-3	. . .	6	5.3	4-9	. . .
mogollonensis	4	3.0	2-4	. . .	4	2.5	2-3	. . .	4	5.5	4-7	. . .
xanthognathus	1	2.0	2	. . .	1	1.0	1	. . .	1	3.0	3	. . .
arvalis	16	2.7	2-5	1.0	16	1.9	1-3	0.6	16	4.6	3-7	1.3
agrestis	5	2.8	2-4	. . .	5	1.0	1-1	. . .	5	3.8	3-5	. . .
oeconomus (palaearctic)	4	3.2	1-8	. . .	4	3.2	1-6	. . .	4	6.5	3-14	. . .
o. operarius	11	2.4	2-3	0.5	11	2.3	1-4	0.9	11	4.6	3-6	1.5
o. innuitus	1	2.0	2	. . .	1	3.0	3	. . .	1	5.0	5	. . .
nivalis	2	2.0	2-2	. . .	2	2.0	2-2	. . .	2	4.0	4-4	. . .
ochrogaster	4	4.0	3-7	. . .	4	2.2	2-3	. . .	4	6.2	4-10	. . .
miurus	4	7.5	5-9	. . .	4	2.0	2-2	. . .	4	9.5	7-11	. . .
Phaiomys leucurus	1	2.0	2	. . .	1	2.0	2	. . .	1	4.0	4	. . .
Pitymys subterraneus	1	2.0	2	. . .	1	3.0	3	. . .	1	5.0	5	. . .
savi	1	3.0	3	. . .	1	2.0	2	. . .	1	5.0	5	. . .
pelandonius	1	3.0	3	. . .	1	1.0	1	. . .	1	4.0	4	. . .
pinetorum	6	2.5	2-5	. . .	6	0.5	0-3	. . .	6	3.0	2-8	. . .
nemoralis	1	3.0	3	. . .	1	1.0	1	. . .	1	4.0	4	. . .
Lagurus pauperrimus	3	2.7	1-4	. . .	3	0.3	0-1	. . .	3	3.0	1-5	. . .
Neofiber alleni	5	8.6	6-13	. . .	5	10.8	5-12	. . .	5	17.6	11-25	. . .
Ondatra zibethica	3	3.6	2-5	. . .	3	2.6	2-3	. . .	3	6.3	4-8	. . .

To check for possible relationships between age or sex and the number of tarsal glands present, 52 specimens (35 males, 17 females) of *Clethrionomys gapperi*, collected during July and August in the states of Oregon, Idaho, Montana, North Dakota, Wyoming, and Colorado, were examined critically. For accurate sex determination each animal was dissected. The appraisals of age in my study were based upon cranial measurements, since it was desirable to compare gland number and age quantitatively and since no true numerical estimate of age could be made. As an index to relative age the sum of three composite skull measurements was taken for each specimen. The measurements, condylobasilar length, condylozygomatic length, and alveolobasilar length, were used, since Howell (1924:993-99) defined them well and made an intensive study of their variation and significance in another microtine, *Microtus montanus yosemite.* The three measurements were taken by Howell's methods. The specimens were then listed in two columns, one for each sex, in the order of relative age as indicated by the cranial measurements. The average number of glands in groups of specimens taken from different segments of these columns was never significantly different. Scatter diagrams of summed cranial measurements plotted against total tarsal gland number were made for each sex separately. These further demonstrated the lack of correlation between relative age and tarsal gland number.

Likewise, the relative size of the tarsal glands was not found to change with age, nor was there any size difference that could be correlated with sex or season.

In a series of 16 specimens of *Microtus longicaudus* the eyelids from both orbits were studied. These showed that the number of glands was frequently different on opposite sides of the head in corresponding eyelids, but that this variation in gland number in corresponding eyelids of the same individual is far less than the variation in corresponding eyelids of different individuals in the same population.

TAXONOMIC VARIATION

The data on the number of tarsal glands occurring in all species of microtines examined in this study are presented in Table I. This information is primarily intended for those who wish to examine the data critically for particular species or groups. The variation in total gland number within the subfamily is seen to better advantage in Figure 1. In this chart the dots are the means; the straight lines on the same axes as the dots are the ranges. The ends of the rectangles enclosing the dots and crossing the range lines stand for the 95 and 99 per cent confidence limits of the means of the populations (by the method of Kenney and Keeping, 1951:184-85). It may be assumed, therefore, with a certain degree of confidence that the actual mean of the population occurs within the enclosed area and that the difference between the means of two populations is significant at a certain confidence

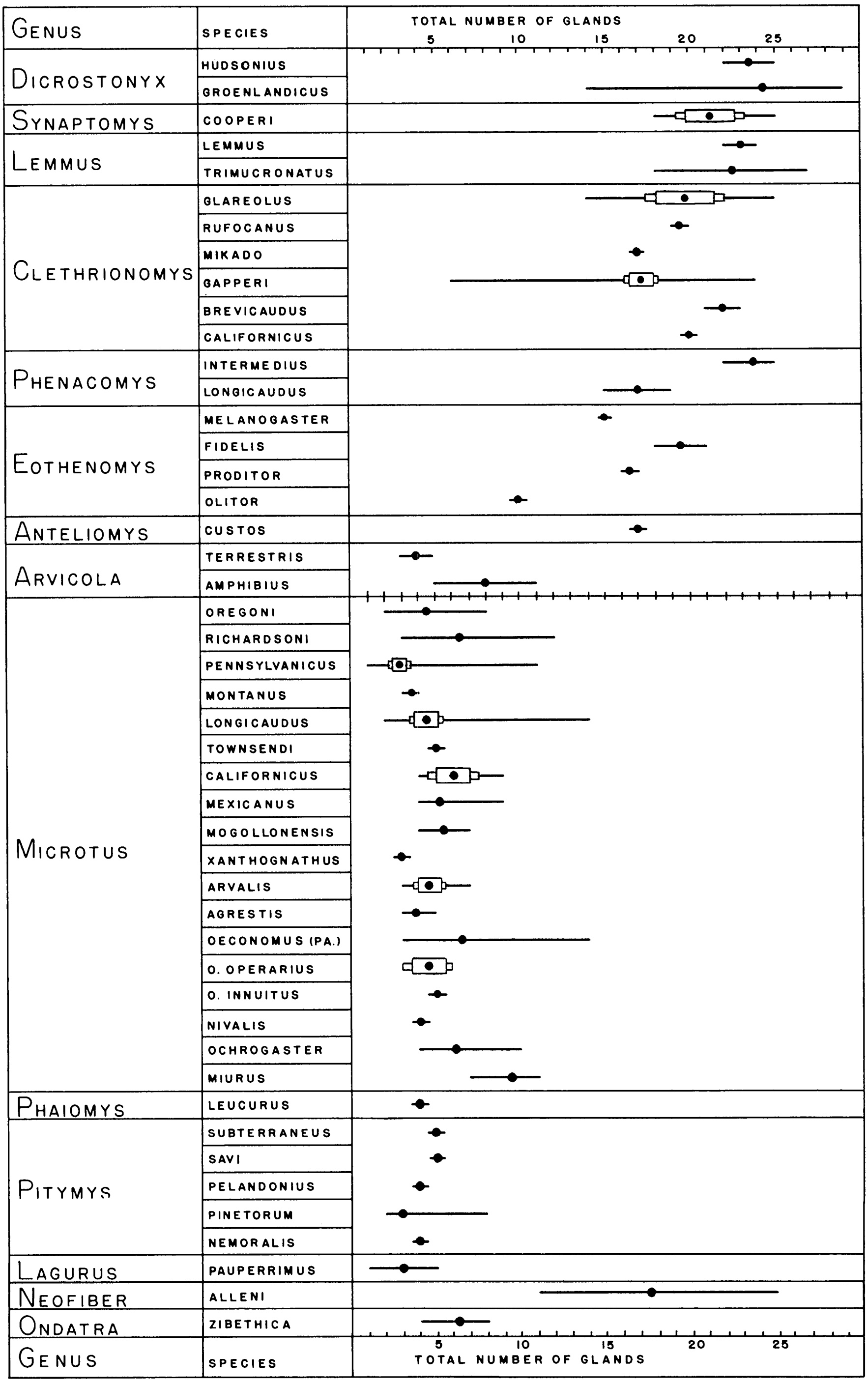

FIG. 1. The total number of tarsal glands occurring in different genera and species of microtines.

The mean number for each species is shown by a dot, the range by a line on the same horizontal axis as the dot, and the 95 and 99 per cent confidence intervals for the mean of the population by rectangles enclosing the dot. For the numerical data used, see Table I.

level. Thus, the difference between the mean gland number of *M. pennsylvanicus* and that of *M. longicaudus* is significant at the 5 per cent level, but not at the 1 per cent level; and the difference between the mean gland number of *M. pennsylvanicus* and that of *M. californicus* is significant at both the 5 and 1 per cent levels. These statistical notations are useful only when the samples are of a satisfactory size, since the confidence limits spread out on either side of the sample mean as the sample size decreases. Figure 1 illustrates the great differences in tarsal gland number within the subfamily and shows that the number of tarsal glands is a well-defined characteristic of taxonomic groups. Besides the differences between species and between genera that are shown here, there is a trend in the reduction in gland number which corresponds rather well in some cases to the phylogenetic position assigned by Hinton (1926) to these genera of microtines on the basis of cranial and dental morphology. Thus, the most primitive Microtinae, the Lemmi, have the least reduction; and of these the most primitive genus, *Dicrostonyx*, has a shade less reduction than the two other lemming genera. Among the voles *Clethrionomys*, one of the most primitive genera, has the least gland reduction. The greatest gland reduction has occurred in the genera *Arvicola*, *Microtus*, *Phaiomys*, *Pitymys*, *Lagurus*, and *Ondatra*.

In Figure 2 the trend in gland reduction is further analyzed in terms of the positions occupied by the various genera and of the relative amount of reduction in dorsal and ventral eyelids. The reduction appears to have occurred symmetrically in the two eyelids throughout the subfamily, except possibly within the genus *Microtus*, which shows some variation in regard to relative number of glands lost in dorsal and ventral eyelids. In *Microtus (Stenocranius) miurus* there is a surprising number of glands in the dorsal lid, considering the great reduction in number in the lower lid (see Pl. II). Plates I, II, and III show the morphological patterns typifying the various genera and species. It will be noted that: (1) the tarsal glands of the lower lid are usually shorter than those of the upper lid; and (2) as reduction in gland number occurs, it is most pronounced in the center of the eyelids and is compensated for in some degree by enlargement of the extrapalpebral glands posteriorly. The inferior extrapalpebral gland varies greatly from species to species, sometimes practically equaling the superior gland (as in *Lemmus lemmus*), and in many species is absent in nearly all individuals.

The distribution of the variation in gland number in three species is shown by histograms (Fig. 3). These represent the frequency distribution of the number of glands in 70 specimens of *Clethrionomys gapperi*, 51 of *Microtus pennsylvanicus*, and 48 of *Microtus longicaudus*. It will be noted that as the number of glands decreases, the frequency distribution becomes more skewed and that the modal number of glands expresses the characteristic pattern within a species better than does the mean. Patterns of this sort emphasize the differences between species, and show where such differences occur, to better advantage than do mean values.

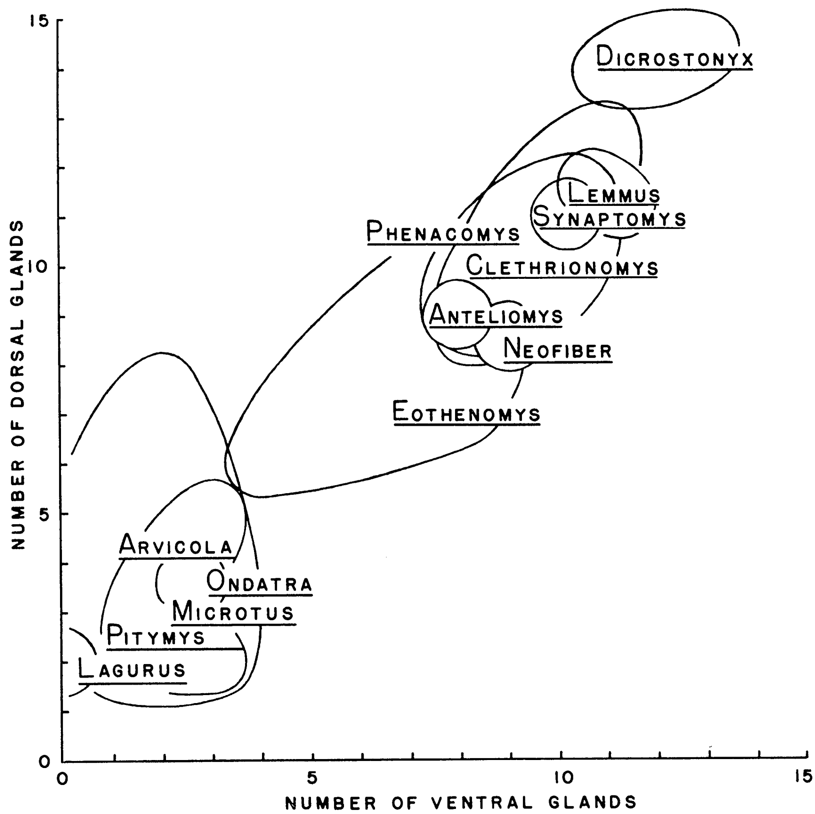

FIG. 2. Graphic representation of the symmetrical and phylogenetic reduction in the number of tarsal glands in certain genera of microtines.

The area enclosed around each genus indicates the location of the mean values for the different species within the genus.

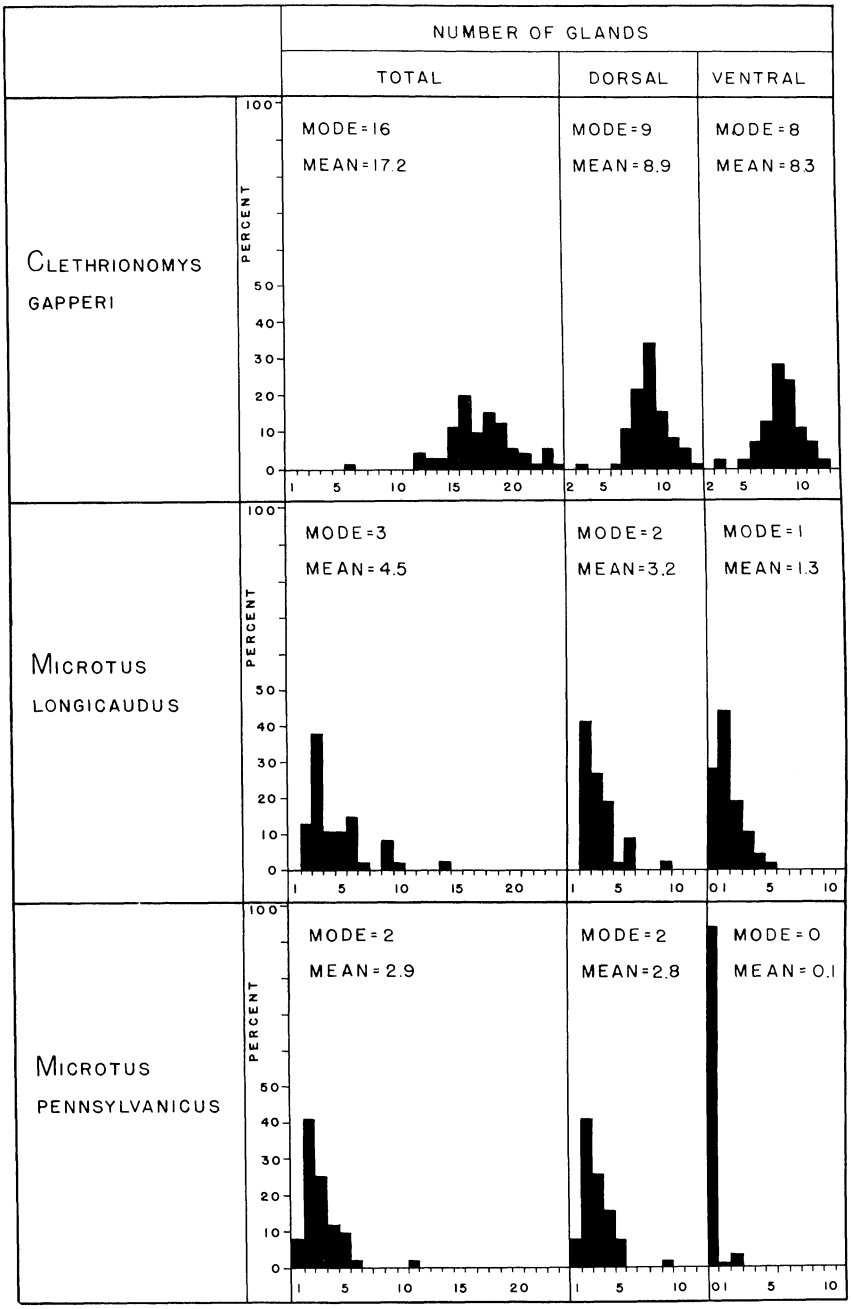

FIG. 3. Frequency distribution of the number of tarsal glands in three species of voles, based on 70 specimens of *Clethrionomys gapperi*, 48 of *Microtus longicaudus*, and 51 of *Microtus pennsylvanicus*, taken from widely scattered localities in their respective ranges. Each vertical bar represents the per cent of the sample which has a particular number of glands. Dorsal refers to glands in the upper eyelid. Ventral refers to glands in the lower eyelid. Total refers to the total number of glands, or the sum total of both dorsal and ventral glands.

The functional or adaptational significance of the changes in Meibomian gland pattern seen in voles and lemmings is obscure. It would appear that the reduction in gland number is balanced by the increase in the size of the remaining glands, especially the extrapalpebral glands. In some of the burrowing species, such as *Microtus oregoni* and *Pitymys pinetorum*, the lengths of the eyelids are reduced and the size of the tarsal glands relative to the size of the eyelids is greater than in other species. One possible explanation for the reduction in gland number and increase in gland size is that fossorial or burrowing habits in the subfamily have been associated with reduction in eye size and the need for increased secretory protection. With the occurrence of smaller eyelids increased tarsal gland development would have to extend beyond the orbit. For reasons yet obscure, the increased development has occurred primarily in a posterior direction and in the superior palpebral glands. In microtine species which are but slightly if at all fossorial, whose eyes are but slightly reduced in size, and in whose eyelids tarsal gland reduction has left vacant areas centrally, one wonders whether the present tarsal gland morphology is a holdover from an ancestral fossorial adaptation and whether the eyes and eyelids have secondarily enlarged. When burrowing rodents of other subfamilies were examined, however, no such enlargement was seen in the tarsal glands. But it should be pointed out that in considering the adaptive significance of tarsal glands in different rodents, one must take into account also the degree of development and functional state of the other orbital glands.

The aquatic genera *Neofiber* and *Ondatra* show several interesting parallels in their tarsal glands. (1) The large tarsal glands are crowded and tend to be fused at the posterior angle of the eyelids. (2) Over most of the length of the eyelids there are only small filiform tarsal glands, similar to those seen in squirrels. (3) The enlarged tarsal glands are compacted together and do not follow the duct of the exorbital lacrimal gland posteriorly. In these characteristics *Ondatra* is more advanced than *Neofiber*, since the crowding and fusing of the enlarged glands is more extensive and since there are fewer of the filiform glands.

SUMMARY

Study of 350 whole mounts of eyelids and their Meibomian glands from 14 genera and 47 species of microtine rodents demonstrates that:

1. Variations in Meibomian gland number cannot be correlated with sex, season, or age.
2. The number of Meibomian glands present and their morphology and location are species characteristics.
3. Within this subfamily of rodents (Microtinae) a reduction in gland number occurs along with an increase in the size of the remaining glands, especially the most posterior ones, which extend beyond the region of the eyelids as extrapalpebral glands.

4. The reduction in gland number occurs nearly equally in upper and lower lids and primarily in their mid-region.

5. The trends in Meibomian gland number and morphology parallel in many instances the currently accepted phylogeny of the subfamily. Thus, the primitive genera have glands which are more numerous, smaller, and more nearly equal in size than do the more advanced genera.

6. One possible explanation for the reduction in gland number and increase in gland size is that fossorial habits in the subfamily have been associated with reduction in eye and eyelid size and with an increased need for secretory protection of the eye.

7. The glandular morphology of the aquatic genera *Neofiber* and *Ondatra* is strikingly similar and is more advanced in the latter.

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PLATE I

Camera lucida drawings of the tarsal glands of microtines. (The anterior corner of the eye is at the left.)

Dicrostonyx groenlandicus, adult female (QC 3-C-112); Baffin Island; right eyelids.

Dicrostonyx hudsonius, adult female (USNM 190376); Chimo, Ungava, May, 1883; left eyelids.

Lemmus lemmus, male (UMMZ 57796); Mjosen Lake, Norway, October 18, 1926; right eyelids.

Lemmus trimucronatus, juvenile female (QC 3-C-174); Nunivak, Alaska; right eyelids.

Synaptomys cooperi (QC 3-C-103); Preble Co., Ohio, February 6, 1950; right eyelids.

Clethrionomys brevicaudus, female (UMMZ 76577); Pennington Co., South Dakota, August 28, 1935; right eyelids.

Clethrionomys rufocanus, male (QC 3-C-92); Tokyo, Japan, September-November, 1950; right eyelids.

Clethrionomys californicus, male (QC 3-C-273); Lane Co., Oregon, July 18, 1951; right eyelids.

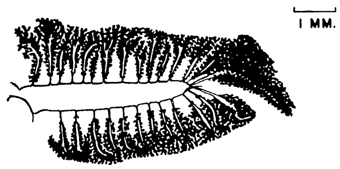
Clethrionomys glareolus, adult female (UMMZ 97673); near Helsinki, Finland, October 7-10, 1950; right eyelids.

Clethrionomys mikado, male (QC 3-C-91); Tokyo, Japan, September-November, 1950; right eyelids.

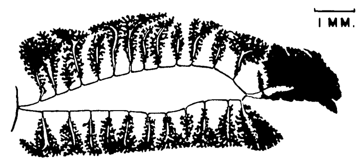
Phenacomys intermedius, male (QC 3-C-311); Teton Co., Wyoming; right eyelids.

Phenacomys longicaudus, adult female (USNM 206390); Carlotta, Humboldt Co., California, February 18, 1915; left eyelids.

PLATE I

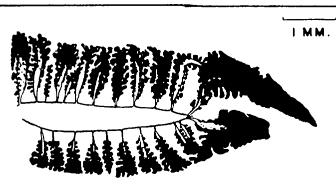


DICROSTONYX GROENLANDICUS

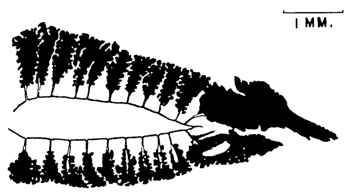


DICROSTONYX HUDSONIUS

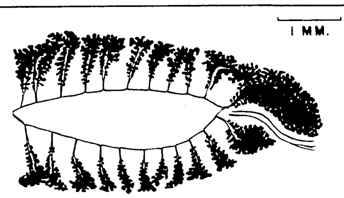
LEMMUS LEMMUS



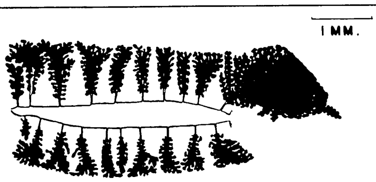
LEMMUS TRIMUCRONATUS



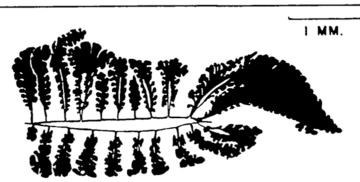
SYNAPTOMYS COOPERI



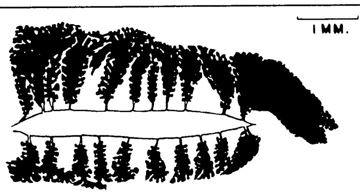
CLETHRIONOMYS BREVICAUDUS



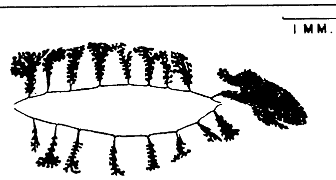
CLETHRIONOMYS RUFOCANUS



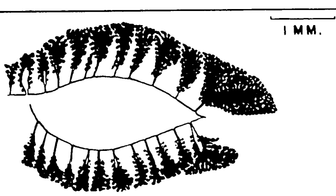
CLETHRIONOMYS CALIFORNICUS



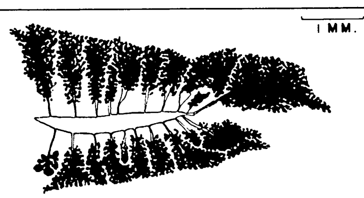
CLETHRIONOMYS GLAREOLUS



CLETHRIONOMYS MIKADO



PHENACOMYS INTERMEDIUS



PHENACOMYS LONGICAUDUS

PLATE II

Camera lucida drawings of the tarsal glands of microtines. (The anterior corner of the eye is at the left.)

Eothenomys melanogaster, adult male (AMNH 44875); Mu-cheng, Salween Dr., Yunnan Prov., China, February 9, 1917.

Eothenomys fidelis, adult male (AMNH 44831); Lichiang, Yunnan Prov., China, October 6, 1916; left eyelids.

Eothenomys proditor, adult male (AMNH 44803); Lichiang, Yunnan Prov., China, October 30, 1916; left eyelids.

Anteliomys custos, adult female (AMNH 44934); Lichiang, Yunnan Prov., China, October 22, 1916; left eyelids.

Arvicola amphibius, adult male (CNHM 48291alc.); Leicestershire, England; left eyelids.

Microtus richardsoni, female (QC 3-C-361); Teton Co., Wyoming, July 26-27, 1951; right eyelids.

Microtus miurus, adult male (MCZ 45234); Seward Peninsula, Alaska, July 9, 1948; right eyelids.

Microtus ochrogaster, male (UMMZ 75010); Custer Co., Nebraska, July 20, 1934; right eyelids.

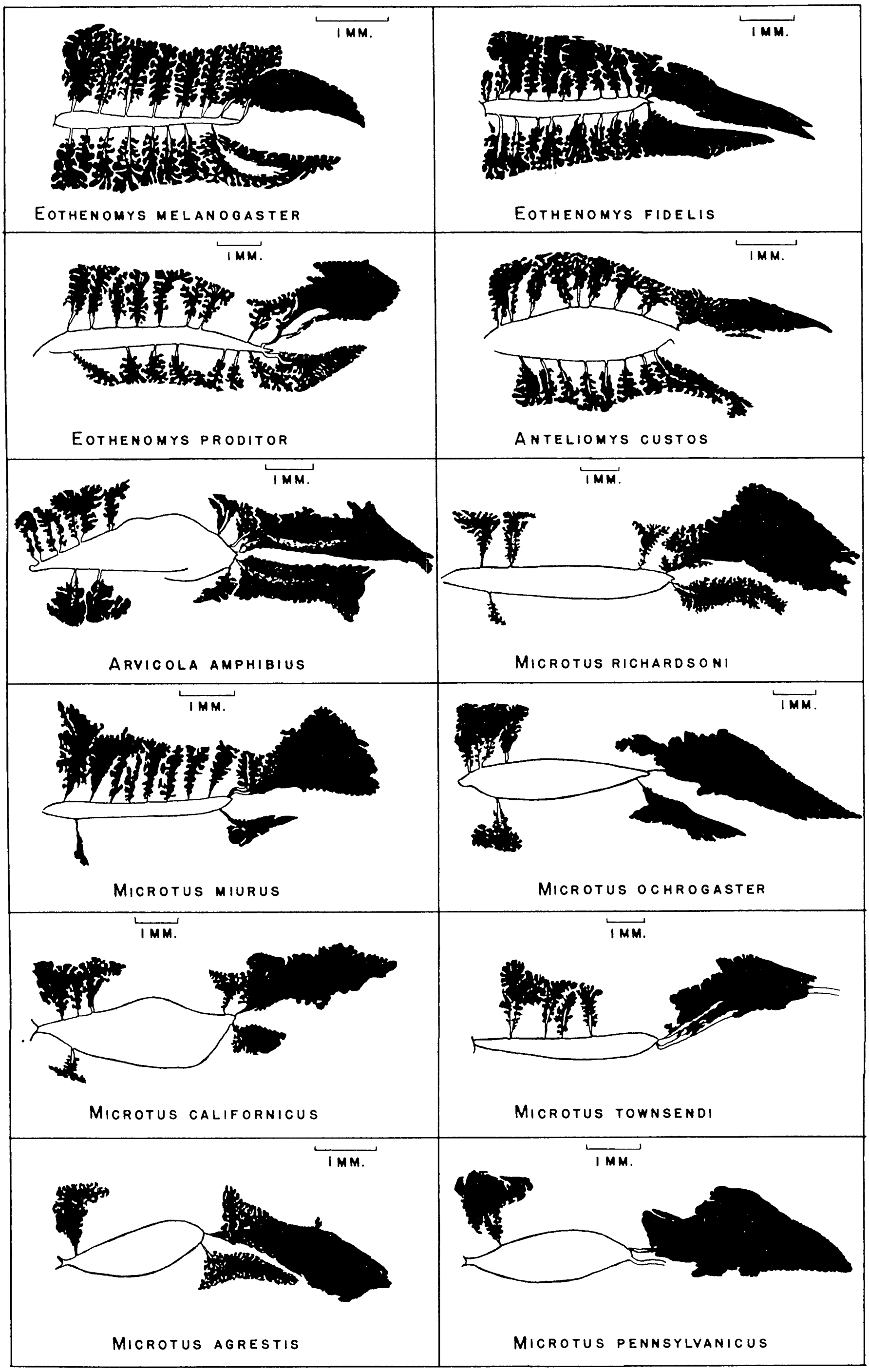
Microtus californicus, female (QC 3-C-471); Contra Costa Co., California, July 25, 1951; right eyelids.

Microtus townsendi, female (UMMZ 52938); Mason Co., Washington, August 9, 1919; right eyelids.

Microtus agrestis, female (QC 3-C-485); Furstenwalde, Spree, Germany, December, 1950; right eyelids.

Microtus pennsylvanicus, female (UMMZ 53275); Ramsey Co., North Dakota, July 19, 1920; right eyelids.

PLATE II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Eothenomys melanogaster
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Eothenomys fidelis
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Eothenomys proditor
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Anteliomys custos
1 MM.
Arvicola amphibius
1 MM.
Microtus richardsoni
1 MM.
Microtus miurus
1 MM.
Microtus ochrogaster
1 MM.
Microtus californicus
1 MM.
Microtus townsendi
1 MM.
Microtus agrestis
1 MM.
Microtus pennsylvanicus

PLATE III

Camera lucida drawings of the tarsal glands of microtines. (The anterior corner of the eye is at the left.)

Microtus arvalis, female (QC 3-C-477); Furstenwalde, Spree, Germany, November, 1950; right eyelids.

Microtus montanus, male (QC 3-C-294); Harney Co., Oregon, July 21-22, 1951; right eyelids.

Microtus oeconomus, adult male (MCZ 45246); Seward Peninsula, Alaska; right eyelids.

Microtus nivalis, male (QC 3-C-510); Piemonte, Italy, August, 1951; right eyelids.

Microtus mexicanus, adult female (QC 3-C-167); Distrito Fed., Mexico, January 25, 1950; right eyelids.

Phaiomys leucurus, adult male (USNM 84125); Ladak, Kashmir, India; left eyelids.

Microtus oregoni, male (QC 3-C-248); Humboldt Co., California, July 12-13, 1951; right eyelids.

Pitymys pinetorum, adult male (USNM 283094); Nicholas Co., West Virginia, May 28, 1943; left eyelids.

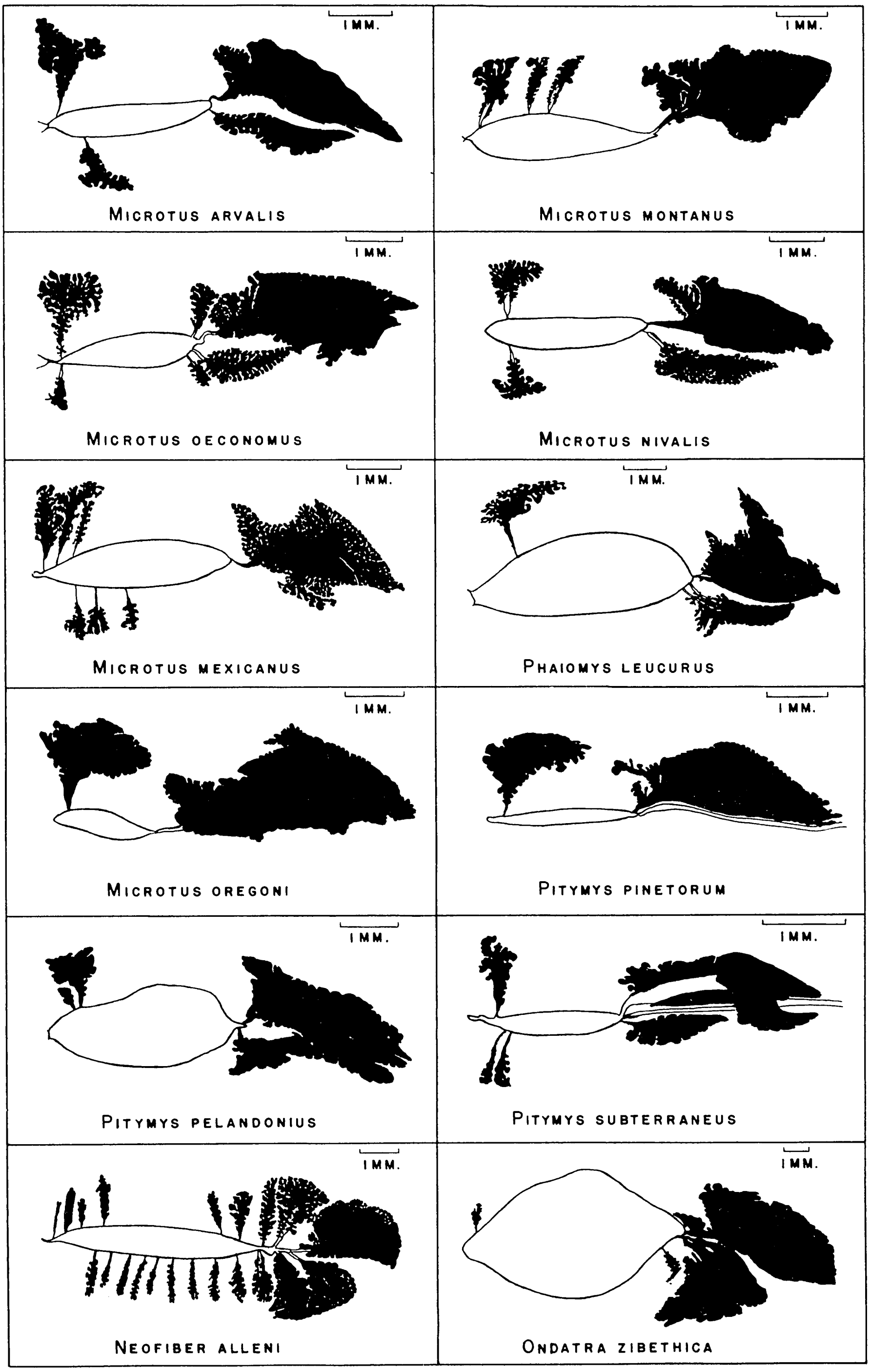
Pitymys pelandonius, adult male (USNM 172327); Silos, Prov. of Burgos, Spain, October, 1906; left eyelids.

Pitymys subterraneus (QC 3-C- 84); Esztergomi, Hungary, 1925; right eyelids.

Neofiber alleni, adult female (QC 2-E-8); Putnam Co., Florida, April 13, 1950; right eyelids.

Ondatra zibethica, male (QC 3-C-371); Washtenaw Co., Michigan, August 14-15, 1951; right eyelids.

PLATE III


1 MM.
MICROTUS ARVALIS
1 MM.
MICROTUS MONTANUS
1 MM.
MICROTUS OECONOMUS
1 MM.
MICROTUS NIVALIS
1 MM.
MICROTUS MEXICANUS
1 MM.
PHAIOMYS LEUCURUS
1 MM.
MICROTUS OREGONI
1 MM.
PITYMYS PINETORUM
1 MM.
PITYMYS PELANDONIUS
1 MM.
PITYMYS SUBTERRANEUS
1 MM.
NEOFIBER ALLENI
1 MM.
ONDATRA ZIBETHICA

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