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MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 83

The Comparative Myology of the Mammalian Genera *Sigmodon*, *Oryzomys*, *Neotoma*, and *Peromyscus* (Cricetinae), with Remarks on Their Intergeneric Relationships

BY

GEORGE C. RINKER

ANN ARBOR
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CONTENTS

	Page
Introduction	7
Acknowledgments	7
Discussion of the Subfamily Cricetinae	8
Remarks on the Genera Studied	10
Objectives of the Study	11
Materials	12
Methods	13
Arrangement and Terminology of the Muscles	14
Description and Comparison of the Muscles	15
Branchiomeric Musculature	15
Masticatory Group	15
Internal Pterygoid Group	18
Mylohyoid Group	19
Superficial Facial Group	19
Hyoid Constrictor Group	36
Glossopharyngeal Group	38
Trapezius Group	38
Lingual Group	41
Myotomic Musculature	42
Dorsal Division	42
Superficial Spino-occipital Group	42
Sacrospinalis Group	42
Semispinalis Group	46
Suboccipital Group	51
Ventral Division	51
Cervical Prevertebral Group	52
Lumbar Prevertebral Group	53
Caudal Flexor Group	53
Medial Ventral Cervical Group	54
Lateral Cervical Group	55
Medial Thoracoabdominal Group	57
Lateral Thoracoabdominal Group	58
Diaphragma	63
Perineal Group	63
Appendicular Musculature	66
Muscles of the Pectoral Girdle and Limb	66
Extensor System	66
Costo-spino-scapular Group	66
Latissimus-subscapular Group	68
Deltoid Group	70
Suprascapular Group	71
Triceps Group	72
Extensor Group of the Forearm	73
Flexor System	77
Pectoral Group	77
Flexor Group of the Arm	79
Flexor Group of the Forearm	81
Flexor Group of the Manus	83

Page

Muscles of the Pelvic Girdle and Limb 87
Extensor System 87
Iliacus Group 87
Gluteal Group 88
Quadriceps Femoris Group 91
Tibial Extensor Group 93
Peroneal Group 95
Flexor System 96
Adductor Group 96
Ischiotrochanteric Group 98
Hamstring Group 100
Flexor Group of the Leg 106
Flexor Group of the Pes 109
Discussion and Conclusions 116
Myological Problems 116
Intergeneric Relationships 116
Literature Cited 121

ILLUSTRATIONS

Figures

(Figures 1-18 follow page 125)

Figure

1A. Lateral view of the superficial muscles of the masticatory group in *Sigmodon*.
B. Lateral view of the deeper muscles of the masticatory group in *Sigmodon*.
2. Lateral view of the superficial facial muscles in *Sigmodon*.
3. Dorsal view of superficial facial muscles in *Sigmodon*.
4A,B. Lateral views of the superficial facial muscles of the rostrum in *Sigmodon*.
5. Lateral views of M. buccinatorius and associated muscles in (A) *Sigmodon*, (B) *Oryzomys*, (C) *Peromyscus*, and (D) *Neotoma*.
6A. Comparison of M. digastricus in *Neotoma* and *Sigmodon*.
B. Ventral view of the submandibular region in *Sigmodon*.
C. Ventral view of deeper levels of the submandibular region in *Sigmodon*.
7A. Lateral view of the intrinsic back muscles in *Sigmodon*.
B. Schematic representation of M. longissimus.
C. Schematic representation of M. iliocostalis.
D. Schematic representation of M. semispinalis dorsi.
E. Sketch of the shorter fascicles of the transversospinal and intertransverse systems in the lower thoracic region.
F. Schematic representation of M. semispinalis capitis and M. longissimus capitis.
G. Schematic representation of M. longissimus cervicis.
8. Ventral view of anterior half of *Sigmodon*.

Figure

9A. Lateral view of neck and thorax of *Sigmodon*.

B. Sketch showing the relationships of Mm. obliquus abdominis externus and internus to the inguinal ligament.

10A. Ventral view of the perineal region in *Sigmodon*.

B. Lateral view of the structures associated with the urethra, anus, and penis in *Sigmodon*.

C. Ventral view of the same.

11. Dorsal view of the anterior part of the body of *Sigmodon*.

12A. Lateral view of the anterior limb of *Sigmodon*.

B. Same as A with many of the superficial muscles removed.

13A. Medial view of the anterior limb of *Sigmodon*.

B. Medial view of the forearm of *Sigmodon*.

C. Sketch showing the manner in which the three heads of M. flexor digitorum profundus unite to form a common tendon in (1) *Sigmodon*, (2) *Neotoma*.

14A. Sketch of left manus of *Sigmodon*.

B. Same as A after removal of the tendon of M. palmaris longus.

C. Dissected view of the same.

D. The deep palmar muscles in *Sigmodon*.

E. The dorsum of the manus of *Sigmodon*.

15A, B, C. Progressively deeper views of the lateral aspect of the posterior limb of *Sigmodon*.

D. Lateral view of the thigh of *Sciurus vulgaris*.

16A. Sketches showing the origin of M. rectus femoris in (1) *Sigmodon*, (2) *Neotoma*, (3) *Oryzomys*, and (4) *Peromyscus*.

B. Diagrammatic representation of cross sections through the posterior pelvic region of (1) *Mustela frenata*, (2) *Sciurus vulgaris*, (3) *Tamias striatus*, and (4) *Sigmodon hispidus*.

C. Medial aspect of the thigh of *Oryzomys*.

D. Medial aspect of the thigh and ventral lumbar region in *Sigmodon*.

17A. Medial view of the leg and foot of *Sigmodon*.

B. Lateral view of A.

C. The dorsum of the foot of *Sigmodon*.

18A, B, C, D. Views of the plantar aspect of the feet of *Peromyscus*, *Neotoma*, *Sigmodon*, and *Oryzomys*, respectively.

E. (1) Plantar, (2) dorsal, and (3) side views of the tendinous rings which surround the tendons of M. flexor digitorum fibularis and M. flexor digitorum profundus in the foot and hand of *Sigmodon*.

F. Plantar aspect of the foot of *Sigmodon*.

G. Deeper view of the same.

H. The deep plantar muscles in *Sigmodon*.

THE COMPARATIVE MYOLOGY OF THE MAMMALIAN GENERA *SIGMODON*, *ORYZOMYS*, *NEOTOMA*, AND *PEROMYSCUS* (CRICETINAE), WITH REMARKS ON THEIR INTERGENERIC RELATIONSHIPS*

INTRODUCTION

KNOWLEDGE of the gross morphology of many of even the most common rodents is very incomplete. Although there has been some recent revival of interest in this field, there are many areas in which the surface has hardly been touched. One of these is the use of comparative gross anatomy in attempts to systematize the lower taxonomic categories. Although this does not seem to be practicable on the specific level, it may prove to be of considerable value in revealing intergeneric relationships within certain families. The results of those studies which have been made appear to indicate that such an approach is both feasible and productive.

Acknowledgments

The investigations upon which this dissertation is based were originally suggested by the late John Eric Hill, of the Division of Mammals, American Museum of Natural History. During the early stages of the work he presented many suggestions, especially with regard to technique, which have been of great assistance in the entire course of the investigations. Many others have helped directly or indirectly. I am especially indebted to Dr. W. H. Burt, curator of mammals, Museum of Zoology, University of Michigan, for his excellent criticism and guidance, as well as for the use of preserved specimens and skeletal material in his charge; to Dr. C. W. Hibbard, curator of vertebrate paleontology, Museum of Paleontology, University of Michigan, for valuable criticism and advice; and to Dr. Russell T. Woodburne, Department of Anatomy, University of Michigan, whose advice on certain anatomical problems has been very helpful. I am also obligated to Dr. E. Raymond Hall, director of the Museum of Natural History, University of Kansas, for the loan of preserved material in his charge, and to Dr. Wilbur Quay, for the gift of preserved specimens of *Oryzomys*. A special note of thanks is due Miss Elsa Hertz for stenographic assistance and Mr. William Brudon for suggestions and for the use of the equipment which aided in the preparation of the illustrations. I wish also to thank the Board of Governors of the Horace H. Rackham School of Graduate Studies for the grant which made possible the publication of this study.

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Discussion of the Subfamily Cricetinae

The four genera with which this study is concerned are assigned by taxonomists to the muroid subfamily Cricetinae. This subfamily includes approximately 60 groups which are currently given generic rank. Ellerman (1941) considered 57 of these groups valid genera and listed an additional five nominal genera which he was unable to examine. These forms are distributed, according to Ellerman (1941: 327), throughout the "entire American continent from Arctic Canada and Alaska south to Southern Patagonia; the greater part of the Palaearctic region (North France, Hungary, Greece, Asia Minor, Syria, Persia, Kashmir eastwards to east coast of Northern China, north to Germany, temperate Russia and temperate Siberia); Southern Africa; Madagascar." Eight of the genera recognized by Ellerman are Old World forms. No genera are common to both hemispheres, although *Calomyscus* from Persia, Baluchistan, Mesopotamia, and South Russian Turkestan is said to be very close to *Peromyscus*.

Various authors have in the past separated segments of the subfamily as distinct taxonomic categories. Merriam (1894) erected the subfamily Neotominae to include *Neotoma, Hodomys, Xenomys,* and two fossil genera. In his opinion "*Sigmodon* should be looked upon as an ancestral rather than a contemporary type. It is almost on the dividing line between the tuberculate and flat crowned groups, and is probably on or near the trunk line along which the Neotominae branched off from the tuberculate series." Merriam believed it probable that some of the species referred to the genera *Oxymycterus, Holochilus,* and *Abrothrix* belong to the Neotominae.

Thomas (1896) accepted Merriam's "Neotominae" and included all other cricetines in "Sigmodontinae"; both subfamilies were placed under the Muridae. Miller and Rehn (1901) recognized the subfamily Neotominae with the genera *Neotoma, Nelsonia, Xenomys, Neotomodon,* and *Hodomys* and relegated all other North American muroid genera except the microtines to the subfamily Cricetinae. This same arrangement was followed by Miller (1912), but later (1924) he dropped the subfamily Neotominae and reunited those genera with the Cricetinae. Since that time, and in some earlier instances, supergeneric groups within the Cricetinae have been designated by terms which have no taxonomic status and little specific meaning unless the author lists the genera to which he considers that the term applies. Thus, the terms "oryzomine (oryzomyine) group," "sigmodont group," and "akodont group," are used. Thomas (1917) spoke of the "*Oryzomys-Oecomys* series" and the "*Rhipidomys-Thomasomys* group." Tate's (1932a, b, c) oryzomine group included *Oryzomys, Nesoryzomys, Zygodontomys, Chilomys, Delomys, Phaenomys, Rhagomys, Rhipidomys, Nyctomys, Oecomys, Thomasomys, Inomys, Aepeomys, Neacomys,* and *Scolomys*. Gyldenstolpe (1932) designated all the neotropical cricetines as "sigmodont rodents," which is reminiscent of the use of the term "Sigmodontinae" by Thomas (1896). Hershkovitz (1944) presented the most recent definitions of some of the supergeneric cricetine groups. He applied the term "oryzomyine" to the genera and subgenera "*Oryzomys, Melanomys, Oligoryzomys, Microryzomys (= Thallomyscus), Oecomys, Nesoryzomys, Neacomys, Scolomys, Nectomys,* and *Sigmodontomys*." Also, he defined

the sigmodont rodents as "a natural supergeneric group of cricetines comparable to the oryzomyine group; it includes *Sigmodon*, *Sigmomys*, *Holochilus*, *Rheithrodon*, and others too little known by me to be assigned here with certainty." In speaking of the "*Rhipidomys-Thomasomys* group" of Thomas (1917), Hershkovitz (1944: 20) stated:

> Included were *Rhipidomys*, *Thomasomys* (= *Aepeomys* and *Inomys*, *fide* Osgood 1933: 161), *Phaenomys*, and *Delomys*, to which may be added the North American *Nyctomys*, *Otonyctomys*, *Megadontomys*, *Peromyscus* (*s.s.*), and *Ochrotomys* (*s.g.*); it would be appropriate to refer to these genera collectively as the peromyscid group were the genus *Peromyscus* disembarrassed of the *Akodon*-like *Haplomylomys* and *Podomys*, which, though frequently retaining the mesostyle and mesostylid, lack the mesoloph and mesolophid. Except for these two, the dental pattern of the group is essentially oryzomyine.

This brief and synoptic resume of the opinions of various taxonomists has been presented primarily to demonstrate the confusion and disagreement which exist in regard to the interrelationships of the cricetine genera. It should also be emphasized that, in addition to those genera which have been mentioned, there are many others, the affinities of which are doubtful or completely unknown. Ellerman's (1941) frank discussion of this situation is particularly pertinent. He stated (1941: 327-28):

> The present group is the most difficult group of all living Rodents to arrange in any natural order.... Cranial characters are of no use in dealing with a group of this description from the point of view of arranging a key, as all being more or less generalized Muridae, there are no characters (with very few exceptions) which will not be duplicated in any of the large genera. External characters are very much the same; even the tail reduction, which might on first view be used to divide off such genera as *Cricetus* and *Onychomys*, is overlapped by short-tailed species of many of the Neotropical genera. One is forced, therefore, to endeavor to divide the genera on dental characters, and a key has been got together which is in many places much more average than absolute, and probably can be broken down; this is chiefly owing to the fact that although such forms as *Neotoma*, *Sigmodon* and *Oryzomys*, representing three extremes, are very widely separated dentally, there are a host of subsidiary genera which have intergrading dental characters; in fact some genera start life in one section, and in the adult appear to develop a dental pattern not distinguishable from that of another section. All American Cricetinae seem to be extremely closely allied, and to have no characters which will constantly separate them from allied genera, in very many instances; even long-standing and well-known genera like *Akodon*, *Peromyscus*, *Oryzomys*, *Phyllotis* and *Hesperomys* are not in all cases clearly distinguishable, and as each of these may have as many as a dozen closely allied subsidiary genera, the task of arranging them in any natural order is almost impossible.

It seems probable that at least some of this confusion and difficulty in arranging these genera is a result of overdependence on an inadequate number of characters and the failure of many workers to recognize the possibility that convergent evolution, especially of the dentition, can occur. Arrangement of such groups, on the basis of the character of the dentition, then leads to an unnatural classification. It is my opinion that this is true among the cricetines and that additional evidence of intergeneric relationships must be sought.

Remarks on the Genera Studied

The representatives of the genus *Sigmodon* (cotton rats) are medium-sized rats, 225 to 330 mm. in total length. The tail is considerably less than half the total length (approximately one-third). They are robust, with short, rounded ears, which are almost hidden by the fur. Pelage is long and coarse, grizzled dark gray and black, brown, or light buffy gray. The fur of the underparts varies from gray to white, with plumbeous base.

The skull is characterized by the heavy rostrum and prominent supraorbital ridges which continue posterolaterad as the temporal ridges. The anterior border of the zygomatic plate is sharply cut back, forming a strong zygomatic spine. The pterygoid fossae are very deep; the auditory bullae are of medium size. The molar teeth are rather high- and flat-crowned, with long narrow enamel loops swinging across the occlusal surfaces. In the lower molars these folds usually form S-shaped patterns. There are about 50 named species and subspecies of *Sigmodon*, distributed throughout the southern United States as far north as Virginia, northern Kansas, southern Colorado, and extreme southern Nevada and south through Mexico and Central America to Venezuela, Colombia, Ecuador, and northern Peru.

The genus *Oryzomys* (rice rats) comprises several well-marked groups. Members of the subgenus *Oryzomys*, with which this paper is concerned, are medium-sized rats, somewhat smaller than most specimens of *Sigmodon* (225 to 315 mm. in total length). The scaly, thinly haired tail usually constitutes about one-half the total length. The ears are small, inconspicuous, and covered with hair. The pelage is rather coarse and long; the upper parts are grizzled brown or buff, and the underparts are white or creamy.

The skull has a somewhat narrow interorbital constriction; the supraorbital and temporal ridges are moderately developed, but not so strongly as in *Sigmodon*. The anterior border of the zygomatic plate is slightly cut back; the auditory bullae are rather small. The molar teeth are low-crowned, with low cusps. The upper molars are symmetrical, with the outer and inner cusps nearly opposite. The enamel pattern of the molars is very complex. Rice rats inhabit the southeastern United States; their habitat extends north to New Jersey along the Atlantic coast, inland to southern Illinois, Missouri, and Oklahoma, west through the Gulf States, throughout Mexico, Central America, and nearly all of South America. There are approximately 186 named kinds.

The species of woodrats (genus *Neotoma*) vary from slightly smaller to somewhat larger than the Norway rat. Total length is 330 to 430 mm. The tail is fairly long, usually slightly less than half the total length. The pelage is long and soft, cinnamon, buff, brown, or gray above and white or creamy white on the underparts. The tail is covered sparsely with short hairs, except in the forms of the subgenus *Teonoma*, which are characterized by large, bushy tails.

The skull has a narrow interorbital constriction; the rostrum is rather long and tapering. Supraorbital and temporal ridges are usually developed, but not so prominently as in *Sigmodon*. The bullae are rather large. The

molar teeth are high-crowned; the occlusal surfaces are flat and have a prismatic pattern of ridges formed by the folds of enamel extending in from the lateral and medial borders.

Representatives of this genus are present in western North America from extreme southwestern Yukon Territory south to Nicaragua and Guatemala, and from the Pacific coast to eastern Montana, Illinois, Missouri, and western Florida. They are found also in the mountainous regions of eastern United States from Connecticut to Kentucky and Tennessee and along the Atlantic coast from South Carolina to central Florida. There are approximately 96 named kinds.

The white-footed mice (genus *Peromyscus*) are small to medium sized, 125 to 255 mm. in total length. The length of the tail varies in different species from less than half to considerably more than half the total length. The pelage is soft and fine. Color of the upper parts varies among the species from dark brown to gray, cinnamon, or light buff. The underparts are white. The tail is moderately hairy, brownish above, lighter below.

The skull has a moderate interorbital constriction. The brain case is rounded, without supraorbital or temporal ridges. The anterior border of the zygomatic plate is nearly straight; the bullae are usually moderately developed. The molar teeth are low-crowned with well-developed cusps, which are alternately disposed. Re-entrant folds of enamel extend between the cusps. The third lower molar is rather strongly reduced.

Representatives of this genus are distributed over nearly the whole North American continent, from Panama to Alaska and Labrador. There are about 180 named kinds.

Objectives of the Study

This study was undertaken in order to determine whether evidence contributing to the systematic arrangement of the cricetine genera could be brought to light by approaching the problem from the standpoint of comparative myology. The four genera, *Sigmodon, Neotoma, Peromyscus,* and *Oryzomys*, were selected for examination because they appeared to represent four widely separated segments of the subfamily. Perimeters might thus be established within which other genera could be placed as they were studied. The evidence discovered in this study now makes it appear that the original estimate of the interrelationships of these genera was somewhat in error. Data are also available to show that systems erected on the basis of the cranial and dental morphology, although perhaps convenient for taxonomic work, may completely fail to express natural relationships.

These objectives have been pursued in the course of the study: (1) preparation of a more or less detailed description of the muscular system of *Sigmodon*; (2) comparison of the musculature of representatives of the genera *Neotoma*, *Peromyscus*, and *Oryzomys* with that of *Sigmodon* and with one another in order to determine whether there are differences or similarities which have phylogenetic significance; (3) discovery of evidence which might suggest the derivation or homologies of muscles among mammals in general; and (4) determination of the practicability of this approach to the problems of rodent taxonomy.

The selection of the genus *Sigmodon* as the focal point of the study was more or less arbitrary. It made little difference which genus was given the detailed treatment, since similarities and differences of all the other genera were treated as well. The anatomy of *Neotoma* has been described by Howell (1926), however, and *Sigmodon* was chosen principally because it is the largest of the remaining three genera, and therefore easiest to dissect.

MATERIALS

The preserved specimens used in this study were:

Sigmodon hispidus texianus Audubon and Bachman
Approximately thirty specimens, from Hamilton, Greenwood County, Kansas.

Neotoma floridana osagensis Blair
Thirteen specimens, from Hamilton, Greenwood County, Kansas.

Neotoma fuscipes macrotis Thomas
Four specimens, from one mile south of Escondido, San Diego County, California.

Oryzomys palustris palustris Harlan
Two specimens, from Locustville, Accomac County, Virginia.

Oryzomys couesi couesi Alston
Four specimens, from Petén, Uaxactún, Guatemala.

Peromyscus difficilis difficilis Allen
Three specimens, from Canyon Contreras, Distrito Federal, Mexico.

Peromyscus leucopus noveboracensis Fischer
Six specimens, from Hamilton, Greenwood County, Kansas.

Peromyscus maniculatus bairdi Hoy and Kennicott
Three specimens, from Hamilton, Greenwood County, Kansas; two specimens, from Ann Arbor, Washtenaw County, Michigan.

Rattus norvegicus Berkenhaut
Four specimens, from Silver Creek, Iosco County, Michigan.

Sciurus vulgaris Linnaeus
One specimen, from Flaten in Aamli, Norway, was used in connection with the analysis of homologies of M. caudofemoralis.

Tamiasciurus hudsonicus loquax Bangs
One specimen, from the vicinity of Ann Arbor, Washtenaw County, Michigan. This and the next specimen were used to check relationships of M. caudofemoralis and M. flexor brevis of the pes.

Tamias striatus rufescens Bole and Moulthrop
One specimen, from the vicinity of Ann Arbor, Washtenaw County, Michigan.

Mustela frenata noveborascensis Emmons
Two specimens, from Peoria, Peoria County, Illinois, were used in connection with the study of M. caudofemoralis.

METHODS

Many of these specimens were not dissected completely, but were used only for checking certain questionable features. In addition to the specimens listed above, skeletal material was drawn from the collection of the University of Michigan Museum of Zoology, Division of Mammals, for use in conjunction with the study of the musculature.

Several preservatives or embalming mixtures were tried. The best fixative for purposes of general dissection was a 2 per cent solution of formaldehyde (1 part of commercial formalin to 18 parts of water), which was saturated with common salt (sodium chloride). The muscles of freshly killed specimens preserved in this fluid retained a nearly natural color and a high degree of flexibility; they were tough enough to permit adequate manipulation. For certain types of dissection, however, such as the tracing of nerves, and when toughness of the muscles is not important, specimens preserved in a 4 per cent solution of formaldehyde (1 part commercial formalin to 9 parts of water) were found to be more satisfactory, provided that they were in an extended position when fixed. In such specimens the nerves are especially tough and the fascial planes are easily followed. Complicated embalming mixtures containing phenol, glycerin, and other ingredients appear to have no advantage over the simple ones just mentioned. Specimens were left immersed in the liquid for storage. Before dissection they were removed from the fluid, allowed to drain, and then kept in an airtight container, suspended above enough fluid to keep the atmosphere of the container saturated.

Much of the general dissection and all of that involving such regions as the feet, distal segments of the limbs, and ventral neck region were done under a binocular dissecting microscope with powers of 9X, 12X, and 18X. For certain critical areas powers of 24X and 27X were used.

After several specimens of *Sigmodon* had been dissected, and a general knowledge of the musculature of that genus had been gained, concurrent dissections were made on specimens of all four genera. The individual muscles in each form were compared directly with the corresponding muscles of each of the other forms. This was repeated at least three times with as many different sets of specimens. Points which appeared questionable or which varied to an appreciable extent were checked in all available specimens.

A number of published works were of particular aid in various phases of this study. Howell's (1926) rather exhaustive account, *Anatomy of the Wood Rat*, and Hill's (1937) excellent treatment entitled *Morphology of the Pocket Gopher Mammalian Genus Thomomys* were the most important of these. Howell's monograph was employed at first as a sort of laboratory manual and was used also as a check on the accuracy of my own observations of the muscles of *Neotoma*, as well as a source for data on variations which did not occur in specimens of that genus which I dissected. Valuable information was also obtained from such works as those of Parsons (1894, 1896), Leche (1900), Alezais (1900), and Greene (1935).

Muscles were found to vary considerably in apparent size and strength even in specimens of the same species, depending on the type of preservation,

degree of dessication, age and condition of the individual, and position in which the animal was fixed. Such variations among specimens of a species make quantitative comparisons between genera questionable, even if it were not for the fact that accurate estimation of relative bulk, or volume, of muscles in animals of different size is almost impossible. Accordingly, apparent quantitative differences in the muscles have not been considered in this study, except in cases where it appears certain that the differences are not due to any of the factors mentioned above. Data based on observations of qualitative differences and similarities (origin, insertion, topographical relationships, and innervations of muscles) are, however, usually dependable and constitute the principal basis of the present study.

ARRANGEMENT AND TERMINOLOGY OF THE MUSCLES

The arrangement of the muscles follows closely that used by Hill (1937), except in certain groups for which later and more exhaustive studies have shown Hill's arrangement to be inadequate. The muscle groups, according to Hill (1937: 102), are set up "on the basis of common or homologous innervation, on evidences of comparative myology, and, whenever possible, on developmental data. The muscles of branchiomeric origin are described first, then the myotomic muscles of the head and trunk, and finally, the muscles of the appendages."

The terminology used by Hill (1937) is adopted here. He says:

> [It is] that of the international system (B.N.A.) or the English equivalents, employed in modern human anatomy, except where certain names are misleading when applied to mammals other than man. In this connection it seems desirable to replace in description, except where no change of meaning is involved (as, for example, in connection with the structures of the head), the terms "anterior," "posterior," "superior," "inferior," by those of more general application, namely, "ventral," "dorsal," "cranial" or "cephalic," and "caudal." It also seems advisable to restrict the adverbial form of these words, namely, that ending in "-ally" (for example, ventrally), to references to position and to use the form ending in "-ad" (for example, ventrad) when course is intended (cf. Bensley, 1926: 43).

In the descriptions and comparisons of muscles which follow, all observed variation is discussed. When there is no statement to the contrary, it is to be assumed that the corresponding muscle in *Neotoma*, *Peromyscus*, and *Oryzomys* is essentially similar to that in *Sigmodon*. I have determined innervation of all but a very few of the muscles in *Sigmodon* and *Neotoma*, but the innervation of the muscles of *Oryzomys* and *Peromyscus* was checked only if there appeared to be a need to answer some specific question.

DESCRIPTION AND COMPARISON OF THE MUSCLES

Branchiomeric Musculature

Masticatory Group
(Figs. 1, 8, 11)

The muscles of this group are supplied by the masticatory nerve.

Tullberg (1899) gave a brief comparison of the masticatory muscles of *Peromyscus leucopus* and *Neotoma cinerea*. Although he described the general morphology of *Sigmodon hispidus*, he did not compare the masticatory apparatus with that of the other two genera. He noted in particular the more strongly developed M. temporalis of *Neotoma*, as compared with that in *Peromyscus*, and said that M. transversus mandibulae appears to be less developed in *Neotoma*.

As in most rodents, the masseter muscle of the cricetines is divided into three principal parts, M. masseter superficialis, M. masseter lateralis profundus, and M. Masseter medialis. Each of the last two muscles is usually further differentiated into two parts. This is true of *Sigmodon*, *Neotoma*, and *Peromyscus*, but the masseter medialis of *Oryzomys* forms a single continuous sheet. In *Sigmodon*, *Peromyscus*, and *Oryzomys*, the pars posterior of M. masseter lateralis profundus is differentiated into two elements.

Various investigators have applied many different terms to the elements of the masseter complex. Published descriptions of this muscle are consequently rather confusing. Hill (1937) gave a list of the synonyms of each part, which is of considerable aid in the interpretation of the muscle.

M. masseter superficialis

Origin. — By a strong, flat tendon from the maxillary, just ventral to the infraorbital foramen and immediately posterior to the maxillary-premaxillary suture.

Insertion. — On the ventrolateral border of the angular process, with a small part reflected on the medial surface of the mandible to insert on the posterior aspect of the bulge over the proximal end of the root of the incisor.

Remarks. — As the tendon of origin passes caudoventrad, it spreads to form a strong aponeurosis, from the deep side of which the muscle fibers take origin. Only minor differences were noted in the relationships of this muscle in the various forms. In *Neotoma* and *Peromyscus* origin is higher on the side of the zygomatic plate, above the level of the ventral limit of the infraorbital foramen. The muscle arises in *Oryzomys* precisely as in *Sigmodon*. In all four forms some fibers insert on the aponeurosis of M. masseter lateralis profundus pars posterior. Only a few insert in this way in *Neotoma* and *Peromyscus*, but a large number do so in *Oryzomys*. *Sigmodon* is intermediate in this respect.

M. masseter lateralis profundus, pars anterior

Origin. — From the dorsal margin of the zygomatic plate and spine and from the lateral aspect of the zygomatic arch as far posteriad as the level of a vertical line through the middle of the eye.

Insertion. — By a broad, heavy aponeurosis on the masseteric crest of the mandible.

Remarks. — The insertional aponeurosis is developed superficially, and most of the muscle fibers insert on its deep side. Only a very few fibers attach directly to the bone.

In *Sigmodon* and *Oryzomys* this part is developed relatively more strongly than in *Neotoma* and *Peromyscus*. Its origin does not extend so far anterior in the other forms as in *Sigmodon*, a condition apparently correlated with the development of the zygomatic spine in this genus.

M. masseter lateralis profundus, pars posterior

Origin. — Along the lateral border of the zygomatic arch from a point below the middle of the eye to the posterior end of the arch.

Insertion. — Onto the entire lateral surface of the angular process, above the masseteric crest.

Remarks. — The fibers of this part are distinguished from the anterior fibers principally by the difference in their course. Those of pars anterior are more nearly vertical, whereas those of pars posterior pass decidedly caudoventrad. The posterior part slightly overlaps the anterior part.

In *Neotoma* this part is differentiated from the anterior part to a much greater extent than in the other genera. In *Sigmodon*, *Oryzomys*, and *Peromyscus* the fibers of the posterior part which arise from the tip of the angular process constitute a discrete slip which passes almost directly dorsad to the arch, posterior to the jugal. This rather well-differentiated segment of the pars posterior has been described also in *Reithrodontomys* (Rinker and Hooper, 1950). No such division is evident in *Neotoma*.

M. masseter medialis, pars anterior

Origin. — From the medial surface of the zygomatic arch anterior to the jugal and from the fossa in the maxillary bone anteromedial to the superior root of the zygomatic arch.

Insertion. — A heavy aponeurosis develops on the medial surface of the muscle, upon which most of the fibers insert; this in turn attaches to the lateral surface of the mandible. Only a few of the more posterior muscle fibers insert directly on the mandible.

Remarks. — The segment which passes through the infraorbital foramen is larger in *Peromyscus* and *Neotoma* than in the other two genera, and in them its origin extends onto the premaxillary bone. In *Peromyscus* and *Neotoma* slightly more than half of the muscle fibers insert directly on the mandible; in *Oryzomys* the posterior two-thirds of the fibers insert directly.

M. masseter medialis, pars posterior

Origin. — From the medioventral surface of the zygomatic process of the squamosal.

Insertion. — On the lateral surface and posterior border of the coronoid process and into the fossa medial to the incisor cap.

Remarks. — The fibers of this part are distinctly differentiated from the anterior fibers; the directions of the fibers of the two parts are nearly at right angles. The masticatory nerve pierces these fibers as it passes out through the notch between the coronoid and condylar processes of the mandible (Hill, 1937). In *Neotoma* insertion is onto more of the lateral surface of the coronoid process. In *Peromyscus* only the most anterior fibers come into contact with the anterior part, and this only at the insertion. Accordingly, a short piece of the arch is left from which no fibers of the masseter medialis take origin. The two parts of the masseter medialis are not differentiated in *Oryzomys*, and their respective limits could not be determined.

M. temporalis

Origin. — From the parietal and squamosal bones in the region between the superior and inferior temporal ridges, from the posterolateral part of the frontal bone in the orbital fossa, and from the lambdoidal crest below its junction with the superior temporal line.

Insertion. — On the tip, anterior border, and anterior part of the medial surface of the coronoid process of the mandible.

Remarks. — Although the fibers of this muscle constitute a rather closely unified mass, two poorly defined sections can be detected. There is an anterior, superficial part, and a posterior, deeper part. The fibers of the superficial part arise within the orbit and from the anterior half of the superior temporal ridge. Many of these fibers insert on the aponeurosis of the deeper part, but most end in a tendon which attaches along the anterior border of the coronoid process and in the groove between the base of that process and the last molar. The deep section is made up of fibers arising along the whole superior temporal ridge (deep to the superficial part in the anterior half of this ridge), from the temporal fossa, and from the lambdoidal crest. These insert on a heavy tendon which develops in the middle of the muscle. This tendon passes down over the base of the zygomatic arch to insert on the tip and medial surface of the coronoid process.

In *Oryzomys*, although the superficial part is slightly more extensive, it is not so well differentiated from the deep part as in *Neotoma* and *Sigmodon*. The two parts are still less distinct in *Peromyscus*, and their limits can hardly be detected. In *Sigmodon* and *Oryzomys* the area of origin of the temporalis is sharply limited by the heavy superior temporal ridge; the muscle does not encroach on the dorsum of the brain case. Only a small part of the parietal, and none of the interparietal, is involved. The temporal ridges are absent in *Peromyscus* and relatively weakly developed in *Neotoma*. In the former genus the temporalis is apparently rather weak, and the area of origin, although more extensive than in *Sigmodon*, is considerably less extensive than in *Neotoma*. In the latter genus the muscle is very strong, and the area of origin includes almost half of the parietal and a part of the interparietal. The mode of origin of

the temporalis in *Oryzomys* is similar to that in *Sigmodon*, but the muscle is not so strongly developed. The apparently greater strength of M. temporalis in *Neotoma* and *Sigmodon* is probably correlated with the more lophodont type of dentition of these forms.

No fibers of this muscle were found to insert on the aponeurosis of M. masseter as was described by Howell (1926).

M. pterygoideus externus

Origin. -- From the lateral surface of the alisphenoid bone, anterior to the buccinator foramen, from the immediately adjacent part of the maxillary bone, and from the anterior third of the lateral pterygoid plate.

Insertion. — On the medial surface of the articular condyle of the mandible.

Remarks. — In *Sigmodon* and *Oryzomys* this muscle does not appear to be so strongly developed as in *Neotoma* and *Peromyscus*. The difference is only slight.

Internal Pterygoid Group
(Figs. 6B, C; 8)

Innervation of this group is by the medial branch of the mandibular nerve.

M. pterygoideus internus

Origin. — From the pterygoid fossa.

Insertion. — On the medial surface of the angular process and on the dorsal surface of its inflected ventral border.

Remarks. — In all four genera this muscle is composed of two groups of fibers which may be separated quite easily. The more ventral group is made up of fibers which take origin from the anterior and medial borders of the fossa and insert along the inflected ventral margin of the angular process. The fibers of the more dorsal group arise from within the fossa and insert on the medial surface of the angular process. A heavy aponeurosis is formed on the ventral surface of this part and tends to separate it from the other part. The course of these fibers is noticeably more directly laterad. The internal pterygoid as a whole is considerably larger in *Sigmodon* and *Neotoma* than in the other two genera.

M. tensor veli palatini

Origin. — From the anteromedial point of the auditory bulla and from the anterolateral surface of the auditory tube.

Insertion. — On the soft palate and posterior part of the lateral surface of the medial pterygoid plate.

Remarks. — The tendon of this muscle passes anteroventromediad, crosses the ventral margin of the medial pterygoid plate, and fans out into the soft palate. The fibers from each side decussate freely with those of the other side. Most of the fibers arising on the auditory tube pass directly anteromediad to insert on the pterygoid plate.

M. tensor tympani

Origin. — From the posterior border of the auditory tube and from the walls of the semicanal in which it lies.

Insertion. — On the manubrium of the malleus.

Remarks. — An aponeurosis develops on the surface of the muscle which is in contact with the cochlea. The muscle fibers insert on this aponeurosis which then develops into a small round tendon, passing over the cochleariform process just before it inserts. As the tendon passes over this process, it changes direction almost 90 degrees. There is no bony septum between the semicanal of the tensor tympani and the auditory tube; the two structures lie in a common groove.

Mylohyoid Group
(Figs. 6A, B; 8)

The three muscles of this group are supplied by the mylohyoid nerve, a branch of the mandibular nerve.

M. mylohyoideus

Origin. — From the medial surface of the mandible along a line just ventral to the alveoli of the molar teeth.

Insertion. — Into the median raphe and the anterior surface of the body of the hyoid.

Remarks. — No significant variation was noticed.

M. transversus mandibulae

This muscle, probably a derivative of the mylohyoid, passes transversely between the mandibles, immediately posterior to the symphysis. Its width in *Sigmodon* averages about 5 mm. It appears to have approximately the same relative development in all the genera studied except *Peromyscus*, in which it is relatively wider anteroposteriorly.

M. digastricus (anterior belly)

Origin. — From the anterolateral surface of the tendon of the posterior belly.

Insertion. — On a small flange immediately lateral to the posterior end of the mental symphysis.

Remarks. — In *Sigmodon*, *Neotoma*, and *Oryzomys* the two anterior bellies are in very close contact except for a slight divergence just before insertion. In *Peromyscus* only the posterior third to half of the medial borders are in contact. (See also remarks under M. digastricus, posterior belly, p. 36.)

Superficial Facial Group
(Figs. 2, 3, 4, 5, 8)

This group comprises all the superficial facial muscles and is equivalent to the constrictor colli group of Hill (1937).

Huber (1931) has grouped these muscles into three layers on the basis of their derivation. These three layers, sphincter colli superficialis, platysma, and sphincter colli profundus, are derived from the reptilian primitive sphincter colli. The true sphincter colli superficialis does not occur in the muroid rodents, although a false superficial sphincter formed by decussating fibers of the deep sphincter has been given that name by several authors.

Huber's (1930: 137) concept of the platysma and sphincter colli profundus may be summed up rather briefly:

> From the "primitive sphincter colli" restricted to the neck region as it is still in the modern reptiles and presumably was in the reptilian ancestors of the marsupials and placentals, there have shed off the undifferentiated platysma and sphincter colli profundus. These two primary muscle layers invaded the face where they subsequently differentiated into the more or less distinct facial muscles. The platysma evidently gave rise to the M. platysma colli et faciei, and to the postauriculo-occipital muscle group, which includes part of the extrinsic and intrinsic ear muscles.... The rest of the superficial facialis was derived from the sphincter colli profundus....

Meinertz' extensive work in this field on rodents and lagomorphs (1932; 1935a, b; 1936a, b; 1941; 1942a, b) has been, in essence, a confirmation of Huber's concepts. The arrangement of the musculature followed here has been taken, with minor modification, from Meinertz' (1941) publication *The Skin Musculature of the Greenland Lemming*. Such an intensive examination of the muscles and their innervation as is presented in that work is far beyond the scope of the present study, and I have drawn much information from Meinertz, particularly with regard to innervation, without attempting to confirm it in detail.

The following outline shows the arrangement used here for the elements of this group.

A. Platysma and derivatives
  1. Platysma
    M. platysma myoides
      Pars buccalis
      Pars mentalis
      Pars auricularis
    M. platysma cervicale

  2. Retroauricular musculature
    a. Cervicoauricular musculature
      Layer 1.
        M. cervicoauricularis
        M. cervico-occipitalis

      Layer 2.
        M. cervicoauricularis medius anterior
        M. cervicoauricularis medius posterior

      Layer 3.
        M. cervicoauricularis posterior profundus

    b. Mm. auriculares proprii
        M. mandibulo-auricularis

B. Sphincter colli profundus and derivatives
1. Pars auris
2. Pars intermedia and derivatives
a. Pars intermedia ventralis
b. Pars intermedia dorsalis and derivatives
(1) Preauricular musculature
Deep layer
"Intermediate plate"
M. zygomaticolabialis
M. auriculo-occipitalis

Superficial layer
M. frontalis (auricular part)
M. auricularis anterior superior
M. auricularis anterior inferior

(2) Orbitonasal musculature
M. frontalis (orbital part)
M. orbicularis oculi
M. nasolabialis
M. nasolabialis superficialis

3. Pars palpebralis

4. Pars oris and derivatives
M. maxillolabialis
M. dilator nasi
M. nasolabialis profundus
Pars interna
Pars media superior
Pars media inferior
Pars anterior
Pars anterior profunda
Pars maxillaris superficialis
Pars maxillaris profunda
M. bucco-naso-labialis
M. buccinatorius
Superficial anterior parts
Pars intermaxillaris
Pars intermaxillaris superficialis
Pars mandibularis anterior
Pars orbicularis
Pars orbicularis oris

Superficial posterior parts
Pars longitudinalis posterior dorsalis
Pars mandibularis posterior
Pars longitudinalis posterior ventralis

A. Platysma and Derivatives

1. Platysma

The platysma proper is divided into two layers, the superficial platysma myoides and the deeper platysma cervicale. The former muscle may again be divided into three parts: pars buccalis, pars mentalis, and pars auricularis.

M. platysma myoides

The fibers of this sheet arise along the middorsal line, from the occiput to the level of the interscapular fossa, with a few fibers arising superficial to the cutaneous maximus in the dorsal part of the shoulder region, and from the ventral part of the ear cartilage.

Pars buccalis. — This part is made up of the fibers arising in the nuchal region. They pass laterad, then turn craniad to pass immediately beneath the ear onto the buccal region. Here the more ventral fibers pass deep to pars palpebralis of the sphincter colli profundus to insert into the corner of the mouth, interlacing with the fibers of M. orbicularis oris. Some of the more dorsal fibers, after passing ventral to the ear, swing dorsad and are lost in the region immediately below and posterior to the eye. The fibers from the anterior 4 or 5 mm. of the origin pass directly laterad, immediately behind the ear, around the base of the ear cartilage, and insert into this cartilage near the middle of its ventral aspect.

Pars mentalis. — This part is composed of the posterior fibers arising from the dorsal mid-line and those which arise on the shoulder region. The fibers pass down around the neck, deep to the superficial part of the sphincter colli profundus, but superficial to partes palpebralis and orbicularis, to insert into the lateral aspect of the mental region. At the insertion the fibers pass deep to the orbicularis oris.

Pars auricularis. — Arising from most of the anterior region of the base of the ear cartilage, the fibers pass dorsocraniad to the posterior corner of the eye where they diverge, some passing above and some below the eye. The inferior border of this part is continuous with the dorsal border of the pars buccalis.

Remarks. — In *Neotoma* the fibers composing pars mentalis arise entirely from the region of the shoulder and extend more onto the throat region than in *Sigmodon*. In *Peromyscus* this layer is so thin that I could not determine the exact area from which the fibers take origin, but few if any fibers appear to come from the shoulder region. *Oryzomys* has numerous fibers arising from this region, but the mentalis part also includes fibers from the dorsal mid-line as in *Sigmodon*. Insertional relationships are similar in all four genera.

The fibers of the dorsal border of pars buccalis in *Sigmodon* turn dorsad and end in the postocular region, as described by Meinertz (1941) for the Greenland lemming and (1942a) for the Norway rat. This occurs also in *Oryzomys*, but not in the specimens of *Neotoma* and *Peromyscus* which I dissected. Meinertz spoke of this as an incipient process of differentiation of a pars orbitalis.

Pars auricularis shows greater variation among the forms studied than do the other two parts. In *Sigmodon* and *Oryzomys* this part fans out over the postorbital region, inserting into the skin both dorsal and ventral to the eye and interlacing with M. orbicularis oculi. In *Neotoma* these fibers pass down over the masseter, posteroventrad to M. zygomaticolabialis, and insert into the corner of the mouth, forming what might be called an M. auriculolabialis, as Howell (1926) designated this slip which inserts

independently, passing deep to pars buccalis and M. zygomaticolabialis. This is a close parallel to the condition described in *Cricetus* by Meinertz (1942a). In *Peromyscus* most of the fibers insert as in *Neotoma*, but some end in the region just behind the eye and ventral to it, a condition more or less intermediate between that in *Sigmodon* and that in the wood rat.

M. platysma cervicale

Origin. — Along the dorsal mid-line for a distance of about 12 mm. anterior to the spine of the second thoracic vertebra.

Insertion. — Into the skin of the ventrolateral part of the throat, piercing and interlacing with the fibers of M. platysma myoides.

Remarks. — At the origin this muscle is covered completely by M. platysma myoides and the superficial cervicoauricular muscles. In *Neotoma* this is a broader layer of fibers, covering the entire side of the neck. The posterior fibers pass ventrad across the shoulder, paralleling the spine of the scapula. In *Peromyscus* and *Oryzomys* many of the fibers appear to merge with pars mentalis of M. platysma myoides. This may not actually be true, as the fibers of p. cervicale pierce the p. myoides, and it is extremely difficult to trace the individual fibers.

Innervation of M. platysma cervicale is by the ramus auricularis posterior.

2. Retroauricular Musculature

According to Meinertz, the retroauricular musculature is derived from the platysma. The muscles may be divided into two groups, the cervicoauricular muscles and the Mm. auriculares proprii. Those of the former group lie in three planes, the most superficial of which is immediately deep to M. platysma myoides; the deepest layer lies in the same plane as the M. platysma cervicale. Of the Mm. auriculares proprii, all are intrinsic to the ear except the M. mandibulo-auricularis, which is the only one treated here.

All the retroauricular muscles receive their innervation from the posterior auricular branch of the facial nerve.

a. Cervicoauricular Musculature
Layer 1

M. cervicoauricularis

Origin. — Along the ligamentum nuchae, from the spine of the second thoracic vertebra to the level of the axis.

Insertion. — By three slips. The anterior slip runs anterolaterad, passes deep to M. auriculo-occipitalis, and curves down around the anterior side of the base of the ear to insert on the anteroventral aspect of the ear cartilage. The middle slip inserts into the middle of the dorsal aspect of the cartilage, and the posterior slip attaches to the posterior bulge of the cartilage. In some specimens the two posterior slips are not differentiated from each other.

Remarks. — The anterior border of this muscle overlaps slightly the posterior border of M. cervico-occipitalis. Variations found in this muscle among the forms studied were only slight. In *Neotoma* its relations were almost exactly as in *Sigmodon*; in *Oryzomys* the muscle is considerably less distinct from M. cervico-occipitalis and divides into its terminal slips only immediately before insertion. *Peromyscus* has this muscle relatively weakly developed; here it inserts mainly on the dorsomedial surface of the conch, with only a few fibers passing around to the anterior side of the ear.

M. cervico-occipitalis

Origin. — From the cranial 8 mm. of the ligamentum nuchae.

Insertion. — The fibers pass craniolaterad, deep to M. auriculo-occipitalis and the intermediate plate, deep to the fibers of the auricular part of M. frontalis, and merge with this last muscle in the midfrontal region.

Remarks. — In at least some specimens of *Sigmodon* the caudal border of this muscle is overlapped by the anterior border of M. cervicoauricularis. This is true also in *Neotoma* and *Oryzomys*. In *Peromyscus* the adjacent borders of these two muscles are continuous. Only in *Sigmodon* do the fibers of M. cervico-occipitalis continue onto the frontal region to merge with the fibers of M. frontalis. In *Neotoma* and *Peromyscus* the fibers end on the deep side of the "intermediate plate" over the posterolateral part of the parietal bone. In *Oryzomys* the muscle approaches the condition seen in *Sigmodon*, extending nearly as far anteriad, but is not so strongly developed.

Layer 2

M. cervicoauricularis medius anterior

Origin. — From the ligamentum nuchae, deep to the origin of M. cervico-occipitalis.

Insertion. — On the dorsocaudal surface of the base of the ear, just deep to the middle segment of M. cervicoauricularis.

Remarks. — This thin band of fibers, approximately 6 mm. wide at the origin, converges rather sharply at first, then passes laterad as a band about half as wide as at its origin. In *Neotoma* and *Peromyscus* this muscle is relatively less than one-half as wide, but otherwise has much the same relationships. In *Oryzomys* this slip appears to be wider than in the last two forms, but is not so broad as in *Sigmodon*.

The relationships of M. cervicoauricularis medius anterior, M. cervicoauricularis medius posterior, and M. cervicoauricularis posterior profundus are almost precisely as shown by Meinertz (1942a: 262, Fig. 3) in the Norway rat.

M. cervicoauricularis medius posterior

Origin. — Along the ligamentum nuchae posterior to M. cervicoauricularis medius anterior, deep to M. cervicoauricularis, and partly superficial to the anterior border of M. platysma cervicale.

Insertion. — Onto the posterior surface of the base of the ear cartilage.

Remarks. — From a rather broad origin the fibers pass craniolaterad, converging strongly. M. cervicoauricularis posterior profundus lies immediately deep to the anterior half of this muscle, and extreme care is required to separate them. Relationships in all four genera are similar.

Layer 3

M. cervicoauricularis posterior profundus

Origin. — From the ligamentun nuchae, immediately deep to the anterior half of M. cervicoauricularis medius posterior.

Insertion. — Onto the posteroventral part of the base of the ear cartilage.

Remarks. — This muscle lies just beneath the anterior half of M. cervicoauricularis medius posterior and is very easily overlooked. The fibers pass more directly laterad, however, emerging from beneath the posterior border of the more superficial muscle just at the insertion of the latter, then pass ventrad around the base of the ear to their insertion.

The M. platysma cervicale lies in the same plane as this muscle, and the two are very nearly continuous.

b. Mm. Auriculares Proprii

Of these, only M. mandibulo-auricularis is described.

M. mandibulo-auricularis

Origin. — From the dorsoanterior part of the base of the ear cartilage.

Insertion. — On the mandible, just inside the border of the posterior semilunar notch.

Remarks. — Although its topographical relationships would hardly allow the inclusion of this muscle in the retroauricular group or, more specifically, among the Mm. auriculares proprii, Huber (1925) has traced its derivation from an intrinsic muscle of the ear.

B. Sphincter Colli Profundus and Derivatives

This muscle and its derivatives constitute the deepest layer of the superficial facial musculature. It is the only one of the layers which actually forms a complete sphincter, passing entirely around the head and neck. The sphincter colli profundus proper forms a continuous sheet from the pectoral region to the mental symphysis, but it is customarily described in four parts. That procedure has been followed here.

Along the ventral mid-line the fibers from each side pass through those from the other side, continuing superficial to them, thus forming a superficial layer of fibers which has been called the sphincter colli superficialis by some authors (e.g. Schreiber, 1929). The use of this term in regard to rodents would only lead to confusion, since they do not possess a true superficial sphincter.

The four parts of the sphincter colli profundus, as treated by Huber and Meinertz, are pars auris, pars intermedia, pars palpebralis, and pars oris. They are discussed in that order.

1. Pars Auris

This part of the muscle sometimes constitutes a discrete slip. Arising from the posterior half of the mid-line of the manubrium sterni, the fibers pass laterocraniad to the side of the neck, then dorsad to insert on the ventral surface of the ear cartilage. No other fibers of the sphincter colli profundus attach to the ear in *Sigmodon*. This is the slip referred to by Howell (1926) as M. sternofascialis, and by Hill (1937) and Bryant (1945) as M. sternoauricularis.

In *Neotoma*, Howell (1926) found this slip only in the subgenus *Homodontomys*. In the specimens of this subgenus which I dissected, it is present as a thin band arising as in *Sigmodon* but merging with the posterior border of pars intermedia ventralis before inserting on the ear. In the specimens of *Neotoma* (*Neotoma*) *floridana* which were dissected this slip was found to be constant and independent of the pars intermedia as in *Sigmodon*. No evidence of continuity of this slip and the pars intermedia was found in *Oryzomys*, except possibly a thin fascia which seemed to connect their adjacent borders. This fascia appears to be present in *Peromyscus*, too, but is very thin.

The relationships of this part, as observed in the forms dissected, seem to show stages in the formation of a discrete sternoauriclar part of the sphincter colli profundus.

2. Pars Intermedia and Derivatives

a. Pars Intermedia Ventralis

These fibers make up the greater part of the sphincter colli profundus. They pass dorsad around the posterior masseteric region, becoming continuous with those of the "intermediate plate" in the region between the eye and the ear. This part lies entirely deep to M. platysma myoides and is continuous with pars palpebralis anteriorly.

b. Pars Intermedia Dorsalis and Derivatives

(1) Preauricular Musculature
Deep Layer

"Intermediate plate"

The fibers of the "intermediate plate," which are for the most part a continuation of the pars intermedia ventralis, cover the dorsal part of the head between the eyes and ears. In the median third of this area the layer becomes almost completely aponeurotic. This layer is so thin, and it is so difficult to establish its exact limits, that a detailed comparison is not justified.

M. zygomaticolabialis

Origin. — Partly as a continuation of the fibers from the intermediate plate and partly from the fascia of the ventral postorbital region, deep to the intermediate plate.

Insertion. — Into the corner of the mouth, deep to the orbicularis oris.

Remarks. — Meinertz (1941) found a similar continuity of the intermediate plate and M. zygomaticolabialis in the Greenland lemming. He interpreted this as evidence of the direct derivation of the zygomaticolabialis from the intermediate plate. Relationships of this muscle are generally similar in the four genera.

M. auriculo-occipitalis

Origin. — From the surface of the posterior part of the intermediate plate, apparently partly continuous with that structure.

Insertion. — On the dorsal (medial) side of the base of the ear cartilage.

Remarks. — This segment, a primary derivative of the intermediate plate, is the most superficial layer of the interauricular region. It is, at least partly, the equivalent of Howell's (1926) M. interscutularis. Meinertz (1935b, 1936a), however, has shown that the true interscutularis occurs only in those forms which have a scutulum. He substituted (1941) the present term for the topographically equivalent muscle in forms not possessing that structure. The fibers of the muscle pass almost directly laterad, superficial to M. cervico-occipitalis and M. cervicoauricularis, converging somewhat as they approach the ear.

Superficial Layer

M. frontalis (auricular part)

Origin. — From the dorsoanterior surface of the cartilage of the ear.

Insertion. — On the surface of the intermediate plate anterior to the ear and, with the orbital part, on the frontal bone just medial to the anterior corner of the eye.

Remarks. — Only a few fibers insert on the surface of the intermediate plate anterior to the ear. Most of them pass beneath the intermediate plate, merge with fibers of M. cervico-occipitalis, and continue anteriad to join and insert with the orbital part of the frontalis. This development of the auricular part of the frontalis beneath the intermediate plate is a departure from the usual relationships. In *Dicrostonyx* and *Rattus* (Meinertz, 1941, 1942a) this part passes entirely superficial to the intermediate plate. This is also the situation found in *Neotoma* and *Peromyscus*; *Oryzomys* is similar to *Sigmodon* in the relationships of this muscle.

M. auricularis anterior superior

This slip is apparently undifferentiated in the forms studied. I have been unable to distinguish a discrete slip in this region.

M. auricularis anterior inferior

Origin. — From the superficial surface of the posterior border of sphincter colli profundus, pars intermedia, immediately anteroventral to the base of the ear cartilage.

Insertion. — Onto the cartilage of the ear just beneath the intertragic cleft.

Remarks. — This small bundle of fibers was seen only in *Sigmodon*. Meinertz (1941) made no mention of its occurrence in the Greenland lemming, and (1942a) stated that it is absent in the Norway rat. The muscle described under this name by Schreiber (1929) in *Agouti paca* [sic] has relationships almost precisely the same as those of the present slip, and I have, therefore, used this term.

(2) Orbitonasal Musculature

M. frontalis (orbital part)

Origin. — From a small prominence on the frontal bone, immediately medial to the corner of the eye.

Insertion. — Into the skin of the frontal and anterior parietal regions.

Remarks. — The medial fibers pass posteromediad, spreading out over the medial part of the frontal region, interlacing with the fibers from the opposite side. The more lateral fibers course posterolaterad, fanning out to end in the fascia of the medial preauricular region. This latter group of fibers passes deep to the intermediate plate and is partly continuous with the auricular segment of the frontalis and M. cervico-occipitalis. The frontalis as a whole is weakly developed in *Neotoma* and *Peromyscus* and in these forms is not reinforced by fibers from the cervico-occipitalis.

M. orbicularis oculi

This muscle does not seem to be very strongly developed in any of the forms studied. The fibers lying in the eyelid arise on the border of the strong medial palpebral ligament and appear to pass entirely around the eyelid to insert on the opposite border of the same ligament. Fibers arising from the skin of the interorbital region pass both anteriorly and posteriorly around the eye to meet again in the suborbital region, interlacing there to a considerable extent. Some of the anterior fibers can be separated from the nasolabialis only with difficulty, and it may be that the two muscles are continuous for a short distance.

A small M. retractor anguli oculi lateralis is present in all four genera. In at least some specimens of *Sigmodon* there is a small bundle of fibers with similar relations at the medial corner of the eye (Figs. 2, 3).

M. nasolabialis

Origin. — From the small prominence on the frontal bone just medial to the medial corner of the eye.

Insertion. — Into the mystacial pad and into the margin of the upper lip, deep to the orbicularis oris.

Remarks. — The anteromedial fibers pass directly anteriad along the maxillary-premaxillary suture for more than half the distance to the nares before turning onto the side of the rostrum. The posterior fibers pass anterolaterad over the zygomatic spine, turning down over the side

of the rostrum just anterior to the bulge of M. masseter. This is the most superficial layer of fibers in the posterior part of the mystacial pad. Those fibers which attach to the bases of the vibrissae do so by forming a simple loop around the follicles. Relationships of the muscle are generally similar in all four genera, but in *Neotoma* and *Peromyscus* origin is not confined to the tubercle on the frontal. In those forms fibers arise also from the premaxillary bone, along a line extending some 8 mm. anteriad from the tubercle parallel to the posterior part of the maxillary-premaxillary suture.

M. nasolabialis superficialis

Origin. — From the galea of the anterior half of the bridge of the rostrum.

Insertion. — Into the skin of the side of the rostrum and the mystacial pad.

Remarks. — This is a thin, even sheet of fibers passing transversely across the rostrum. It is so thin that exact limits of its extent could not be determined. It appears, however, to be about equally developed in *Sigmodon* and *Oryzomys*. In both *Neotoma* and *Peromyscus* the muscle is much better developed and extends over the entire dorsal surface of the rostrum as far back as the level of the anterior border of the zygomatic plate.

3. Pars Palpebralis

The pars palpebralis of the sphincter colli profundus is a direct continuation of the pars intermedia. Its posterior limit is easily seen on the cheek region where the pars buccalis of the platysma, after crossing superficial to the pars intermedia, goes deep to this part. It covers the entire suborbital region in all four genera.

4. Pars Oris and Derivatives

All the remaining muscles of the rostral region are derivatives of the pars oris of the sphincter colli profundus. This part has lost connection with the pars palpebralis and has been given over in its entirety to the formation of the discrete muscles of the rostral and oral regions. Innervation of all the elements of this group is by branches from the buccal plexus.

M. maxillolabialis

Origin. — From a shallow groove in the maxillary bone, which extends craniad from the anterior border of the alveolus of M^1 for approximately 3 mm., and from the inferior part of the anterior border of the zygomatic plate.

Insertion. — Into the base of the mystacial pad.

Remarks. — The fibers extend dorsad and craniad, interlacing with the fibers of M. nasolabialis around the bases of the vibrissae. In *Neotoma* relations are much the same, except that the prealveolar part of the origin

is from a rather strong oblique ridge which extends anteromediad from the anterior border of the alveolus to the margin of the incisive foramen. In *Peromyscus* and *Oryzomys* the ridge from which this part of the muscle arises begins at the alveolar border and curves slightly anteromediad, then parallels the border of the incisive foramen. This differs only very slightly from the condition seen in *Sigmodon*.

M. dilator nasi

Origin. — From the medial half of the dorsal margin of the zygomatic notch.

Insertion. — Into the lateral part of the dorsal border of the rhinarium.

Remarks. — This is a very slender muscle which becomes tendinous in its distal third. At the origin it lies deep to M. nasolabialis. Near the middle of the rostrum it is superficial to the dorsal fibers of M. nasolabialis profundus pars media superior and then passes deep to part of pars interna near the insertion. Part of the fibers of pars interna arise from the tendon of this muscle. There is very little variation in this muscle among the genera studied.

M. nasolabialis profundus

This muscle consists of six rather well-differentiated parts which lie on the side of the rostrum. Some of these attach to the nasal cartilage, others to the premaxillary bone. There appears to be little variation in these muscles among the four genera studied. Their dissection is, however, so difficult that although all have been seen and compared in the different forms, data on relative development, size, and exact insertion may not be dependable in all cases.

Pars interna

Origin. — From the nasal cartilage, dorsolateral to the naris.

Insertion. — Into the skin over the nasal bone for approximately 8 mm. posterior to the rhinarium, and onto the tendon of M. dilator nasi.

Remarks. — There are usually three parts to this slip. The most superficial passes caudodorsad onto the bridge of the nose, superficial to the tendon of M. dilator nasi; the deepest passes to the same region but goes deep to that tendon; the most posterior part attaches to the lateral border of the same tendon. Relationships appear to be constant in the forms dissected.

Pars media superior

Origin. — From the premaxillary bone between the incisors, deep to the origin of pars media inferior.

Insertion. — Into the skin of the dorsum of the rostrum, piercing the nasolabialis superficialis, and into the skin of the mystacial pad.

Remarks. — This part consists of two rather well-differentiated slips. The anterior slip arises from the side of the median raphe between the incisors, superficial and medial to the origin of the other slip. The fibers

pass around the base of the nasal cartilage, coursing posterodorsad, deep to the tendons of pars maxillaris superficialis and pars maxillaris profundus, deep to pars interna and M. dilator nasi, onto the bridge of the rostrum, where they pierce the nasolabialis superficialis and insert into the skin. The fibers of the deeper, posterior slip arise from the anterolateral aspect of the incisive alveolus and pass onto the side of the rostrum where some insert into the mystacial pad. Most of the fibers continue caudodorsad, deep to the dilator nasi, to the dorsum of the rostrum, where they insert in the same manner as do those of the other slip. Some of the fibers extend into the region of the origin of M. dilator nasi and lie between that muscle and M. nasolabialis, with which they appear to be continuous.

In some specimens of *Sigmodon* there is also a third slip which lies deep to those described above (Fig. 4). This slip has a divided origin. Some of the fibers arise from the lateral border of the nasal bone immediately anterior to the point where its suture with the premaxillary begins; other fibers arise deep to the posterior part described above. These two groups of fibers meet and merge, passing directly caudad beneath the mystacial pad and are lost among the bases of the vibrissae. In one specimen these fibers continue posteriad and emerge from beneath the posterior border of the nasolabialis to end on the fascia of the M. sphincter colli profundus pars palpebralis immediately below the eye. A slip similar to this was found in *Peromyscus*, but it did not have the fibers arising from the free border of the nasal bone, nor could it be traced through the mystacial pad. In *Neotoma* pars media superior is similar to that of *Sigmodon*, but the third slip was not found in any of the specimens dissected. In *Oryzomys* the muscle is not so strongly developed, nor is it so well differentiated into the two parts.

Pars media inferior

Origin. — From the median raphe between the incisors immediately ventral to the nasal cartilage and from the adjacent margin of the upper lip.

Insertion. — Into the mystacial pad and the posterior part of the margin of the upper lip.

Remarks. — This part seems to be similar in all forms dissected. Most of the fibers attach to the bases of the vibrissae, each fiber forming a loop around a follicle.

Pars anterior

Origin. — From the nasal cartilage at the dorsolateral margin of the naris.

Insertion. — Into the margin of the upper lip.

Remarks. — This is a very thin slip of fibers passing around the side of the nasal cartilage, immediately caudal to the rhinarium. It passes superficially across the anterior end of pars media superior.

Pars anterior profunda

Origin. — From the nasal cartilage, deep to pars anterior.

Insertion. — Into the skin of the anterior part of the mystacial pad.

Remarks. — This bundle passes directly caudad and is lost among the fibers of pars media inferior.

Pars maxillaris superficialis

Origin. — By a tendon from the dorsolateral aspect of the nasal cartilage posterior to the naris.

Insertion. — By a very thin, loose aponeurosis onto the ventral part of the anterior border of the zygomatic plate and onto the body of the maxillary bone below this.

Remarks. — This slip lies deep to pars media inferior and M. maxillolabialis. It broadens somewhat posteriorly, becoming a very thin membrane which is pierced by many branches of the infraorbital nerve. In *Sigmodon* and *Oryzomys* the tendon by which this slip arises is only 1 or 2 mm. in length. In the former it is so short that origin sometimes appears to be directly by fleshy fibers. In *Neotoma* origin seems to be always direct, but in *Peromyscus* the muscle is tendinous for at least half of its length.

Pars maxillaris profunda

Origin. — By a short tendon from the lateral side of the nasal cartilage, ventral to the naris.

Insertion. — By a very thin aponeurosis onto the anterior margin of the zygomatic plate.

Remarks. — The remarks concerning the length of the tendon of origin of the preceding muscle apply equally to this muscle. The course of the fibers is almost directly caudad, turning slightly dorsad. The muscular fibers end in the region deep to the posterior part of the mystacial pad and are continued by a thin fascial sheet which is very weak and is pierced by most branches of the infraorbital nerve.

M. bucco-naso-labialis (M. buccinatorius of Howell, 1926)

Origin. — From the lateral side of the premaxillary and maxillary bones in the depression posteroventral to the bulge over the root of the incisor and anterior to the bulge of the nasolachrymal canal.

Insertion. — Into the anterior part of the margin of the upper lip and into the mucous lining of the mouth, after piercing the fibers of pars intermaxillaris of M. buccinatorius.

Remarks. — This muscle has two slightly differentiated parts. The anterior segment arises partly deep to the anterior border of the posterior part. Its fibers course more anteriad than do the posterior fibers and insert more laterally. This part, according to Meinertz (1942a), is the homologue of the M. bucconasalis which occurs in certain other rodents (e.g., *Dicrostonyx*). Differentiation is but slightly indicated in *Sigmodon*, however, and it is even less in *Neotoma*, *Peromyscus*, and *Oryzomys*.

The posterior part arises by fibers which overlap those of the anterior segment, passes caudoventrad, pierces the fibers of M. buccinatorius pars intermaxillaris near its posterior border, and inserts into the lining of the mouth.

In *Peromyscus* and *Neotoma*, as well as in *Oryzomys*, this muscle constitutes a single, continuous sheet in which I can find no evidence of differentiation into two segments except for a slight hiatus distally between the fibers which insert on the upper lip and those which insert into the lining of the mouth. The muscle is relatively much broader in *Neotoma* and *Peromyscus* than in the other two genera. This is probably correlated directly with the greater length of the rostrum in those forms, but is not entirely due to that factor since the origin is not restricted to the region posterior to the bulge over the incisor, but rather it encroaches to a considerable extent on the anterodorsal aspect of that bulge.

M. buccinatorius

The buccinator muscle is rather sharply differentiated into a number of discrete parts. Meinertz has described these parts in great detail in *Dicrostonyx* (1941) and in the Norway rat (1942a). Such a finely detailed analysis of relationships is beyond the scope of the present work, but the more important parts are described below in sufficient detail to allow comparison with other forms.

Superficial Anterior Parts

Pars intermaxillaris

Origin. — Along the premaxillary bone and median raphe of the palate from a point just posterior to the incisors, to the level of the junction of the anterior and middle thirds of the incisive foramina.

Insertion. — Into the margin of the upper lip, the skin of the chin, and the mucous lining of the mouth along a line extending posterodorsad from the corner of the mouth.

Remarks. — There is a slight differentiation of this sheet of fibers into two parts. The anterior half of the fibers insert primarily into the margin of the lip; some fibers continue around the corner of the mouth, merging with those of pars orbicularis oris to insert into the skin of the chin. The fibers of the posterior half of the sheet pass slightly more caudad, to the region posterodorsal to the corner of the mouth, where they interlace with the fibers of pars mandibularis anterior, turning deep to insert into the lining of the mouth. Relationships in this region are somewhat obscured by the insertion of M. platysma myoides pars buccalis.

Shortly laterad from its origin the pars intermaxillaris is pierced by two groups of fibers, those of M. bucco-naso-labialis and of pars intermaxillaris superficialis. There is little variation of this part among the forms studied. In *Neotoma* and *Peromyscus* it is somewhat wider anteroposteriorly, a condition correlated, no doubt, with the greater rostral length.

Pars intermaxillaris superficialis

Origin. — From the lining of the mouth, just lateral to the insertion of M. bucco-naso-labialis.

Insertion. — Into the skin of the upper lip.

Remarks. — This is an extremely thin layer of fibers which, after emerging from the pars intermaxillaris, are lost almost immediately among the fibers of pars media superior of M. nasolabialis profundus and of M. maxillolabialis. I was able to locate the proximal ends of the fibers and to confirm the presence of these fibers in the four genera, but was unable to trace them well enough to justify comparison.

Pars mandibularis anterior

Origin. — From the slight crest on the dorsomedial surface of the diastema of the mandible, just posterior to the symphysis.

Insertion. — Into the lining of the mouth along the line of insertion described under pars intermaxillaris.

Remarks. — In *Sigmodon* and *Oryzomys* this part is small, relatively less than half the width, anteroposteriorly, of that in *Neotoma* and *Peromyscus*. *Peromyscus* has a small posterior segment differentiated from the main part, which extends posterodorsad, overlying the ventral border of pars longitudinalis posterior ventralis.

The fibers of pars mandibularis anterior interlace with those of pars intermaxillaris, and many appear to be continuous with that part. Details of relationships in this region, however, are complicated by the insertion of M. platysma myoides pars buccalis.

Pars orbicularis

Origin. — From the dorsal surface of the mandible, immediately lateral to the posterior end of the symphysis.

Insertion. — Into the skin of the region ventral to the symphysis.

Remarks. — Fibers of this part pass at first caudolaterad, then turn ventrad around the lateral surface of the mandible. At the insertion there is some interlacing with the corresponding fibers from the opposite side. There is little variation in this muscle among the forms studied.

Pars orbicularis oris

Origin. — From the skin of the upper lip, principally in the posteroventral part of the mystacial pad.

Insertion. — Into the skin of the lower lip and subsymphysial region.

Remarks. — Fibers of this part appear to be continuous in the upper lip with those of M. nasolabialis profundus pars media inferior, and at the corner of the mouth with those of pars intermaxillaris. Meinertz (1941:49) described these same relationships in *Dicrostonyx*, and in regard to the continuity with M. nasolabialis profundus stated: "It is undoubtedly here a question of an original muscular connection between these two muscles."

Superficial Posterior Parts

Pars longitudinalis posterior dorsalis

Origin. — From the maxillary bone, just lateral to the alveoli of the molar teeth.

Insertion. — Principally into the lining of the mouth, just posterior to the junction of the upper and lower lips, piercing the fibers of pars intermaxillaris and pars mandibularis anterior. A few fibers pass into the skin, superficial to the latter part.

Remarks. — The fibers pass almost directly anteriad, turning very slightly ventrad. There is considerable variation in the development of this part among the forms studied. In *Sigmodon* it covers well over half the surface of the posterior part of the buccinator. In *Neotoma* it makes up at least two-thirds of the superficial posterior surface, and in *Oryzomys* and *Peromyscus* less than half of this area is taken up by this part. In *Sigmodon* and *Oryzomys* a few of the fibers pass into the skin at the corner of the mouth, but in the other two all the fibers pass deep to pars intermaxillaris and pars mandibularis anterior. Near the insertion the fibers of the dorsal border of this part are pierced by, and interlaced with, fibers of the posterior border of M. bucco-naso-labialis.

Pars mandibularis posterior

As used here, this term is the equivalent of the same term as applied by Meinertz (1942a) for the Norway rat, but is not equivalent to his use of it for *Dicrostonyx* (1941).

Origin. — From the mandible, along a line just lateral to the alveoli of the molars.

Insertion. — Into the skin of the mouth after piercing the pars longitudinalis posterior dorsalis, and, anteriorly, passing deep to pars mandibularis anterior.

Remarks. — The fibers run dorsoanteriad, becoming more nearly horizontal in the anterior part. Only the most anterior fibers reach and pass deep to pars mandibularis anterior. In *Sigmodon* this slip occupies nearly all the surface of the posterior part of the buccinator, except that covered by pars longitudinalis posterior dorsalis. In the other three forms less of the surface is covered by this segment. *Neotoma* approaches *Sigmodon*, having only a slightly less extensive pars mandibularis posterior. In *Peromyscus* this part is restricted to the caudal half of the posterior extension of the buccinator, leaving a large segment of pars longitudinalis posterior ventralis exposed. *Oryzomys* is almost directly intermediate in this respect between *Sigmodon* and *Peromyscus*.

Pars longitudinalis posterior ventralis

Origin. — From the mandible, just lateral to the alveoli of the molars and deep to pars mandibularis posterior.

Insertion. — Into the lining of the mouth, deep to pars mandibularis anterior and pars intermaxillaris, and into the lower lip.

Remarks.— This part appears to be rather consistent in the forms studied. Its fibers pass almost directly anteriad at first, but at the level of the first molar they begin to turn ventrad. In *Sigmodon* only a small part of this slip is visible superficially; most of it is covered by the pars mandibularis posterior. In the other forms it occupies more of the surface area, in inverse proportion to the development of pars mandibularis posterior (*q. v.*).

Hyoid Constrictor Group
(Figs. 6, 8, 9)

M. stylohyoideus, M. jugulohyoideus and the posterior belly of M. digastricus are supplied by the digastric branch of the facial nerve; M. stapedius receives its innervation from the stapedial branch of the facial nerve. This last branch is given off before the nerve trunk leaves the stylomastoid foramen.

M. digastricus (posterior belly)

Origin. — From the jugular process.

Insertion. — By a tendon which fans out over a triangular area anterior to the hyoid, with its apex on the mylohyoid raphe about one-fourth the distance from the hyoid to the symphysis.

Remarks. — With regard to the relationship of the posterior belly to the anterior belly, *Oryzomys* is similar to *Sigmodon*, and *Peromyscus* to *Neotoma*. Only *Sigmodon* and *Neotoma* will be discussed, therefore, and the remarks apply also to the other member of each pair.

As the digastric passes from its origin to the region of the hyoid, it converges to a small round bundle which becomes completely tendinous in *Sigmodon*. Immediately posterolateral to the hyoid bone it begins to curve mediad and at the same time commences to splay out, becoming more or less aponeurotic. This aponeurosis meets and interlaces with its mate from the opposite side, and the fibers attach on the ventral surface of the mylohyoid anterior to the hyoid. None of the tendon fibers continues directly into the anterior belly of the digastric. The fleshy fibers of the anterior belly arise from the anterolateral surface of the tendon of the posterior belly from the point where it begins to turn mediad to its insertion. In *Neotoma*, after the muscle has become partly tendinous, approximately half of the fibers continue directly into the anterior belly, becoming fleshy again. The medial half of the fibers turn mediad, as does the whole tendon in *Sigmodon*, and insert on the mylohyoid raphe immediately anterior to the hyoid arch. This half of the tendon gives rise along its anterior surface to fibers which make up the medial part of the anterior digastric belly.

Parsons (1894:254) has described two distinct types of digastric muscles: "In the Hystricomorpha the two bellies are not separated by a real tendon as in Man, although there is a slight constriction of the muscle, and a thin layer of tendon on the surface especially below; the attachment to the hyoid is very feeble...." Of the sciuromorphine type, he said:

"The anterior and posterior bellies are separated by a distinct tendon which is firmly attached to the hyoid bone. From the inner surfaces of the tendons of the two sides fibrous bands run inwards to meet one another, forming a tendinous arch with its convexity in front. From the front of this arch the two anterior bellies spring; . . ." It is seen that *Sigmodon* and *Oryzomys* possess the true sciuromorphine type of digastric. Hill (1937) has already pointed out that the digastric in *Neotoma* is intermediate in character between the two types.

If Edgeworth's (1914) conclusion that the mandibular belly of the digastric muscle is derived from the interramal muscles be accepted, the conditions found in the genera under consideration here lead to the conclusion that *Neotoma* and *Peromyscus* have passed through a stage represented by *Sigmodon* and *Oryzomys*, which possess a nearly typical sciuromorphine type of digastric.

M. stylohyoideus

Origin. — From the craniolateral aspect of the paroccipital process and from the aponeurosis, which also gives rise to the styloglossus.

Insertion. — On the deflected segment of the thyrohyoid bone.

Remarks. — In *Neotoma* the superficial fibers arise from the jugular process, but the deeper fibers arise from the stylohyal cartilage. In *Peromyscus* the origin is only from the stylohyal. *Oryzomys* presents relationships similar to those in *Sigmodon.*

The origin of part of the fibers of this muscle from the jugular process in *Neotoma* strongly suggests a transitional stage between the condition seen in *Peromyscus* (apparently the primitive condition) and that seen in *Sigmodon* and *Oryzomys.*

M. jugulohyoideus

The presence of this muscle in *Neotoma* was established by Sprague (1942). He stated: "Deep to the superficial fibers of the stylohyoideus, and not clearly delineated from them, a triangular group of fibers is found originating from the jugular process and inserting on the stylohyal, opposite the point of attachment of the stylohyoid. These apparently represent the jugulohyoid, a muscle frequently found when a stylohyal is present." I have found this description applicable to all specimens of *Neotoma* dissected. In *Peromyscus*, in which no fibers of the stylohyoideus extend across the stylohyal, a muscle is present which corresponds in all respects with a typical jugulohyoideus, and there can hardly be any doubt of its identity.

This muscle is much reduced in *Sigmodon* and *Oryzomys*, in which forms it is represented by a small, compact group of fibers lying in the cavity bounded by the jugular process, the mastoid bone, and the posterolateral corner of the bulla. These fibers arise from the lateral aspect of the jugular process, immediately deep to the aponeurosis of the styloglossus. They pass directly craniad to insert on a small cartilaginous or ligamentous structure which lies on the surface of the bulla and appears to be imbedded in the styloglossus aponeurosis. This "ligament" lies nearly at

right angles to the fibers of that aponeurosis, and its lateral end passes into the stylomastoid foramen, where it attaches to the mastoid process. It is my opinion that this structure is the vestige of the stylohyal, since its relationships correspond closely with those of the stylohyal in *Neotoma* (Sprague, 1942:406) and in *Peromyscus*.

M. stapedius

Origin. — From the walls of the depression between the mastoid bone and the cochlea, within the bulla.

Insertion. — On the "shoulder" of the posterior crus of the stapes, just before the crus turns to join the neck.

Remarks. — The stapedius muscle is relatively rather large in all four genera studied and completely fills the groove in which it lies. It is more or less conical, converging to a very thin, round tendon. In *Sigmodon* the greatest length is approximately 3 mm.; the thickness is about 1.5 mm. The facial nerve passes immediately lateral to the tendon and lies on the ventrolateral surface of the anterior half of the muscle. Relationships of this muscle appear to be quite similar in all four general.

Glossopharyngeal Group
(Fig. 6B, C)

M. stylopharyngeus, the only member of this group discussed here, is supplied by a small branch from the glossopharyngeal nerve.

M. stylopharyngeus

Origin. — By aponeurosis from the jugular process.

Insertion. — Into the pharynx, beneath the caudal border of the middle constrictor.

Remarks. — The aponeurosis by which this muscle arises is described in the remarks under M. styloglossus. In some specimens of *Sigmodon* the muscle is divided shortly before insertion, and a branch of the glossopharyngeal nerve passes between the two segments. This same divided condition was described by Sprague (1942) for *Neotoma*, but no mention was made of the relationship to the nerve. I have seen no specimens of *Neotoma* or *Peromyscus* in which this division occurred, but it does occur in at least some specimens of *Oryzomys*. Whether or not the muscle is split is probably a matter of individual variation in those forms, as well as in *Sigmodon*. In *Neotoma* and *Peromyscus* this muscle arises from the stylohyal, just medial to the insertion of M. jugulohyoideus.

Trapezius Group
(Figs. 8, 9, 11)

These muscles have a dual innervation, from the inferior branch of the spinal accessory nerve and from branches of the second and third cervical nerves, through the subtrapezial plexus.

M. sternomastoideus

Origin. — From the cranial half of the ventral side of the manubrium sterni and the immediately adjacent part of the clavicle.

Insertion. — In common with M. cleidomastoideus, on a small tubercle on the caudal rim of the auditory meatus.

Remarks. — Only *Neotoma* has relationships which differ essentially from those seen in *Sigmodon*. In that form some of the fibers insert on the end of the mastoid process of the squamosal; however, most of the fibers attach as in *Sigmodon*.

M. cleidomastoideus

Origin. — From the clavicle, just medial to the origin of M. cleido-occipitalis.

Insertion. — By tendon onto a small protuberance on the border of the auditory meatus, just ventral to the end of the mastoid process of the squamosal.

Remarks. — This muscle lies deep to M. sternomastoideus and M. cleido-occipitalis and is between them. The other three forms differ slightly from *Sigmodon* in the manner of insertion of this muscle. In *Neotoma* approximately half the fibers insert as in *Sigmodon*, and the remaining fibers attach to the mastoid bone, along the dorsal rim of the stylomastoid foramen. This same relationship is found in *Peromyscus* and *Oryzomys*, but in these forms even more of the fibers pass to the mastoid bone.

M. cleido-occipitalis

Origin. — From the middle third of the clavicle.

Insertion. — Onto the posterior aspect of the most ventral part of the lambdoidal crest, just dorsal to the end of the mastoid process of the squamosal and ventral to the junction of the lambdoidal and superior temporal crests.

Remarks. — In *Sigmodon* this muscle does not come into direct contact with the M. acromiotrapezius, but in *Neotoma* and *Peromyscus* the insertion is very broad, extending along the entire superior nuchal line and onto the dorsal mid-line for some 7 to 10 mm. posterior to the occiput. Here its posterior border is in such close contact with the anterior border of M. acromiotrapezius that the two muscles appear to form a continuous sheet of fibers. In *Oryzomys* the muscle is narrow and inserts as in *Sigmodon*. The close relationship of the cleido-occipitalis and the acromiotrapezius apparently led Howell (1926) to identify the former with the clavicular part of the trapezius. The two muscles are, however, separated by the greater auricular nerve (Hill, 1937). Wood (1870) first described and named this muscle in the Norway rat and certain other mammals. Greene (1935:35) called it M. clavotrapezius but also recognized it as M. cleido-occipitalis.

M. acromiotrapezius

Origin. — Along the dorsal mid-line, from just caudal to the superior nuchal line, to the spine of the second thoracic vertebra.

Insertion. — On the distal two-thirds of the scapular spine, the acromion, and the lateral one-fourth to one-third of the clavicle.

Remarks. — This is probably homologous with both the acromial and clavicular segments found in other mammals (Hill, 1937). The clavicle is not involved in the insertion of this muscle in either *Neotoma* or *Peromyscus*. In the former the fibers insert as far distad as the proximal two-thirds of the acromion; in the latter they hardly encroach on the acromion at all. *Oryzomys* resembles *Sigmodon* in having some, though fewer, of the fibers attached to the clavicle.

M. spinotrapezius

Origin. — Along the dorsal mid-line from the level of the seventh thoracic vertebra to the third lumbar vertebra.

Insertion. — Onto approximately 5 mm. of the spine of the scapula near the junction of its proximal and middle thirds.

Remarks. — Origin of this muscle is aponeurotic below the level of the eleventh or twelfth thoracic vertebra. The insertion is much restricted in relation to that in *Neotoma*, in which the whole dorsal third of the scapular spine is involved in addition to a ligament or tendon which extends dorsad from the end of the spine (Howell, 1926:46, and Fig. 6). *Peromyscus* presents relationships similar to those in *Neotoma*. *Oryzomys* closely resembles *Sigmodon* in the insertional relations of this muscle.

There is a small band of fibers which detaches from the lateral border of the spinotrapezius and, instead of inserting on the scapula, continues anteriad into the neck region, passes deep to M. platysma myoides, and is lost in the region immediately behind the ear. This is a well-defined band in *Sigmodon* and *Oryzomys* but is much reduced in the other two forms, particularly in *Neotoma*, in which it often consists only of a strip of fascia that does not appear to contain muscle fibers. Various authors have described this slip in many rodents. It is present in the following rodents: *Marmota* (Bryant, 1945), *Mus* (Alezais, 1900), *Dicrostonyx* (Meinertz, 1941), *Rattus* (Meinertz, 1942a), and certain others. I have also seen it in *Tamiasciurus*, *Microtus*, *Ondatra*, and *Pitymys*. In all instances checked this slip has been innervated by a branch of the accessory nerve. The topographical relations of the band at its origin and for most of its course are the same as those of the "Retractor der Backentasche" described in *Cricetus* by Schreiber (1929), and also the same as those of the posterior part, at least, of the retractor of the pouch in the Geomyidae (Hill, 1937). It would appear that this slip is actually homologous with that mentioned in *Cricetus* and partly homologous with the retractor of the pouch in the pocket gophers. All the muscles of the cheek pouch of the sciurids, as described by Bryant (1945), appear to be derived from the facialis musculature and probably have no relation to the present slip.

Lingual Group
(Fig. 6B, C)

The three muscles of this group are supplied by small branches of the hypoglossal nerve.

M. genioglossus

Origin. — From the medial surface of the mandible, just posterior to the symphysis.

Insertion. — Onto the hyoid bone, deep to M. hyoglossus, and into the median fascial plane or raphe of the tongue.

Remarks. — In *Oryzomys* the anterior, superficial part of this muscle is divided into two slips, and a branch of the hypoglossal nerve passes between them. This condition was described by Howell (1926) for *Neotoma*. No such splitting of the muscle was seen in *Sigmodon* or *Peromyscus*, but it might have been overlooked.

M. hyoglossus

Origin. — From the anterior aspect of the basihyal and the thyrohyal.

Insertion. — Into the lateral part of the tongue.

Remarks. — The fibers pass craniolaterad to merge with those of M. styloglossus and continue craniad in the ventrolateral part of the tongue.

M. styloglossus

Origin. — By a broad, thin aponeurosis from the jugular process, the mastoid bone, and the posterolateral aspect of the bulla, including the ventral rim of the auditory meatus.

Insertion. — Into the lateral part of the tongue.

Remarks. — The nearly complete suppression of the stylohyal in *Sigmodon* and *Oryzomys* has, of course, been accompanied by shiftings of the muscles which ordinarily attach to that structure. The relationships of these muscles in *Peromyscus* appear to be the most primitive. In this genus the styloglossus arises almost entirely from the stylohyal, with only a very few fibers of the lateral border of the muscle taking origin from the rim of the auditory meatus. Howell (1926) said that the origin of this muscle in *Neotoma* "should apparently be considered as from the slight process upon the infero-posterior margin of the auditory meatus rather than from the mastoid, as is usually stated to be the case in rodents." According to my observations, however, Sprague (1942) was correct in pointing out that "only a small part of its origin is from the auditory meatus. Most of the relatively broad tendon by which the styloglossus takes its origin is attached to the stylohyal." This differs from the condition found in *Peromyscus* only in that a larger part of the muscle finds origin on the margin of the meatus. From this stage there is needed only an extension of the attachment to the bulla and a reduction of the stylohyal to bring about the condition found in *Sigmodon* and *Oryzomys*. This has resulted in a broad, thin aponeurosis lying in intimate contact with the ventral surface of the bulla, attaching along the inferior border of the meatus to the mastoid

process and to the jugular process. Imbedded in this aponeurosis is the vestigial stylohyal (see remarks under M. jugulohyoideus, p. 37).

Myotomic Musculature

Dorsal Division

The dorsal division comprises all the epaxial muscles of the body. These muscles are supplied by branches of the dorsal (posterior) primary divisions of the spinal nerves. No attempt was made to determine precisely the innervation of any muscles of this group except M. splenius and the suboccipital muscles. The splenius is innervated by lateral branches of the posterior divisions of at least the second, third, and fourth cervical nerves. Innervation of the muscles of the suboccipital group is given under that heading.

Superficial Spino-occipital Group
(Figs. 9A, 11)

M. splenius

Origin. — Along the ligamentum nuchae from immediately posterior to the occiput to the level of the spine of the second thoracic vertebra.

Insertion. — Onto the ridge formed by the lateral part of the parieto-interparietal suture and onto the lambdoidal crest as far laterad as the mastoid process of the squamosal.

Remarks. — In some specimens of *Sigmodon*, *Oryzomys*, and *Neotoma* a narrow band of the lateral fibers is separate, as described by Howell (1926). When this separation occurs, the lateral slip always inserts by aponeurosis. In *Sigmodon* this muscle encroaches on the dorsum of the skull, extending across and covering the lateral part of the interparietal. In *Neotoma* and *Peromyscus* this does not occur, and the fibers insert along the interparieto-occipital suture. In *Oryzomys*, although the splenius does not cover any part of the interparietal, insertional relations are more like those in *Sigmodon*. Here the fibers insert on the parieto-exoccipital suture immediately lateral to the end of the interparietal. If this line of insertion were extended across the top of the brain case, it would pass anterior to the interparietal, whereas the line of insertion in *Neotoma* and *Peromyscus* is at a level posterior to the interparietal.

Sacrospinalis Group
(Figs. 7A, B, C, F, G; 9; 11; 16)

In rodents the general mammalian tendency toward fusion of the elements of this group with one another and with the transversospinal fascia has been carried almost to completion. In the lumbosacral region there is formed a single muscle mass which is usually called M. erector spinae. Additional attachment to the spines of the lumbar and sacral vertebrae has been gained by the development of the heavy superficial lumbosacral aponeurosis, consisting of broad flat tendons (Slijper, 1946:49).

Howell (1926) considered all this lumbosacral muscle mass as M. longissimus pars lumborum and divided it into parts "lateralis" and "medialis" on the basis of origin of the fibers. His discussion of the relations of these fibers to the fascia applies almost equally well to all four genera under consideration here, but it is my opinion that those fibers which he assigned to his M. longissimus pars lumborum lateralis actually represent the M. iliocostalis lumborum.

In the thoracic region analysis of the spinal muscles is complicated by the origin of fascicles of the longissimus and the transversospinal system from the metapophyses by common tendons. Furthermore, M. spinalis is not completely differentiated from the transversospinal muscles. All this leads me to emphasize that the assignment of certain fascicles to one muscle or another is perhaps questionable.

The erector spinae mass takes origin from both surfaces of the lumbosacral aponeurosis, the metapophyses and sides of the anterior sacral and all the lumbar vertebrae, and the anteromedial surface of the ilium (these last fibers represent the M. iliolumbalis, Slijper, 1946). The fibers arising from the superficial surface of the aponeurosis are restricted to the lateral side of the mass, not extending medial to a line drawn directly anteriad from the crest of the ilium. These fibers pass anteroventrad around the border of the muscle mass, then anteromediad to their insertions on the transverse processes of the vertebrae. At the level of the fourth lumbar vertebra the more superficial fibers begin to take a course more directly anteriad and separate from the other fibers, forming a small but discrete slip which inserts on the last two ribs. This slip constitutes the only separate part of the iliocostalis lumborum.

The lumbosacral aponeurosis consists of two definite layers. The more superficial layer arises by broad, flat tendons from the spines of the second lumbar to third sacral vertebrae, passing anterolaterad. As this layer passes over the region of the metapophyses, it is joined on its deep side by similar tendons which arise from the metapophyses and reach the surface by passing dorsocraniad between the medial (transversospinal) muscles and the longissimus. Muscle fibers of the longissimus arise from these last-mentioned tendons and from the deep surface of the common aponeurosis formed by their fusion with the tendons from the spines. The deepest fibers of this common lumbar mass take origin directly from the mammillary processes of the vertebrae and insert on various parts of the more anterior vertebrae, so that the various fascicles might be referred to as Mm. mammillostyloidei, intertransversarii, and mammillotransversarii (Slijper, 1946, Fig. 47).

M. iliocostalis lumborum

This muscle has been described above. In *Neotoma* the segment which inserts on the last two ribs is relatively much smaller than in *Sigmodon*. It does not appear to be so reduced in *Peromyscus*. In *Oryzomys* insertion is onto the last three ribs (10-12), and the slip is at least as robust as in *Sigmodon*.

M. iliocostalis dorsi

Origin. — From the anterior borders of ribs 8 to 11 by fleshy slips.

Insertion. — By three thin, flat tendons onto the posterior borders of ribs 4 to 6.

Remarks. — The thoracic and cervical parts of the iliocostalis are well differentiated from M. longissimus and are easily separated from it. The dorsal part varies only slightly among the forms studied. In *Neotoma* there is occasionally a slip from the twelfth rib, but usually origin is from ribs 8 to 11, and the insertion extends to the third rib, except in the subgenus *Teonoma* in which there is no attachment to the third rib, and origin is only from ribs 8 to 10 (Howell, 1926). *Peromyscus* is similar to *Sigmodon*, but with a slip inserting on the seventh rib as well as the three on ribs 4 to 6. In *Oryzomys* fibers of this part take origin from ribs 8 to 10, with insertion on ribs 3 to 6.

This part of the iliocostalis is relatively much thinner in *Neotoma* and *Peromyscus* than in the other two genera.

M. iliocostalis cervicis

Origin. — From the anterior borders of ribs 4 to 8.

Insertion. — On the transverse processes of the seventh cervical and first thoracic vertebrae and on the tubercle of the first rib.

Remarks. — In *Neotoma* and *Oryzomys* there is also a slip from the third rib. Insertion may extend as far anterior as the transverse process of the fourth cervical vertebra in *Oryzomys* and to the sixth cervical vertebra in *Peromyscus* and *Neotoma*.

The small variations in the attachments of the various parts of the iliocostalis described above are probably of little significance. Indeed, one might expect the entire range of variation observed in the four genera to be covered in individuals of the same genus. The relative size, or amount of development, of the muscle, however, seems to be rather constant for each genus. In this respect *Neotoma* and *Peromyscus* are similar in having this muscle poorly developed in contrast to the condition found in *Sigmodon* and *Oryzomys*.

M. longissimus

The lumbar part of this muscle has been partly described above. As was stated, Howell assigned the entire sacrospinalis mass to the longissimus. It seems more reasonable, however, to consider the "longissimus lumborum lateralis" of Howell as the lumbar part of M. iliocostalis. This interpretation was followed by Hill (1937:110) whose remark on the fibers of this mass which insert on the transverse processes of the lumbar vertebrae was: "Since these processes are serially homologous to ribs, the slips probably should be considered as representing part of the iliocostalis." It appears that only the fibers of the sacrospinalis mass which arise from the spinous processes and metapophyses of the lumbar and sacral vertebrae (longissimus lumborum medialis of Howell) are more properly considered to represent the longissimus in that region. There is

no differentiation of this lumbar part from the thoracic part of the longissimus, the mass being directly continuous.

M. longissimus dorsi

Origin. — Continuous with the lumbar segment of this muscle, from the lumbosacral aponeurosis formed by the fused tendons from the spines of the second lumbar to fourth sacral vertebrae, and from the metapophysis of the second lumbar to second sacral vertebrae. Additional fibers take origin from the lateral sides of tendons which arise from the metapophyses of the eleventh thoracic to first lumbar vertebrae but do not enter into the formation of the lumbosacral aponeurosis.

Insertion. — On the accessory processes of the lumbar and last three thoracic vertebrae, the undivided processes of the sixth to ninth thoracic vertebrae, the metapophyses of the lumbar and last two thoracic vertebrae, the last ten ribs, and the costal elements of the last three cervical vertebrae.

Remarks. — In the thoracic region the tendons arising from the metapophyses give rise on their medial sides to fibers of the transversospinal system; there are no discrete tendons of origin for that system.

Only minor variations in the longissimus dorsi were encountered. In *Neotoma* origin from the spines extends one or more segment anteriad, and the insertions on the metapophyses extend forward to the tenth thoracic segment. *Peromyscus* has the origin from the spines only as far forward as the third lumbar vertebra. In this form, in addition to slips which correspond with those described for *Sigmodon*, there are slips which insert on the superficial aponeurosis of the levatores costarum of the second to sixth ribs, thus attaching indirectly to the transverse processes of the first five thoracic vertebrae. In *Oryzomys* slips insert as far forward as the process of the third cervical vertebra. As in *Sigmodon*, there are no fibers which insert on the transverse processes of the first five thoracic vertebrae. The fascicle which in *Sigmodon* inserts on the transverse process of the sixth thoracic vertebra attaches in *Oryzomys* on the surface of the levator costae of the seventh rib.

M. longissimus cervicis

Origin. — From the anterior aspect of the tubercles and necks of ribs 2 to 6, the transverse process of the first thoracic vertebra, and the sides of the superior articular processes of the last five cervical vertebrae.

Insertion. — On the costal elements of the last six cervical vertebrae.

Remarks. — The cervical part of the longissimus is a discrete element in all four genera. In *Neotoma* origin is as in *Sigmodon*, except that there are fibers arising also from the transverse processes of the second and third thoracic vertebrae. *Peromyscus* is similar to *Neotoma* in this respect, but has no fibers arising from the sixth rib. In *Oryzomys* this muscle is very small. Its origin is from the second and third ribs and from the transverse processes of the third cervical to first thoracic vertebrae.

M. longissimus capitis (*M. complexus* Howell, 1926; *M. trachelomastoideus* autt.)

Origin. — From the anterior borders of the fourth to sixth ribs, immediately lateral to their tubercles and from the transverse processes of the second and third thoracic vertebrae.

Insertion. — On the end of the mastoid process of the squamosal and on the immediately adjacent part of the lambdoidal crest.

Remarks. — The slips of this muscle which arise from the second and third thoracic vertebrae and the slip from the sixth rib are very small; most of the muscle is made up of those fibers which take origin from the fourth and fifth ribs.

This muscle lies between the cervical segment of the longissimus and the semispinalis capitis. It is distinct from both. A distinct tendinous inscription crosses the muscle between its anterior and middle thirds.

In *Neotoma* this part of the longissimus is relatively small and rises only from the transverse processes of the first two thoracic vertebrae and the sides of the articular processes of the last three cervicals. *Peromyscus* differs in having the origin of this muscle from the tubercle and neck of the fourth rib, the transverse processes of the first three thoracic vertebrae, and the sides of the last two cervical vertebrae; in this form the muscle is considerably thinner than in *Sigmodon.* In *Oryzomys* this muscle appears to be at least as robust as in *Sigmodon,* although the origin is somewhat more restricted; the fibers take origin from the transverse process of the third thoracic vertebra and the tubercles of the third to fifth ribs.

Semispinalis Group (M. transversospinalis, *s. l.*)
(Figs. 7A, D, E, F; 9; 11)

The term "transversospinalis" is used here, as it was used by Slijper (1946:52), to include all the muscle elements lying between the zygapophyses and the spines of the vertebrae. His definitions of the parts of this complex are also applied here. Slijper (1946:52) supposed that the primitive transversospinal muscle is "composed of semispinalis-, multifidus-, submultifidus-, interspinalis-, and intermammillaris-fascicles fused into a solid mass, in which the separate elements cannot be clearly distinguished." This situation still obtains in the postdiaphragmatic region of *Sigmodon* and in the other three genera investigated.

The transversospinal elements of the sacral and caudal regions make up a distinct muscle which is described below as M. extensor caudae medialis. The following discussion applies to that part of the system which arises posterior to the eleventh thoracic vertebra, exclusive of that caudal muscle.

In the anterior sacral and lower lumbar region short tendons arising from the metapophyses of each vertebra give off muscle fibers which insert on the sides of the spinous processes of the next three vertebrae anterior to the level of origin. These fibers represent the rotatores breves, rotatores longi, and the multifidus, according to whether they span one, two, or three segments, respectively. The fibers are not grouped into fascicles,

but form a continuous mass across the entire lumbar region. In this mass there are no fibers which can be considered as semispinalis elements, if that term be restricted to fibers which insert on the fourth (or more) vertebra from their origin. Some of the fibers which arise from the tendon attaching to the zygapophysis of the first lumbar vertebra do extend as far forward as the tenth thoracic vertebra, thus establishing the posterior limit of the semispinalis, which is well developed in the region between the first and last thoracic vertebrae. The muscle fibers of the semispinalis take their origin from the mediodorsal borders of the same tendons which give rise on the opposite borders to fibers of M. longissimus. The appearance of these tendons and the muscle fibers is thus distinctly penniform.

The semispinalis mass is continuous laterally with a group of fibers which take origin from the surface of the anteromedial part of the lumbodorsal fascia. The latter fibers are interpreted as representing the M. spinalis. They are actually continuous with many of the fibers of the aponeurosis which have their ultimate origin on the spines of the first two lumbar vertebrae, and since the insertion is with the semispinalis on the spines of the anterior thoracic vertebrae, they do, in a sense, connect the spinous processes of the vertebrae. Except for the difference in their origin, the semispinalis and spinalis fibers form a single, indivisible mass. Howell (1926) treated these combined (or undifferentiated) muscles as M. spinalis dorsi, a procedure which has been followed by certain other authors (e.g. Winckler, 1939). As Slijper (1946:52) pointed out, however, they should not be so considered (cf. also Virchow, 1916, and Plattner, 1922).

The spinalis is also developed in the sacrolumbar region. Here, fibers arise from the sides of the spinous processes of the last two or three lumbar vertebrae and pass posteriad, deep and medial to M. flexor caudae medialis, to insert on the second or third vertebra caudal to the origin.

The Mm. interspinales are developed between all the consecutive spines anterior to the sacrum, except in the mid-thoracic region (fifth to ninth thoracic vertebrae).

The region between the eleventh and thirteenth thoracic vertebrae is a transitional zone where the shorter elements of the transversospinal system begin to separate into discrete fascicles. Anterior to the eleventh thoracic segment, the rotatores breves and rotatores longi occur as distinct muscles. This is in keeping with Slijper's (1946:53) statement that differentiation of the transversospinal system into its different components has taken place first in the prediaphragmatic region. Thus, the four genera under discussion might be added to his list of mammals "that show in this region a highly differentiated transversospinalis, while in the postdiaphragmatic region the muscle shows still the undifferentiated structure...."

The intermammillares occur as far anterior as a position between the seventh and eighth thoracic vertebrae. Slijper found them in the prediaphragmatic region only in *Choloepus* and *Psammomys*.

The variation in the general relationships of the semispinalis is rather small among the four genera studied, but if the muscle is examined with close attention to the insertion of the fibers which arise from individual vertebrae, certain facts come to light which may be significant. These are shown in Table I.

TABLE I

Comparison of Insertion of the Semispinalis in the Four Genera

Origin	Insertion			
	Sigmodon	*Neotoma*	*Peromyscus*	*Oryzomys*
L 2	T 12, 13, L 1	T 12, 13, L 1	T 12, 13, L 1	T 13, L 1
L 1	*T 10-13	*C 7-T 13	*T 1-or 2-13	T 12, 13
T 13	*T 1-11 or 12	*T 1-12	*T 1-12	*T 1-12
T 12	*T 1-10	*T 5-or 6-11	*T 5-10	*T 2-10 or 11
T 11	*T 3-9 or 10	T 9, 10	T 8-10	*T 2-10
T 10	T 8, 9	T 8, 9	T 8, 9	T 8, 9

*Semispinalis
L, T, and C signify lumbar, thoracic, and cervical, respectively.

It may be seen from this table that the posterior attachments of the semispinalis in *Neotoma* and *Peromyscus* are one segment anterior to the corresponding attachments in *Sigmodon* and *Oryzomys*. It is true that the fibers which arise from the first lumbar vertebra and insert on the tenth thoracic vertebra in *Sigmodon* might be considered as part of the semispinalis, but they certainly do not stand in the same class with those fibers in *Neotoma* which span the entire thoracic series of vertebrae. Note should also be made of the fibers from the twelfth thoracic vertebra. Here again *Neotoma* and *Peromyscus* are similar in that the fibers extend only as far anteriad as the fifth thoracic vertebra, whereas in *Sigmodon* and *Oryzomys* these fibers continue as far as the first and second thoracic vertebrae.

The only transversospinal elements which arise from the eighth to tenth thoracic vertebrae are the rotatores and intermammillares. At the level of the seventh thoracic segment, and anterior to it, fascicles of the M. semispinalis capitis and M. semispinalis cervicis are found.

The semispinalis capitis takes origin by slips from the tubercles and necks of the fourth to seventh ribs, the transverse processes of the first four thoracic vertebrae, and the laminae of the last five cervical vertebrae. Insertion is along the occipital crest, dorsal and medial to the mastoid bone. As in many mammals, this muscle in *Sigmodon* is divided into two distinct parts. One of these (M. biventer cervicis autt.) comprises the fibers arising from the fourth thoracic vertebra and the fourth to seventh ribs. These fibers merge into a sheet which passes almost directly anteriad, to insert on the medial 4 to 5 mm. of the occipital crest and onto the superficial aponeurosis of the other part. Two tendinous inscriptions divide this sheet of fibers into approximate thirds.

The other part (M. complexus autt.) is made up of those fibers arising from the third cervical to third thoracic vertebrae, inclusive. These fibers insert on an aponeurosis which develops on the superficial surface of the sheet and attaches in turn to the occipital crest, from the mid-line to the dorsomedial margin of the mastoid bone. This part is crossed near the middle by a tendinous inscription.

In *Neotoma* the two parts of the semispinalis capitis are not clearly separated, although the origins are distinct. Howell (1926) treated both parts as M. biventer cervicis and applied the term M. complexus to the longissimus capitis. In this genus origin of the posterior part is from the tubercle and neck of the third to seventh ribs, inclusive, and from the transverse processes of the second and third thoracic vertebrae. These fibers, although not separate from those of the anterior part, have the same relationships otherwise as in *Sigmodon*. The anterior part arises from the transverse process of the axis and the laminae of the third cervical to first thoracic vertebrae. Insertion of this part is aponeurotic as in *Sigmodon*. Two tendinous inscriptions are present in the muscle. The more posterior inscription crosses only the fibers of the "complexus"; the other extends across the entire muscle.

The two elements of the semispinalis capitis of *Peromyscus* are separate as in *Sigmodon*. Origin of the caudal part is from the fifth to seventh ribs and from the transverse process of the fourth thoracic vertebra. Two tendinous inscriptions are present, of which the posterior crosses only those fibers from the sixth and seventh ribs. The anterior part of the muscle arises from the transverse processes of the three anterior thoracic vertebrae and from the laminae of the last five cervical vertebrae. A single tendinous inscription crosses this part, as in *Sigmodon*. Relationships of the semispinalis capitis in *Oryzomys* are almost the same as in *Sigmodon*.

The transversospinal fibers of the anterior thoracic and cervical regions, which lie deep (medial) to the semispinalis capitis, form a discrete muscle mass which must be considered as the semispinalis cervicis. The fibers composing this mass take origin from the tubercles and necks of the fifth to seventh ribs, the transverse processes of the second to fifth thoracic vertebrae, and the laminae of the last four cervical vertebrae. Insertion is on the spines of the first thoracic and last six cervical vertebrae. This muscle is generally similar in all four genera, with the minor differences that no fibers arise from the seventh rib in *Neotoma* or from the sixth and seventh in *Peromyscus*.

M. extensor caudae medialis

This muscle is the direct posterior continuation of the transversospinal system. The fibers are first noticeably differentiated at the level of the last lumbar vertebra, and fibers continue to arise from the vertebrae well into the tail. The muscle fibers end in long tendons which pass into the tail to attach to the dorsal parts of the caudal vertebrae. In *Oryzomys* this muscle is developed to approximately the same extent as in *Sigmodon*, but in *Neotoma* and *Peromyscus* fibers from the fifth, and perhaps even the fourth, lumbar vertebra are included in this muscle.

Mm. intertransversarii dorsales

The lateral elements of the dorsal intertransverse muscles of the neck region are discussed later. There are other short fascicles in the neck, however, which I believe represent the medial elements of this series.

These are small bundles of fibers which arise from the sides of the cervical vertebrae, pass craniolaterad, and insert on the transverse processes of the first or second vertebra anterior to the origin. There is a tendency for the more anterior fascicles to extend across more segments. Those fibers which arise from the third to fifth cervical vertebrae and insert on the transverse process of the atlas have been referred to by Howell (1926) and Bryant (1945) as M. longus atlantis. The applicability of this term is discussed later.

In order to establish a basis for the identification of these elements, it is necessary to quote from Grant, in Morris' *Human Anatomy* (10th ed., p. 482):

> In the cervical region there is typically an anterior and a posterior intertransverse muscle in each intervertebral space, the posterior muscle being divisible into a lateral and a medial portion. Actually, then, there are three distinct muscle elements – ventral, lateral, and dorsal. An *anterior intertransverse* muscle (ventral element) is a small, flat, quadrilateral muscle-sheet connecting the opposed borders of the anterior limbs of two adjacent transverse processes and also their anterior tubercles. The muscle between the atlas and axis is suppressed; so is that between the seventh cervical and the first thoracic vertebrae (though perhaps represented by the occasional scalenus minimus). The *posterior intertransverse* muscles are similar to the anterior muscles in shape, direction, and extent of attachment; each connects the opposed borders of the posterior limbs of two adjacent transverse processes and also their posterior tubercles. The anterior muscles and the lateral parts of the posterior muscles (lateral element) are homologous with intercostal muscles and are supplied by the anterior divisions of the corresponding spinal nerves; the medial parts of the posterior muscles (posterior element) belong to the intrinsic muscles of the back and are supplied by posterior divisions. The three elements are represented between the atlas and the skull by the rectus capitis anterior, rectus capitis lateralis, and obliquus capitis superior, respectively; and the nerve-supply of these muscles is homologous with that of the intertransversarii. The vertebral artery runs vertically between each pair of muscles above the sixth, and the anterior division of each cervical nerve passes laterally between the artery and the posterior muscle in each case and then out between the anterior and posterior muscles. The posterior division of each cervical nerve passes medial to each posterior muscle (Cave).

In the four genera under consideration here, the muscles to which I apply the term intertransversarii dorsales lie lateral to M. semispinalis capitis and medial to the origin of M. levator scapulae; the last muscle separates them from the lateral intertransverse elements. They are dorsal to the vertebral artery. The posterior divisions of the cervical nerves send small branches to these muscles and pass dorsad on their medial surfaces. These relationships are so similar to those given in the quotation above that the muscles in question must be, in my opinion, homologous with the medial elements of the human intertransversarii dorsales.

As was pointed out above, the fascicles of this group which attach to the transverse process of the atlas have been called M. longus atlantis by Howell (1926) and Bryant (1945). Such an application of this term leads only to confusion, since it has long been used to designate the superior oblique part of M. longus colli (Hoffmann and Weyenbergh, 1870; Leche, 1900). Furthermore, since they are a part of the series of intertransversarii dorsales, there is no need for a more specific term for these particular fibers.

Suboccipital Group
(Not Figured)

The four muscles of this group have the typical relationships and show almost no variation. Innervation of Mm. rectus capitis posterior major and minor and M. obliquus capitis superior is from the suboccipital nerve (dorsal division of the first cervical nerve). The M. obliquus capitis inferior is supplied by the dorsal division of the second cervical nerve.

M. rectus capitis posterior major

Origin. — From the anterolateral surface of the tip of the axis.
Insertion. — On the supraoccipital region, lateral to the rectus fossa.

M. rectus capitis posterior minor

Origin. — From the anteromedial surface of the dorsal arch of the atlas.
Insertion. — On the supraoccipital region, medial to the rectus fossa, deep and medial to M. rectus capitis posterior major.
Remarks. — All but the most medial part of this muscle is covered by the rectus capitis posterior major.

M. obliquus capitis superior (*M. rectus capitis lateralis* Howell, 1926)

Origin. — From the dorsoanterior part of the transverse process of the atlas.
Insertion. — On the exoccipital, just lateral to the insertion of M. rectus capitis posterior major, and posteromedial to the caudolateral corner of the occiput.

M. obliquus capitis inferior

Origin. — From nearly the whole dorsolateral surface of the lamina and spine of the axis.
Insertion. — On the dorsoposterior surface of the transverse process of the atlas.
Remarks. — This muscle appears to be considerably stronger in *Oryzomys* than in the other three genera.

Ventral Division

Included here are all the skeletal muscles of the body which have not been treated above. These are innervated by the branches of the ventral (anterior) primary divisions of the spinal nerves. In treating these muscles the arrangement of Hill (1937) has been followed, except for one change. The Mm. extensores breves of the second and third digits of the foot have been placed in the tibial extensor group, rather than in the peroneal group, for reasons given in the discussion of those particular muscles. Hill (1937:111) gave separate treatment to the appendicular muscles since "it is not possible to homologize satisfactorily muscles of the appendages with those of the body wall...."

Cervical Prevertebral Group
(Not Figured)

As the ventral rami of the cervical and anterior thoracic spinal nerves leave the intervertebral foramina, they give off small branches to the muscles of this group.

M. rectus capitis anterior

Origin. — From the anteroventral margin of the transverse process of the atlas.

Insertion. — On the posterolateral part of the ventral surface of the basioccipital.

Remarks. — M. rectus capitis anterior lies in contact laterally with M. rectus capitis lateralis and is separated from it by the anterior (ventral) primary division of the first cervical nerve, from which both muscles receive branches.

M. longus colli

The superior and inferior parts of this muscle are not sharply differentiated. The inferior part arises from the ventrolateral aspect of the last two cervical and first five thoracic vertebrae. The origin of the thoracic slips encroaches on the heads of the ribs attaching to those vertebrae. Insertion is on the carotid tubercle of the sixth cervical vertebra, on the superficial aponeurosis of the posteromedial part of the superior segment of this muscle, and on the bodies of the second to fifth cervical vertebrae. *Peromyscus* and *Neotoma* have slips arising from the head of the fifth rib, from the bodies of the vertebrae and heads of the ribs in the first four thoracic segments, and from the body of the seventh cervical vertebra. In *Oryzomys* there is an additional slip from the head of the sixth rib. Insertion in these forms is like that in *Sigmodon*.

The superior part takes origin from the medial surface of the carotid tubercle and lateral part of the ventral surface of the sixth cervical vertebra and from the lateral part of the ventral surface of the bodies of the second to fifth cervical vertebrae. Insertion is onto the medial ventral tubercles of the axis and atlas. This part has similar relations in all four genera.

M. longus capitis

Origin. — From the lateral surface of the carotid tubercle of the sixth cervical vertebra and from the ventral surfaces of the transverse processes of the third to seventh cervical vertebrae.

Insertion. — Onto the ventral surface of the basioccipital and basisphenoid bones.

Remarks. — This muscle is similar in all four genera.

Lumbar Prevertebral Group
(Figs. 10A, 16D)

Innervated by branches of the lumbar nerves, primarily of the first.

M. quadratus lumborum

Origin. — By a strong tendon from the anterior border of the transverse process of the first sacral vertebra and directly by fleshy fibers from the transverse processes of all the lumbar vertebrae.

Insertion. — By fleshy fibers onto the transverse processes and bodies of the lumbar and the last thoracic vertebrae, by strong tendons onto the ventrolateral angles of the bodies of the eleventh and twelfth thoracic vertebrae, and onto the eleventh rib immediately lateral to the head.

Remarks. — In *Neotoma* and *Peromyscus* attachment is to the heads of the eleventh and twelfth ribs and the ventrolateral angle of the body of the eleventh vertebra. Posterior to this, attachments are as in *Sigmodon*. *Oryzomys* differs from *Sigmodon* only in that the most anterior attachment is to the fibrous investment of the eleventh costovertebral articulation rather than to the head of the rib.

M. psoas minor

Origin. — From the bodies of the first three lumbar vertebrae.

Insertion. — By a long, thin tendon onto the iliopectineal eminence.

Remarks. — Howell (1926) described a thin, tough aponeurosis connecting the medial border of this muscle with the remaining lumbar and the anterior sacral vertebrae in *Neotoma*. Apparently, this is a rather constant structure, as it appears in all four genera studied. In *Oryzomys* this aponeurosis is as extensive as in the other forms but is rather thin and weak.

In *Neotoma* and *Peromyscus* this muscle arises from only the second and third lumbar vertebrae. It is reduced in *Oryzomys* to a few fibers which arise from the body of the second lumbar vertebra, and its tendon is very small and weak.

Caudal Flexor Group
(Figs. 10A, 16D)

The nerve supply of this group is by small twigs directly from the sacral and anterior caudal nerves.

M. flexor caudae lateralis

Origin. — From the ventral surface of the bodies and transverse processes of the fifth lumbar to the second caudal vertebrae.

Insertion. — By long thin tendons onto the ventral surfaces and haemal arches of the caudal vertebrae.

Remarks. — This is a complex muscle, made up of many fascicles, each of which terminates in a tendon. Certain of the fascicles are difficult to differentiate from M. flexor caudae medialis. In *Neotoma* the most anterior vertebra from which this muscle arises is the sixth lumbar; in *Peromyscus*, the fourth lumbar; and in *Oryzomys*, the third lumbar vertebra.

M. flexor caudae medialis

Origin. — From the ventral surface of the bodies of the last lumbar to third caudal vertebrae.

Insertion. — By long tendons into the ventral surfaces and haemal arches of the caudal vertebrae.

Remarks. — There are two separate parts of this muscle. The anterior part arises from the last lumbar and first two sacral vertebrae, and the posterior part arises from the third sacral and first three caudal vertebrae. In *Neotoma* fibers of this muscle arise as far posterior as the sixth caudal segment; in *Peromyscus*, as far as the fourth. In *Oryzomys*, the relationships are as in *Sigmodon*.

Medial Ventral Cervical Group
(Figs. 6B, C; 8; 12B; 13A)

The infrahyoid muscles are supplied by a nerve formed from the loop between the first and second cervical nerves and a small element from the third cervical nerve. This trunk also communicates with the descendens hypoglossi to form the ansa hypoglossi. M. geniohyoideus is supplied by a small branch which leaves the sheath of the hypoglossal nerve after that nerve has entered the space immediately deep to M. mylohyoideus.

M. geniohyoideus

Origin. — With M. genioglossus from the medial surface of the mandible, just posterior to the symphysis.

Insertion. — Into the body of the hyoid, superficial to M. genioglossus and M. hyoglossus, deep to M. mylohyoideus.

Remarks. — The geniohyoideus is very similar in all four genera.

M. sternohyoideus

Origin. — From the internal surface of the first sternebra and the anterior border of the cartilage of the second rib.

Insertion. — On the posterior surface of the body of the hyoid.

Remarks. — Origin is continuous laterally with that of M. sternothyroideus. At the level of the anterior end of the manubrium a distinct tendinous inscription crosses the combined fibers of the two muscles, which continue from that level as distinct slips. The relationships of both muscles are the same in all four genera. In specimens of *Neotoma* which I dissected origin of M. sternohyoideus was always as described above; it was not from the first costal cartilage as given by Howell.

M. sternothyroideus

Origin. — Within the thoracic cavity, from the cartilage of the second rib, continuous medially with the sternohyoideus.

Insertion. — On the thyroid cartilage of the larynx.

Remarks. — Relationships of this muscle are similar in all four genera. *Neotoma* has this muscle arising as in *Sigmodon*, rather than from "the sternum beneath the sternohyoid," as given by Howell.

M. thyrohyoideus

Origin. — From the ventrolateral aspect of the thyroid cartilage, immediately cranial to the insertion of M. sternothyroideus.

Insertion. — On the posterior side of the body of the hyoid, deep to M. omohyoideus.

M. omohyoideus

Origin. — From the cranial border of the suprascapular notch.

Insertion. — On the body of the hyoid, deep and somewhat lateral to M. sternohyoideus.

Remarks. — The topographical relationships of this muscle are constant in the four genera. In *Sigmodon* and *Oryzomys* it is considerably more robust than in *Peromyscus* and *Neotoma.*

Lateral Cervical Group
(Figs. 8, 9)

Small dorsal branches of the ventral rami of the cervical and anterior thoracic spinal nerves supply these muscles.

M. rectus capitis lateralis (*M. obliquus capitis superior*, Howell)

Origin. — From the ventroanterior surface of the transverse process of the atlas.

Insertion. — Primarily on the caudomedial surface of the jugular process; a few of the more lateral fibers pass across the posterolateral surface of the mastoid bone to insert just dorsal and posterior to the stylomastoid foramen.

Remarks. — Those fibers which insert on the mastoid bone constitute a discrete slip which is separated from the deeper fibers by the occipital artery. Innervation of these fibers, however, is by the same branch of the first cervical nerve which serves the deep part of this muscle. Medially, this muscle is almost in contact with M. rectus capitis anterior, from which it is separated by the ventral division of the first cervical nerve.

The superficial slip of this muscle is considerably more robust in *Sigmodon* and *Oryzomys* than in *Peromyscus* and *Neotoma.* This is the element which Howell (1926:53, Fig. 11) identified as M. obliquus capitis superior. Except for the difference in size, the muscle is similar in all four genera.

M. intertransversarius lateralis longus

Origin. — From the transverse processes of the last four cervical vertebrae and the tubercle of the first rib.

Insertion. — On the transverse process of the first four cervical vertebrae and on the tendons of M. scalenus which attach to these vertebrae.

Remarks. — This bundle of fibers is nearly completely separate from the scalenus and lies medial to it. The fibers lie immediately dorsal to the brachial plexus, but lateral to M. levator scapulae. Since they are

separated in this manner from the epaxial musculature, they can hardly belong to that division. It seems that they must represent the lateral intertransversarii, and since the fibers have the same relationships as the inconstant intertransversarius lateralis longus in man (Grant, in Morris' *Human Anatomy*, 10th ed., p. 419), that term is used here.

Hill (1937:112), in describing the scalenus of the pocket gopher, stated: "Judging from the cervical insertion, the ventral muscle contains bundles which represent the lateral intertransversarii. In the neck region, the scalene muscles are separated from the epaxial muscles by M. levator scapulae, so it seems improbable that there are any epaxial elements present in the scalenus complex of rodents, whether or not such may be found in other mammals." The present observations are in complete agreement with this opinion, except that here the bundles which represent the lateral intertransversarii are not directly continuous with the scalenus muscle.

The long intertransverse fibers are more intimately associated with the scalenus in *Peromyscus* and *Neotoma* than they are in *Sigmodon*, but otherwise they have the same relations. In *Oryzomys* they are at least as distinct as in *Sigmodon*, appearing in some specimens to be even more distinct.

M. scalenus

Origin. — By slips from the first and third to fifth ribs.

Insertion. — On the transverse processes of the cervical vertebrae.

Remarks. — That part which arises from the first rib constitutes a discrete slip. These fibers insert on the transverse processes of the last six cervical vertebrae. The superficial fibers pass to the axis, the deepest to the seventh vertebra. Some of the fibers insert directly on the processes; others insert indirectly by joining the tendons of the dorsal part of the scalenus.

The dorsal part is larger than the part just described; it arises by slips from the third to fifth ribs. The dorsal half of the fibers from the fifth rib arise deep to the slip of M. serratus from the fourth rib; the other half pass superficial to that slip, but deep to the most anterior fibers of M. obliquus externus abdominis. The slips from the three ribs merge into a single mass which then passes dorsocraniad. Most of the fibers (dorsal two-thirds) end on a strong aponeurosis which develops on the superficial surface and, becoming tendinous, inserts on the transverse process of the atlas. The remaining fibers of the mass terminate in three thin tendons which insert on the transverse processes of the second to fourth vertebrae.

The scalenus in *Neotoma* is usually similar to that in *Sigmodon*, but there is considerable variation in the genus (Howell, 1926:35). *Peromyscus* and *Oryzomys* differ constantly from the other two genera in that some of the fibers from the fourth rib pass deep to the slip of M. serratus anterior which arises on the third rib. *Oryzomys* usually has no fibers from the fifth rib, but in one specimen examined there were a few. Of all genera but *Peromyscus*, specimens were seen in which a few fibers arose from the second rib.

Individual variation in the number of slips which make up the scalenus and in the relationship of these slips to the serratus anterior is such that little significance is attached to the variations just described.

Medial Thoracoabdominal Group
(Figs. 8, 9)

The rectus abdominis is innervated by the anterior divisions of the last nine to ten thoracic nerves and possibly by the ilioinguinal nerve.

M. rectus abdominis

Origin. — From the pubis immediately lateral to the symphysis.

Insertion. — On the entire lateral side of the manubrium sterni, the first costal cartilage, and the extreme medial end of the clavicle.

Remarks. — At the origin the muscle is made up of two or three separate slips which decussate with those from the opposite side in the manner described by Howell (1926). Howell, however, described only two decussating slips from each side. In the specimens of *Sigmodon*, *Neotoma*, and *Peromyscus* which I dissected there were never fewer than five slips of the two muscles, and in some specimens there were six. In the cases where there were five slips the deep slip contained fibers from both sides, but passed entirely to one side or the other. When there were three slips from each side, decussation of the deepest usually occurred, but in one specimen of *Neotoma* these two slips arose and remained on the same side. Thus, in this specimen each rectus abdominis muscle was made up of two bundles of fibers which arose on the opposite side of the mid-line, and one slip from the side on which the muscle lay.

From the origin the muscle passes craniad as a flat band of fibers lying immediately lateral to the linea alba. Just posterior to the xiphisternum it broadens considerably, reaching a width of approximately 15mm. At the level of the xiphisternum it begins to diverge from the mid-line, at the same time becoming narrower. In the mid-thoracic region, the medial border lies some 6 or 7 mm. from the mid-line. As it approaches the insertion, the muscle curves gradually mediad, and the medial fibers insert on the posterior end of the manubrium. Width at the insertion is usually 6 or 7 mm. Insertion in *Neotoma*, *Peromyscus*, and *Oryzomys* is on the first costal cartilage and the manubrium, but not on the clavicle.

The relationship of the oblique and transverse abdominal muscles to the rectus sheath is described in the discussion of those muscles.

M. pyramidalis

Origin. — From the pubis, just lateral to the symphysis.

Insertion. — Into the ventral mid-line for approximately 1 cm. anterior to the symphysis.

Remarks. — The pyramidalis is present in all the genera dissected. It lies superficial to M. rectus abdominis and M. obliquus abdominis internus. Its relationship to the external oblique muscle was not determined with certainty, but the fascial extension of that layer appears to pass superficial to the pyramidalis.

Lateral Thoracoabdominal Group
(Figs. 8, 9, 11)

The muscles of this group are arranged in three primary layers. These layers are represented in the abdominal region by the M. obliquus abdominis externus, M. obliquus abdominis internus, and M. transversus abdominis. In the thoracic region the external oblique layer is split into a superficial layer, represented by the posterior serrati, and a deeper layer, represented by Mm. levatores costarum, Mm. intercostales externi, M. sternocostalis, and (when present) Mm. supracostales. The internal oblique layer is represented in the thorax by the internal intercostal muscles. The two oblique layers lie external to the anterior divisions of the thoracic and upper lumbar nerves and the vessels which accompany them. The third, or transverse layer, in the thorax comprises the Mm. subcostales, the deepest layer of intercostal muscles (when they are present), and the M. transversus thoracis. This deepest layer of intercostal muscles lies deep to the intercostal nerves and vessels. Malmsley (1915) applied the term "intracostals" to them. Eisler (1912:522-26), however, called these the true internal intercostal muscles and applied the term "intercostales intermedii" to that layer which represents the internal oblique.

The interpretation of the homologies of the lateral thoracoabdominal muscles just outlined is supported by relationships observed in the forms dissected for this study, except for one detail. In the forms treated here, as well as in certain other rodents (Hill, 1937), the plane of the posterior serrati is continuous with that of M. obliquus abdominis internus, so that it is impossible to separate the caudal border of M. serratus posterior inferior from the cranial border of M. obliquus abdominis internus. This continuity must, then, be considered as a secondarily derived condition, if the opinions of many anatomists (e.g., Malmsley, 1915; Grant, in Morris' *Human Anatomy*, 10th ed., 1942) are to be accepted.

I have given special attention to the formation of the sheath of M. rectus abdominis. This was studied by careful dissection and by cross sections taken at various levels along the sheath. The character of the sheath changes at four levels between the sternum and the pubic symphysis. At the level of the xiphisternum the superficial wall is formed by the external oblique, the deep wall by the internal oblique and the transverse abdominal muscles. At the level of the end of the xiphisternum the internal oblique layer splits into two laminae, one of which shifts to the superficial surface of the rectus. Approximately 1.5 cm. caudal to the end of the xiphisternum the other lamina of the internal oblique shifts superficially. Near the middle of the linea alba (near the umbilicus) the transverse layer splits, and one sheet shifts to the superficial side of the rectus. Approximately 1.5 cm. anterior to the pubic symphysis the remainder of the transverse layer becomes superficial. Thus, in the region immediately above the symphysis the deep side of the rectus abdominis is in direct contact with the transversalis fascia.

The inguinal ligament is formed as a specialization of the common border of the internal oblique and transverse muscular layers and does

not involve the border of the external layer except in the ventromedial third of its length. The internal oblique and the transverse layers present a common, strong tendinous border which is attached to the superior spine of the ilium dorsolaterally and to the symphysial part of the pubis ventromedially. Fibers of both layers arise from most of the length of this ligament. The fibers of the external oblique muscle which enter this region terminate on a separate tendinous border which merges with the common border of the internal layers only in the ventromedial third of its length. The caudal margin of the border of the external layer is, however, connected with the inguinal ligament by a thin but tough fascia (Fig. 9B). The inguinal ligament is developed in a similar fashion in all four genera studied. According to Howell (1926), this ligament, in *Neotoma*, "extends from the inferior tuberosity of the ischium just caudad of the symphysis to the anterior crest of the ilium." This was not found to be true in any of the specimens which I dissected. In all four genera this ligament attaches along the ventral border of the pubis, from a point just anterior to the symphysis nearly to the level of the pectineal eminence.

M. serratus posterior superior

Origin. — By a thin aponeurosis along the ligamentum nuchae for about 6 mm. anterior to the spine of the second thoracic vertebra.

Insertion. — By three or four slips into the angles of the fourth to sixth or seventh ribs, inclusive.

Remarks. — According to Howell (1926), the insertion of this muscle in *Neotoma* varies considerably, attaching to ribs 4 to 7 (subgenus *Neotoma*), or to as many as ribs 4 to 10 (subgenus *Teonoma*). I have dissected this muscle only in individuals of the subgenus *Neotoma*, but have found, as Howell did, that attachment to ribs 4 to 7 is constant. In *Peromyscus* insertion is on ribs 5 to 8; in *Oryzomys*, on ribs 5 to 7.

M. serratus posterior inferior

Origin. — By a thin aponeurosis along the dorsal mid-line from the level of the tenth thoracic to the third lumbar vertebra, inclusive.

Insertion. — On the angles of the last five ribs (8 to 12).

Remarks. — The posterior border of this muscle is continuous with M. obliquus abdominis internus. Insertion in *Peromyscus* and *Neotoma* is on the last five ribs (9 to 13); in *Oryzomys* the slips attach only to the last four ribs (9 to 12).

M. sternocostalis (not *M. sternocostalis* of Howell, 1926)

This muscle was not found in *Sigmodon*, but is apparently constantly present in *Peromyscus* and *Oryzomys*, and at least occasionally in *Neotoma*. Origin in *Peromyscus* and *Oryzomys* is by a thin aponeurotic band from the ventral mid-line at the level of the posterior half of the first sternebra. The muscle passes anterolaterad, across the superficial surface of M. rectus abdominis, and inserts on the posterior border of the first rib. In *Peromyscus* muscle fibers develop only in the insertional half of the

length; in *Oryzomys* it is a stouter muscle and is fleshy for considerably more than half its length. In five out of six specimens of *Neotoma* examined for this muscle no trace of it was found. In the sixth specimen it was apparently represented by a slip which arose at the costocartilaginous junction of the third rib and was continuous laterally with the scalenus slip from that rib. Insertion was on the first rib as in *Peromyscus* and *Oryzomys*.

The sternocostalis, as this term is used here, is apparently the same muscle referred to by Keith (1894) as supracostalis anterior, by Langworthy (1924) as the fourth layer of the pectoral muscles, and by Bryant (1945) as the entopectoralis profundus. Lander (1918) and Langworthy (1924) placed this muscle in the pectoral group. Bryant (1945) followed Lander's interpretation of the relationships. Keith (1894) concluded that it was derived from the external oblique muscle, and Hill (1937) concurred with this opinion, apparently on the basis that innervation is from the second intercostal nerve in pocket gophers. In *Oryzomys* innervation is from the first intercostal nerve by a small branch which enters the deep side of the muscle just before insertion. Because of this, I have placed the sternocostalis in the present group and am inclined to accept Keith's and Hill's opinions as to its derivation. This muscle may be the equivalent of the rare M. supracostalis anterior of man.

Mm. intercostales externi

These muscles have the usual relationships in all four forms. They are restricted to the region between the tubercles of the ribs and the junction of the ribs with their cartilages. In the superior thoracic region some of the fibers arising on the third and fourth ribs may insert on the first rib. Dorsomedially, this layer is fused with the levatores costarum.

Mm. levatores costarum

Origin. — From the transverse processes of the anterior thoracic vertebrae and from the accessory processes of the posterior thoracic vertebrae.

Insertion. — On the anterior borders of the ribs, near the angles.

Remarks. — These muscles are rather well fused to the external intercostals. In the anterior thoracic region slips of the longissimus dorsi insert on the superficial aponeuroses of these muscles, thus gaining indirect attachment to the transverse processes. There is little variation in these muscles among the four genera, except that *Neotoma* and *Peromyscus* have one more pair than do the other two genera, attached in each to the thirteenth rib.

M. obliquus abdominis externus

Origin. — From the last eight ribs (5 to 12) and to a small extent from the aponeurosis of origin of M. obliquus abdominis internus.

Insertion. — Into the linea alba, superficial to M. rectus abdominis, into a tendinous margin which extends from the anterior spine of the ilium to the pubis, and directly into the pubis near the symphysis.

Remarks. — The tendon, or ligament, extending from the ilium to the pubis, into which many of the fibers of this muscle insert, merges with the inguinal border of the internal oblique and transverse muscles in its ventromedial third.

The slips which arise from the fifth to eighth ribs interdigitate with the slips of M. serratus anterior which arise from those ribs. The course of the fibers is generally caudoventrad, becoming almost directly caudad in the inguinal region.

Only minor variations among the four genera are presented by this muscle. In *Neotoma* origin may extend as far forward as the fourth rib. All specimens of *Oryzomys* examined had a slip also from the fourth rib. *Peromyscus* resembles *Sigmodon* in that the most anterior slip is from the fifth rib.

Mm. intercostales interni

In the thorax these muscles represent the internal oblique layer of the abdomen. All the fibers of this layer lie external to the intercostal nerves and vessels. They extend between adjacent costal margins from the vicinity of the angles of the ribs to the sternum.

M. obliquus abdominis internus

Origin. — By a thin aponeurosis along the dorsal mid-line from the third to the last lumbar vertebra.

Insertion. — Onto the posterior aspect of the ends of the last two ribs, on the costocartilaginous junctions and cartilages of the eighth to tenth ribs, on the lateral aspect of the xiphisternum, and along the linea alba.

Remarks. — Those fibers which insert on the eleventh rib are directly continuous with the internal intercostal muscle between the eleventh and twelfth ribs.

The relationship of this muscle to the rectus abdominis changes at two levels along the abdomen. Those fibers which insert on the xiphisternum pass entirely deep to the rectus. At the level of the end of the xiphisternum, the aponeurosis splits, and one sheet shifts to the superficial side of the rectus. Approximately 1.5 cm. posterior to this, the other sheet also becomes superficial, and from here to the pubis the entire layer passes superficial to the rectus.

Mm. subcostales

These muscles are somewhat irregular in their occurrence and are found to differ even on the two sides of the same individual. In one specimen fibers were found to arise, on one side, from the last two ribs and to insert on the caudal borders of the ninth and tenth ribs. No fibers arose from ribs 7 to 10, but ribs 3 to 6 gave origin to fibers which attached to the first four ribs. On the other side of this specimen fibers arose from ribs 3 to 6 and from ribs 10 to 12. In another specimen fibers arose from all the ribs of the left side except the first two; on the right side, there were no fibers from ribs 7 to 9.

A complete series was present in one specimen of *Neotoma*, arising from ribs 3 to 13 on one side. On the other side the series was complete except for the absence of fibers from the seventh rib. A specimen of *Peromyscus* had the complete series on one side, but lacked fibers from the seventh to tenth ribs on the other side. Three specimens of *Oryzomys* had the complete series on both sides.

The Mm. subcostales lie in the fascial plane which is continuous with that of M. transversus abdominis and M. transversus thoracis and which is separated from the internal intercostal muscles by the intercostal nerves and vessels. Although no intercostal fibers are developed in this fascia among the forms under discussion, this apparently is the plane of the deepest layer of intercostal muscle fibers (Mm. intracostales, Malmsley, 1915) of man.

M. transversus thoracis

Origin. — From the internal surface of the xiphisternum and from all but the first sternebrae.

Insertion. — On the second to ninth costal cartilages and on the fascia of the intervening internal intercostal muscles.

Remarks. — In *Neotoma* and *Peromyscus* insertion is on the cartilages of ribs 2 to 10. In *Oryzomys* insertion is like that in *Sigmodon*.

M. transversus abdominis

Origin. — From the caudomedial aspects of the eighth to tenth ribs, from the posterior borders of the ends of the last two ribs, from the deep surface of the aponeurosis by which M. obliquus abdominis internus arises from the dorsal mid-line, and from the lateral three-fifths of the inguinal ligament.

Insertion. — Into the linea alba along its entire length.

Remarks. — In the region above the umbilicus this muscle passes entirely deep to M. rectus abdominis. Near the umbilicus, however, one lamina of the aponeurosis shifts to the superficial surface of the rectus. The other layer shifts from the deep to the superficial side of the rectus at a level approximately 1.5 cm. cranial to the symphysis.

M. cremaster

This muscle is made up of two distinct layers of fibers which cross nearly at right angles to each other. The outer and inner layers are direct continuations of the internal oblique and transverse abdominal layers, respectively. The cremaster is well developed in males of all four genera, completely enveloping the testis when it is in the scrotal position. When the testis is within the abdominal cavity, the cremaster fibers remain as a small pouch protruding from the external inguinal ring.

Innervation is by the genitofemoral nerve.

Diaphragma (*M. sternocostalis* Howell, 1926) (Fig. 16D)

The crura arise from the bodies of the twelfth thoracic to third lumbar vertebrae. Other slips arise from the last five ribs and their cartilages and from the deep side of the xiphisternum. The central tendon is irregularly circular, with a deep excavation from the dorsal side where the crura insert. The openings through the diaphragm have the usual relationships.

A few minor differences are presented by the other genera. In *Neotoma* the crura arise (subgenus *Neotoma*) from the first two lumbar vertebrae and the other slips from ribs 6 to 12, or (subgenus *Teonoma*) the crura arise from the first four lumbar vertebrae and the other slips from ribs 6 to 13. In *Peromyscus* the crura arise as in *Teonoma*, the other slips from ribs 7 to 13. *Oryzomys* is similar to *Peromyscus*, except that the slip from the thirteenth rib is, of course, not present.

Innervation is by the phrenic nerve, which arises from the anterior divisions of the fourth and fifth cervical nerves.

Perineal Group (Figs. 10, 15B, 16D)

The muscles of this group receive their innervation from branches of the sacral plexus. M. ischiocavernosus, M. bulbocavernosus, M. sphincter ani externus, and M. sphincter urethrae membranaceae were examined in the males of all four genera, but in the female of *Sigmodon* only. These muscles are, of course, present in the females, but are so small that it would be almost impossible to compare them satisfactorily.

M. iliococcygeus (*M. abductor caudae internus* Howell, 1926)

Origin. — From the ventral part of the pelvic surface of the ilium, between the level of the gluteal notch and the anterior border of the acetabulum.

Insertion. — By a single tendon, some fibers of which attach to the transverse processes of each of the fourth to eighth caudal vertebrae.

Remarks. — In *Neotoma* this muscle comprises several fascicles, terminating in at least four tendons which join those of M. flexor caudae medialis and M. flexor caudae lateralis to insert on the caudal vertebrae distal to the fourth or fifth vertebra. In *Peromyscus* as many as six tendons may proceed from this muscle. *Oryzomys* usually resembles *Sigmodon* in having only one tendon from this muscle, but may have two. In one specimen there were two tendons on the right side and one tendon on the left.

M. pubococcygeus (*M. abductor caudae externus* Howell, 1926)

Origin. — Along the medial surface of the horizontal ramus of the pubis from the symphysis almost to the iliopectineal eminence.

Insertion. — On the transverse processes of the third and fourth caudal vertebrae and on the tendon of M. iliococcygeus.

Remarks. — In *Oryzomys* the origin extends anteriad nearly to the level of the femoral process (anterior inferior spine) of the ilium. In this genus there is a small hiatus near the anterior border of the muscle through which the obturator nerve passes. In *Neotoma* and *Peromyscus* the muscle is similar to that in *Sigmodon.* (See also remarks under M. coccygeus.)

M. coccygeus

Origin. — From the "spine" of the ischium, from the anterior border of the obturator foramen, and from most of that part of the medial surface of the obturator membrane which is ventral to the M. obturator internus.

Insertion. — On the transverse processes of the first four caudal vertebrae.

Remarks. — Those fibers arising from the area on the ischium which is equivalent to the spine (although no spine is developed) pass almost directly caudad to the transverse process of the first caudal vertebra. The fibers trend progressively more dorsad as the posterior border of the muscle is approached. Approximately half the medial surface of this muscle is covered by the M. pubococcygeus, and the two muscles are apt to appear as a continuous sheet. The fibers of M. pubococcygeus, however, run in a more caudal direction, crossing those of the coccygeus at an angle of approximately ten degrees. Moreover, these two sheets of fibers receive separate nerves from the sacral plexus. The nerve to M. pubococcygeus passes caudad on the medial surface of the muscle, sending twigs into it. The nerve to M. coccygeus passes between the two layers (medial to M. coccygeus, lateral to M. pubococcygeus).

In *Peromyscus* and *Neotoma* M. coccygeus does not extend so far posteriad on the obturator membrane and is only slightly overlapped by the pubococcygeus; insertion of the most anterior fibers is on the last sacral vertebra. In these two forms the two muscles (M. coccygeus and M. pubococcygeus) appear as one continuous sheet even more definitely than in *Sigmodon,* and particular care is required to separate them. Howell (1926) apparently included both these muscles in his discussion of "M. abductor caudae externus." The relationships of this muscle in *Oryzomys* are similar to those in *Sigmodon,* except that the insertion includes the transverse process of the last sacral vertebra.

M. ischiocavernosus

Origin. — From the entire length of the caudal border of the inferior ramus of the ischium.

Insertion. — Onto the crus of the corpus cavernosum penis.

Remarks. — As the crus of the corpus cavernosum penis extends dorsolaterad to its attachment on the ischium, it is completely invested by this muscle. In all the forms investigated these relationships were similar.

M. bulbocavernosus

In the four genera treated here, the bulbar part of the urethra of the male is distinctly bilobed and forms a Y-shaped structure with the penile

urethra. The muscle fibers which surround each lobe are distinct from those of the opposite side, and the M. bulbocavernosus might thus be considered as a paired muscle. The description which follows applies only to the muscular investment of one lobe and is duplicated on the other side. The fibers take their origin from the dorsal (posterior) mid-line of the bulbus penis, in the cleft between the two lobes. They pass caudad and ventrad, turn anterodorsad around the lobe, then mediad to insert near their origin, having passed entirely around the lobe. A group of fibers which arises in the posteroventral part of the cleft between the lobes is differentiated from the other fibers. This bundle passes directly distad (anteriad) to insert on the ventromedial aspect of the crus of the corpus cavernosum penis.

There is great variation in the size of the parts of the urethra, depending upon the stage of the individual's sexual cycle. In a sexually active male *Sigmodon*, for example, one lobe of the bulbus penis, including its muscular investment, may be as much as 15 mm. long and 10 mm. wide, whereas the respective dimensions of this part in a sexually quiescent male are usually less than half as large. This seasonal, individual variation makes impossible any attempt to compare relative development of the muscles associated with the urethra in the different genera. General relationships (origin, insertion, position) of the muscle are, however, similar in all four genera.

M. sphincter ani externus

This bundle of fibers arises from the caudal end of the lobe of the bulbus penis on one side, passes directly across the mid-line, dorsal to the rectum, and attaches to the corresponding part of the other lobe of the bulb. At the mid-line the fibers are attached loosely to the caudal vertebrae by connective tissue.

Tullberg (1899) considered this muscle a part of M. bulbocavernosus, and, to judge from its attachments, it seems to me that this may be correct. It is possible that the true sphincter ani externus is represented by a layer of striated muscle fibers which invests the terminal 10 to 12 mm. of the rectum. This layer was identified by Howell (1926:97) as the internal anal sphincter. It is superficial to the anal glands, as well as to a layer of scattered, longitudinal, striated fibers, and is equally developed in the male and female. Since the sphincter ani internus of man is made up of smooth muscle and is deep to the longitudinal layer of striated fibers, it is hardly possible to consider it the homologue of the layer to which Howell applied the term. If the muscle here called M. sphincter ani externus actually is the homologue of the one so called in man, one would expect it to be almost equally developed in both sexes. Such is not the case, however; only a vestige of this fascicle is present in the female.

In spite of these discrepancies, I am following the precedent set in several more or less recent works (Howell, 1926; Mossman, Lawlah, and Bradley, 1932) in applying the term M. sphincter ani externus to the fibers which attach to the ends of the lobes of the bulbus penis, but with considerable reservation. This muscle might correspond to that which Hill (1937) called M. rectocavernosus. As Howell (1926) pointed out, there is a need

for extensive investigation of the perineal muscles throughout the mammals in order to establish homologies of certain fascicles.

M. sphincter urethrae membranaceae

The fibers of this muscle form a continuous investment of the membranous urethra, from the ejaculatory ducts to the level where the bulbourethral ducts enter.

Appendicular Musculature

Muscles of the Pectoral Girdle and Limb

Extensor System

Costo-spino-scapular Group (Figs. 8, 9, 11)

Innervation is described under each muscle.

M. levator scapulae and *M. serratus anterior*

Origin. — From the transverse processes of the last five cervical vertebrae and from the craniolateral surfaces of the first eight ribs near their costochondral articulations.

Insertion. — Along the entire vertebral border of the scapula and on a small part of its costal surface near the caudal angle.

Remarks. — In some specimens there is also a slip from the ninth rib. Those slips which arise from the cervical vertebrae and first three ribs are medial to the scalenus; the slip from the fourth rib arises deep to the ventral half of the scalenus fibers from the fifth rib, but lies superficial to the dorsal half of those fibers. The slips from the fifth to eighth ribs interdigitate with the slips of M. obliquus abdominis externus which arise from those ribs. At the insertion the fibers of the posterior border are twisted in such a manner as to insert on the medial surface of some of the more anterior fibers.

The adjacent borders of these two muscles are continuous, with no indication where one ends and the other begins. At least, there is no way in which this can be determined by gross examination.

The part of this sheet which arises from the cervical vertebrae and the first three ribs is supplied by the dorsal scapular nerves. The posterior part of the sheet receives its innervation from the long thoracic nerve, which is made up of fibers from the sixth to eighth cervical nerves. The slip from the fourth rib appears to be supplied by branches from the dorsal scapular nerve as well as by the long thoracic nerve, and it might thus be considered to belong either to the levator scapulae or to the serratus anterior. Howell (1926) described the part anterior to the fifth rib (including that slip from the fifth rib in the subgenus *Teonoma*) as M. levator scapulae and the remaining posterior part as M. serratus magnus. This procedure is, of course, entirely justified on the basis of the difference in innervation of the two parts, as well as by the fact that the two muscles are entirely separate

in so many mammals. The problem of determining just how much of the sheet should be called by one name and how much by the other appears to be impossible to solve from the standpoint of gross anatomy, and it is here considered best to describe the entire mass as a unit, as Hill (1937) and Bryant (1945) saw fit to do.

In *Neotoma* this muscle has essentially the same relationships as in *Sigmodon*, but in the subgenus *Teonoma*, according to Howell, there may be slips from as many as 11 ribs. Howell described the insertion of these two muscles in *Neotoma* as restricted to the part of the dorsal border of the scapula caudal to the spine. I have not found this to be true; it is, rather, along the entire dorsal border of the scapula, as in all three other genera under consideration.

In *Peromyscus* and *Oryzomys* the slip arising from the third rib, as well as that from the fourth, passes superficial to the dorsal part of the scalenus.

M. rhomboideus

This muscle is divided into anterior and posterior parts in all four genera, but in *Neotoma* and *Peromyscus* the relationships of the two parts differ from those in *Sigmodon* and *Oryzomys*. Innervation is from the dorsal scapular nerves.

M. rhomboideus anterior

Origin. — From the cranial 7 to 8 mm. of the ligamentum nuchae.

Insertion. — Along the caudal half of the vertebral border of the scapula.

Remarks. — As the band of fibers passes caudolaterad from the origin, it undergoes a tortion of approximately 90 degrees, so that the plane of the muscle is vertical at the level of the cranial angle of the scapula, and the deep side lies in contact with the part of M. occipitoscapularis which passes deep to the scapula. In specimens which do not have the divided occipitoscapularis, the rhomboideus anterior lies flat against the medial surface of M. levator scapulae and M. serratus anterior. As it traverses the region medial to the scapula, this muscle lies immediately deep to M. rhomboideus posterior. Insertion on the vertebral border of the scapula begins at a level just posterior to the scapular spine and extends to the caudal angle. This description of the muscle in *Sigmodon* applies equally well to that in *Oryzomys*. In both forms the anterior segment of the rhomboideus is considerably smaller than the posterior part.

In *Neotoma* and *Peromyscus* the anterior part is the larger. It arises as a broad sheet of fibers along the ligamentum nuchae, from the spine of the axis to the spine of the first thoracic vertebra. Howell (1926:47) described the insertion in *Neotoma* as "hardly at all upon the scapular border but rather it is practically confined to an area upon the scapula at right angles to the border and opposite the spine." This description has not been applicable to any of the specimens which I dissected, in all of which the insertion was similar to that described above for *Sigmodon*. Indeed, the interposition of M. serratus anterior and M. levator scapulae between the rhomboideus and the medial scapular surface precluded the possibility of the rhomboideus inserting on the medial surface of the scapula.

M. rhomboideus posterior

Origin. — From the remaining part of the ligamentum nuchae posterior to the origin of M. rhomboideus anterior and from the spine of the second thoracic vertebra.

Insertion. — On the vertebral border of the scapula, caudal to the spine.

Remarks. — In bulk this part is approximately twice as large as the anterior part. Its anterior fibers extend caudolaterad, superficial to those of rhomboideus anterior. The posterior fibers pass latero-dorso-caudad from the spine of the vertebra to the border of the scapula when the scapula is in a normal position. The rhomboideus posterior in *Oryzomys* is similar to that in *Sigmodon*. In *Neotoma* and *Peromyscus* it is relatively smaller and arises only from the spine of the second thoracic vertebra. Insertional relationships, however, are similar to those in *Sigmodon*.

M. occipitoscapularis

Origin. — From 6 to 8 mm. of the lambdoidal crest immediately dorsal to the end of the mastoid process of the squamosal bone.

Insertion. — Immediately anterior to the cranial border of the scapula the muscle divides and sends about half of its fibers to insert on the vertebral border of the scapula anterior to the spine and on the dorsal 6 to 8 mm. of the spine; the other half of the fibers pass deep to the scapula to insert on the vertebral border near the caudal angle.

Remarks. — The part of this muscle which passes deep to the scapula lies between the rhomboideus anterior and the combined levator scapulae and serratus anterior. This muscle is not divided in any of the three other genera examined, in all of which the insertion extends along the lateral margin of the anterior two-thirds of the vertebral scapular border. Very few fibers attach to the spine, and these only at the extreme dorsal end. In *Peromyscus* and *Neotoma* the muscle is broader at the origin than in *Sigmodon* and *Oryzomys* and extends farther dorsad along the lambdoidal crest.

Innervation is from the dorsal scapular nerve.

M. omocervicalis (*M. atlantoscapularis* Howell, 1926)

Origin. — From the ventral arch of the atlas.

Insertion. — On the posterior border of the metacromion.

Remarks. — The origin of this muscle is from the ventral arch of the atlas in all four genera. I have failed to find any basis for Hill's (1937) statement that *Neotoma* has retained the primitive attachment to the transverse process of the atlas. Insertion is similar in all four genera. Innervation is supplied by a branch of the third cervical nerve.

Latissimus-subscapular Group
(Figs. 11, 12, 13A)

Innervation is by the subscapular nerves.

M. latissimus dorsi

Origin. — Along the dorsal mid-line from the level of the seventh to eleventh thoracic vertebrae and from the lumbodorsal fascia as far caudad as the level of the fourth or fifth lumbar vertebra.

Insertion. — On the humerus deep to M. coracobrachialis, 3 to 4 mm. below the lesser tuberosity.

Remarks. — The fibers of this muscle pass anteroventrad around the thorax to the axillary region, converging to form a band approximately 12 mm. wide. In the axillary region this band abruptly decreases in width to form a tendon some 6 mm. wide which continues anteriad, to pass deep to the brachial artery and nerves and deep to M. coracobrachialis. The ventral fibers of M. teres major insert along the dorsal margin of this tendon. The dorsoepitrochlearis arises from the ventral border of the tendon at the point where it narrows abruptly.

In *Neotoma* some of the fibers continue superficial to the brachial artery and nerves, inserting by aponeurosis which spreads out over the coracobrachialis and M. biceps. The fibers of the dorsal border of this aponeurosis curve proximad to attach to the base of the greater tuberosity of the humerus. This aponeurosis is also partly continuous with the tendon of origin of M. dorsoepitrochlearis. The relationships here strongly suggest an intermediate stage in the transferal of the origin of M. dorsoepitrochlearis from the humerus to the tendon of M. latissimus dorsi. The principal part of the latissimus dorsi tendon passes deep to the brachial artery and nerves as in *Sigmodon*. M. teres major does not insert on this tendon in *Neotoma*.

In *Peromyscus* the relationships of M. latissimus dorsi are almost exactly as in *Neotoma*. *Oryzomys* presents only very minor variation from the condition described for *Sigmodon*.

M. teres major

Origin. — From the dorsal (proximal) half of the axillary border of the scapula and from the immediately adjacent superficial fascia of M. subscapularis.

Insertion. — On the dorsal border of the tendon of M. latissimus dorsi. The common tendon of the two muscles inserts 3 to 4 mm. distal to the lesser tuberosity.

Remarks. — In *Neotoma* and *Peromyscus* this muscle inserts independently, proximal and partly deep to the tendon of M. latissimus dorsi. In *Oryzomys* relationships are as in *Sigmodon*.

M. subscapularis

Origin. — From the whole subscapular surface except a small area along the vertebral border.

Insertion. — Into the intertubercular groove and onto the adjacent part of the lesser tuberosity.

Remarks. — The fibers of this muscle are arranged in a number of fascicles. As Howell reported for the wood rat, these groups of fibers are not separable and are complexly related, varying considerably from specimen to specimen. An anterior and a posterior part, however, become rather distinct distally. Differences among the genera studied are hardly greater than among individuals.

Deltoid Group
(Figs. 8, 11, 12A, 13A)

These muscles are innervated by the axillary nerve.

M. clavo-acromiodeltoideus

Origin. — From nearly the whole length of the clavicle and from the ventral border of the tip of the acromion.

Insertion. — The clavicular fibers are inserted on the anterior border of the deltoid crest of the humerus. Acromial fibers are inserted on the fascia of the distal third of the clavicular fibers and on the posterior lip of the deltoid crest opposite the insertion of the clavicular fibers. Some fibers insert on the aponeurosis of M. spinodeltoideus.

Remarks. — There is very little difference among the four genera. Individual variation in the distinctness of the clavicular and acromial parts appears to be as great as the variation among the different genera.

M. spinodeltoideus

Origin. — From the distal two-thirds of the posterior lip of the scapular spine and from the adjacent fascia of M. infraspinatus.

Insertion. — By a thin aponeurosis on the caudal border of the deltoid crest.

Remarks. — Some of the fibers of the acromial part of M. clavo-acromiodeltoideus insert on the aponeurosis of this muscle. Relationships are generally similar in all four genera with the exception that in *Peromyscus* no fibers take origin from the superficial fascia of M. infraspinatus.

M. teres minor

Origin. — From the distal two-fifths of the axillary border of the scapula and from the heavy aponeurosis which attaches to this border of the scapula (see below).

Insertion. — On the greater tuberosity, just below the insertion of M. infraspinatus.

Remarks. — The aponeurosis mentioned above arises along the border of the scapula between the origins of M. teres minor and M. teres major, passes ventrolaterad around the teres minor, then turns dorsocraniad to pass up over the lateral surface of that muscle and the distal part of M. infraspinatus, and attaches to the caudal border of the free part of the scapular spine and to the metacromion. Thus, the teres minor and the infraspinatus are enclosed in an aponeurotic envelope.

This aponeurosis is well developed in *Sigmodon* and *Oryzomys*, but only weakly developed in *Neotoma* and *Peromyscus*. Parsons (1894, 1896) described such a structure in *Lagostomus* and *Rhizomys*. According to him (1894:263): "The teres minor was seen most distinctly in *Lagostomus*, in which animal a fibrous band was found running from the metacromial process to the origin of the long head of the triceps, covering the infraspinatus and teres minor near their insertion." He also wrote (1896:168-69): "It is interesting to note that a strong ligament was seen in *Rhizomys* running from the axillary border of the scapula, between the origins of the teres major and minor, across the latter muscle to the metacromion process." There is little doubt that this "ligament" represents the same structure found so well developed in *Sigmodon* and *Oryzomys*. As this sheath passes over the ventral border of M. teres minor, it gives origin to many of the fibers of M. triceps caput longus. The teres minor presents only very slight variations in the genera studied.

Suprascapular Group
(Figs. 11, 12, 13A)

The two suprascapular muscles are innervated by the suprascapular nerve.

M. supraspinatus

Origin. — In two parts: (1) from the entire cranial surface of the spine of the scapula and from the intermuscular septum between this muscle and M. infraspinatus, and (2) from the suprascapular fossa and the lateral surface of the superior transverse scapular ligament (which could more appropriately be called a membrane in this form).

Insertion. — By a strong, flat tendon on the craniodorsal part of the greater tuberosity of the humerus.

Remarks. — Most of the fibers which take origin from the scapular spine insert on the aponeurosis which develops on the caudolateral surface of the other part; only the distal fibers of the first part insert directly on the humerus (Howell, 1926). This muscle is not essentially different in any of the four genera.

M. infraspinatus

Origin. — From the posterior surface of the spine and from the entire infraspinous fossa.

Insertion. — On the greater tuberosity of the humerus, immediately caudolateral to the insertion of M. supraspinatus.

Remarks. — The fleshy fibers insert in a bipennate fashion onto an aponeurosis which divides the muscle into approximately equal anterior and posterior parts (Howell, 1926).

Like M. supraspinatus, this muscle is similar in all four genera.

Triceps Group
(Figs. 8, 11, 12, 13A)

These muscles are supplied by the radial nerve. The three heads of the triceps are so nearly distinct that they are treated separately.

The term M. anconeus has been applied so loosely in the literature that a few remarks regarding this muscle seem justified. The muscle running from the lateral epicondyle of the humerus to the olecranon, apparently derived from the triceps, and innervated by the radial nerve appears to be the homologue of the anconeus muscle of man and should thus deserve the name M. anconeus, or perhaps M. anconeus lateralis. There is, however, a similar muscle, situated on the medial aspect of the elbow, which has frequently been called M. anconeus (Howell, 1926). If this muscle in a particular form is innervated by the radial nerve and can therefore be assumed to have been derived from the triceps matrix, the term M. anconeus medialis may most properly be applied. There is in many forms, however, a muscle in this position which is innervated by the ulnar nerve and appears to be derived from the ventral matrix of the forelimb. This muscle is properly called M. epitrochleoanconeus. (Howell, 1936a, b). Greene (1935:48) correctly described M. anconeus in text, but in her figure (Fig. 83, p. 74) this name is applied to the muscle on the medial side of the elbow. Greene's (1935:48) text description of "M. epitrochleoanconeus" leaves no doubt that she referred to M. dorsoepitrochlearis, which is, however, correctly labelled (pp. 73-74, Figs. 82, 83). The muscle on the medial side of the elbow, passing from the medial epicondyle to the olecranon, has been invariably innervated by the ulnar nerve in all muroid rodents which I have dissected and should therefore be called M. epitrochleoanconeus. These remarks have been inserted here with the hope that perpetuation of errors in the literature will be prevented.

M. triceps brachii, caput lateralis

Origin. — By aponeurosis from the greater tuberosity of the humerus and from the upper third to half of the deltoid crest.

Insertion. — On the lateral part of the dorsal surface of the olecranon.

Remarks. — Relationships of this muscle are similar in all four genera.

M. triceps brachii, caput medialis

Origin. — From the posteromedial surface of the distal two-thirds of the shaft of the humerus.

Insertion. — On the dorsal surface of the olecranon.

Remarks. — Little if any variation occurs among the four genera.

M. triceps brachii, caput longus

Origin. — From the distal third of the axillary border of the scapula and from the surface of a heavy aponeurosis which attaches to the distal two-thirds of the axillary border (see M. teres minor, p. 70).

Insertion. — On the proximal end of the olecranon.

Remarks. — In *Neotoma* and *Peromyscus* the origin is confined almost completely to the border of the scapula. In *Oryzomys* relationships are nearly as in *Sigmodon*, with a large part of the fibers taking origin from the aponeurosis. In these last two forms the muscle is shorter and more massive than in the former.

M. anconeus (not *M. anconeus* of Howell; see *M. epitrochleoanconeus*, p. 81)

Origin. — From the caudal surface of the lateral epicondyle of the humerus.

Insertion. — On the lateral aspect of the olecranon, deep to M. triceps c. lateralis.

Remarks. — This muscle is not well differentiated from the medial head of the triceps (Hill, 1937), but it is supplied by a branch of the radial nerve distinct from that which serves the latter muscle. Relationships do not differ essentially in any of the four genera, but *Oryzomys* shows the greatest amount of differentiation of this muscle from the triceps.

M. dorsoepitrochlearis (*M. epitrochlearis* Howell, 1926)

Origin. — From the ventral border of the latissimus dorsi at the point where that muscle becomes tendinous and by a thin aponeurosis from the caudal border of M. teres major.

Insertion. — On the mediocaudal aspect of the olecranon.

Remarks. — In *Neotoma* and *Peromyscus* the cranial border of this muscle is continuous with an aponeurosis which attaches to the humerus just below the greater tuberosity. The relationships here are not greatly different from those found in *Geomys* and in the squirrels (Hill, 1937; Bryant, 1945). No fibers take origin from M. teres major in *Neotoma* or *Peromyscus*, and the insertion in these forms extends farther along the olecranon. The origin of this muscle in *Oryzomys* is like that in *Sigmodon*, but the width of the insertion is intermediate between that of the latter and that of *Neotoma*.

Extensor Group of the Forearm
(Figs. 8, 12, 13, 14E)

The muscles of this group are all supplied by branches of the radial nerve. As in most, if not all, muroid rodents (Parsons, 1896) and in certain other rodents (Hill, 1937) there is no brachioradialis in the genera studied.

M. extensor carpi radialis longus

Origin. — From the proximal part of the lateral epicondylar ridge.

Insertion. — On the dorsum of the second metacarpal, near the middle.

Remarks. — This muscle arises most proximally of all those which take origin from the lateral epicondyle. Its tendon passes beneath that of M. extensor pollicis brevis and that of M. abductor pollicis longus. A small tubercle is developed on the bone at the point of insertion. Topographical relationships are similar in all four genera. The muscle is somewhat reduced in *Neotoma*.

M. extensor carpi radialis brevis

Origin. — From the lateral epicondyle distal to the origin of M. extensor carpi radialis longus.

Insertion. — On the middle of the dorsum of the third metacarpal.

Remarks. — This muscle is a little larger than the preceding one. It is reduced in *Neotoma*, but only slightly. Topographical relationships are similar in all four genera.

M. supinator

Origin. — By a heavy tendon from the lateral end of the capitulum of the humerus, deep to the radial collateral ligament.

Insertion. — On the cranial and lateral surfaces of the proximal half of the radius.

Remarks. — The origin of this muscle in *Neotoma* and *Peromyscus* is from the annular ligament of the radius. In these forms and in *Oryzomys* there is a sesamoid bone in the tendon as it passes over the head of the radius. This is absent in *Sigmodon*. The tendon of origin in *Oryzomys* has the same relationships as in *Sigmodon*. In these last two forms a strong radial collateral ligament arises from the lateral epicondyle immediately lateral to the point at which it meets the capitulum; it extends across the radiohumeral joint to attach to small adjacent areas of the radius and ulna about 2 mm. below the head of the radius. This ligament was not found in *Neotoma* or *Peromyscus*, or in any other rodent which I have dissected, except those already mentioned and the Norway rat. Parsons (1896:172), however, mentioned that "... in some cases, as in that of *Bathyergus*, there is a well marked external lateral ligament, situated behind the tendon [of M. supinator], but in others, of which *Cricetomys* is an example, the tendon itself seems to form the lateral ligament, and has the orbicular ligament attached to it." This latter situation appears to approach closely the situation found in *Neotoma* and *Peromyscus*.

M. extensor pollicis brevis (*M. abductor metacarpi pollicis* Howell, 1926, part)

Origin. — From all but the distal 4 to 5 mm. of the distal half of the interosseus surface of the ulna.

Insertion. — Onto the radial side of the falciform bone.

Remarks. — (See also under M. abductor pollicis longus.) The tendon passes distomediad, superficial to the tendons of the flexores carpi radiales, around the wrist, in the first osteofibrous canal. In the canal it becomes partly fused in some specimens with the tendon of M. abductor pollicis longus. In other specimens the two tendons are separate. In the canal this tendon crosses over that of the abductor so that near the insertion it lies proximal to that tendon rather than distal to it as at the original end.

Insertion of this muscle is into the radial side of the falciform bone in all the forms studied. Greene's (1935) statement that insertion in the Norway rat is on the first phalanx of the thumb is not consistent with my

observations. In *R. norvegicus* I have found the insertion always to be on the falciform. The origin in this form has been found to be principally from the ulna and the interosseus membrane, with a few fibers arising from the radius. According to Greene, origin is "from the ulnar surface of the radius and from the interosseus membrane just distal to extensor pollicis longus [=my abductor pollicis longus]."

M. abductor pollicis longus (*M. abductor metacarpi pollicis* Howell, 1926, part)

Origin. — From the middle half of the interosseus aspect of the radius and from the proximal half of the corresponding surface of the ulna.

Insertion. — Almost entirely on the radial side of the first metacarpal; a few fibers insert on the falciform.

Remarks. — The propriety of the terminology here applied to this and to the preceding muscle is perhaps questionable. Greene (1935) called this muscle "M. extensor pollicis longus." This I do not believe to be correct, for reasons given below. Howell (1926), failing to recognize the presence of two muscles here because of their nearly complete fusion in *Neotoma*, described both as "M. extensor metacarpi pollicis."

In *Sigmodon* M. abductor pollicis longus passes distomediad around the radius, accompanied by M. extensor pollicis brevis, in the first (radial) osteofibrous compartment. In the compartment its tendon is sometimes partly fused with that of the short extensor, but is always easily separated from it. In its course it passes beneath the other tendon and comes to lie on the distodorsal side of it. In *Peromyscus* and *Neotoma* the two tendons are almost completely fused, but the individual fibers, if traced, run as in *Sigmodon*. Insertion in these two forms is into the base of the first metacarpal, but there is a small slip which separates from the main tendon and passes to the dorsal side of the terminal phalanx of the pollex. In *Oryzomys* there is no fusion of the two tendons. That from M. abductor pollicis longus passes beneath the tendon of the extensor to insert, as in *Neotoma* and *Peromyscus*, with the small slip passing to the terminal phalanx.

Greene's (1935) description and figure (p. 75, Fig. 87) showing this muscle in the Norway rat both fail to express the relationships found in the specimens of that species which I have dissected. In both forefeet of three specimens of *Rattus norvegicus* I have found the relationships of this muscle to be almost precisely as described above for *Neotoma* and *Peromyscus*. I cannot agree with her identification of this muscle as M. extensor pollicis longus. It passes through the first osteofibrous canal of the wrist, arises from both the ulna and radius, and inserts principally on the base of the first metacarpal. These relations are all typical of M. abductor pollicis longus. M. extensor pollicis longus, on the other hand, typically arises from the ulna only, passes through the third osteofibrous canal, and inserts on the distal phalanx of the thumb. Acceptance of the present muscle as M. extensor pollicis longus would necessitate the acceptance of the belief that this muscle has transferred its route through the carpal region from the third compartment to the first. This does not seem likely. If my identification of this muscle is correct, however, the attachment to the

distal phalanx of the thumb must be considered as a secondarily derived condition, possibly attained by "capture" of a part of the extensor tendon by the abductor.

M. extensor digitorum communis

Origin. — From the lateral epicondyle between M. extensor carpi radialis brevis and M. extensor digiti quinti.

Insertion. — Into the dorsum of the terminal phalanges of the second to fifth digits.

Remarks. — The relationships and arrangement of the tendons of this muscle in all four genera are almost exactly as Howell described them for *Neotoma*. There are, however, certain minor differences in the fleshy parts of the muscle. Howell found three parts of this muscle, of which the middle part gives rise to two tendons which pass to digits 3 and 4. In specimens available to me this part was readily divisible into two slips. Thus there are, in all, four rather discrete slips. The most medial (ulnar) slip lies in contact with M. extensor indicis. Its tendon splits; the main branch passes directly to the fifth digit; the smaller division crosses deep to the tendon to the fourth digit, to insert on the base of the third digit. In *Neotoma*, *Peromyscus*, and *Oryzomys* this division of the medial slip is small but easily located. In *Sigmodon* it is a very thin tendon which requires careful dissection to be found. In some specimens it seemed to be absent, but was possibly overlooked. The two middle divisions of the muscle lie deep between the other two parts and are usually not visible from a superficial view. These two slips are mostly tendinous, with very short fleshy bellies. The lateral (radial) part lies in contact with M. extensor carpi radialis brevis.

On the dorsum of the hand all four tendons are closely bound together by a rather heavy fascia. The muscle as a whole is much more robust in *Sigmodon* and *Oryzomys* than in the other two genera.

M. extensor indicis

Origin. — From the middle fifth of the lateral surface of the ulna.

Insertion. — On the base of the second digit.

Remarks. — The tendon of this muscle passes through the compartment of the wrist with the tendons of M. extensor digitorum communis. In *Neotoma* and *Peromyscus* a thin tendinous branch passes to the pollex. In *Peromyscus* origin is slightly more proximal (from the third sixth of the ulna).

M. extensor digiti quinti proprius

Origin. — From the lateral epicondyle distal to M. extensor digitorum communis.

Insertion. — Into digits 4 and 5.

Remarks. — This tendon passes through its own compartment in the wrist, superficial to, and on the ulnar side of, the extensor digitorum communis. The tendons pass over the ulnar side of the metacarpophalangeal

joints and are rather closely bound there by a fascia. It appears from this that they might act as abductors, as well as extensors, of the two ulnar digits.

In *Peromyscus* and *Neotoma* this muscle is quite small, appearing to be relatively about half as robust as in *Sigmodon* and *Oryzomys*.

M. extensor carpi ulnaris

Origin. — By two heads: (1) from the caudolateral aspect of the extreme distal part of the lateral epicondyle, distal to the radial collateral ligament; and (2) along the lateral ridge of the ulna, from the middle of the olecranon to a point one-fourth the distance from the semilunar notch to the distal end of the ulna.

Insertion. — Onto the base of the fifth metacarpal.

Remarks. — In *Sigmodon* and *Oryzomys* the fibers which arise from the ulna constitute at least half of the mass of the muscle. In *Neotoma* and *Peromyscus* these make up only approximately a third of the muscle. In *Neotoma* the origin of the ulnar head begins well below the semilunar notch (a distance about equal to the length of the olecranon). In *Peromyscus* origin of this head is as in *Sigmodon*, whereas in *Oryzomys* it takes origin from the entire length of the olecranon.

Flexor System

Pectoral Group
(Figs. 8, 9)

The pectoral musculature is supplied by the lateral anterior thoracic nerves, from the fifth and sixth cervical nerves, and by the medial anterior thoracic nerve, from the eighth cervical and first thoracic nerves. M. subclavius is supplied by a special branch from the plexus.

M. subclavius

Origin. — From the anterior border of the cartilage of the first rib, immediately adjacent to its junction with the rib.

Insertion. — On the dorsocaudal surface of the distal third of the clavicle.

Remarks. — No variation was noted.

M. pectoralis major

Origin. — From the mid-ventral line of the manubrium, from all the sternebrae, and from the anterior third of the xiphisternum.

Insertion. — On the lateral ridge of the humerus.

Remarks. — This muscle, as in many other rodents, is separable into a small, superficial, anterior part and a larger posterior part. The superficial part arises from the anterior half of the manubrium and extends almost directly laterad; its cranial border passes beneath the posteromedial border of M. deltoideus. This part inserts on the distal two-thirds of the

lateral ridge of the humerus, deep to the insertion of M. deltoideus and superficial to the insertion of the other part of M. pectoralis major.

The posterior, deeper part of this muscle arises from the mid-line of the posterior half of the manubrium, all the sternebrae, and the anterior third of the xiphisternum. The fibers pass anterolaterad, converging to form a broad, thin tendon which inserts along the entire length of the lateral crest of the humerus.

In *Peromyscus* and *Neotoma* the origin is similar, except that it extends only as far caudad as the anterior end of the xiphisternum. The superficial part is not discrete in *Neotoma*, but is easily discernible because of the difference in the directional tendency of the fibers. Insertional relationships are much the same in all four genera.

M. pectoralis minor

Origin. — From all of the sternebrae, the xiphisternum, and the anterolateral part of the surface of the xiphisternal cartilage.

Insertion. — Anterior part: on the capsule of the shoulder joint and the most proximal part of the lateral ridge of the humerus. Posterior part: with the tendon of M. cutaneus maximus, on the lateral ridge deep to the insertion of the anterior part.

Remarks. — The large posterior part of this muscle arises only from the xiphisternal cartilage and the extreme posterior part of the xiphisternum. It parallels the posterior border of the anterior part, then diverges laterad to meet M. cutaneus maximus, with which it fuses.

The tendon of the anterior part passes across the tendon of the short head of M. biceps brachii onto the head of the humerus, where it merges with the tendon of M. supraspinatus and the capsule of the joint. In *Neotoma* and *Oryzomys* a small part of the tendon attaches to the clavicle. In *Peromyscus* and *Neotoma* the posterior part is not so distinct from the anterior part. In these two forms the posterior part does not diverge from the anterior part, but continues parallel to it and fuses with the tendon of M. cutaneus maximus very near its insertion. In *Oryzomys* the divergence of the two parts is even greater than in *Sigmodon*, and the fusion of the tendon of the posterior part with that of M. cutaneus maximus is some distance from the insertion.

M. cutaneus maximus

Origin. — From the skin of the thorax, abdomen, and lumbar region (see remarks).

Insertion. — Onto the entire length of the lateral ridge of the humerus, partly deep to the insertion of the anterior part of M. pectoralis minor.

Remarks. — Howell's (1926:37) description of this muscle in *Neotoma* applies almost equally well to *Sigmodon*, *Peromyscus*, and *Oryzomys*. "The muscle diverges from the axillary fossa with strongly developed fibers, joining its fellow of the opposite side upon the midventral line at a point slightly craniad to the xiphoid process of the sternum, and upon the middorsal line at a point immediately dorsad of the axillary fossa [over the middle of the interscapular fossa]. The fibers disappear in the fascia

covering the posterior half of the belly, the groins and the gluteal region, and the lower back. Fibers again develop, however, at the base of the tail." These last mentioned fibers insert into the spines and transverse processes of the third to fifth caudal vertebrae and the superficial fascia of the tail. This part of the muscle is most strongly developed in *Neotoma* and *Peromyscus*.

A detailed comparison of the extent of this muscle in the four genera could not be made because of the impossibility of determining exactly where the fibers ended. It appears, however, that although the area of the body concerned is nearly the same, the muscle is thicker and stronger in *Sigmodon*, possibly also in *Oryzomys*, except for that part which inserts on the tail.

M. pectoralis abdominalis

Origin. — By aponeurosis from the mid-ventral line of the caudal half of the xiphoid cartilage, along the linea alba to a point 10 to 12 mm. posterior to that process, and then laterad for about 8 mm.

Insertion. — Into the lesser tuberosity of the humerus immediately adjacent to the bicipital groove.

Remarks. — This muscle is a thin, flat band running parallel to the caudal border of M. pectoralis minor. It soon converges to about one-half its original width. Medial to the tendon of M. cutaneus maximus it turns anteriad and passes deep to the other pectoral muscles to its insertion.

Insertion in *Neotoma* is on the coracoclavicular ligament and the clavicle. The muscle was not found to attach directly to the humerus in any specimens of this genus. In *Peromyscus* the aponeurosis passes over the biceps tendon to insert partly on the lateral lip of the bicipital groove and partly with M. pectoralis minor on the proximal aspect of the greater tuberosity. *Oryzomys* has an insertion similar to that in *Sigmodon*.

Flexor Group of the Arm
(Figs. 9, 11, 12, 13)

M. biceps brachii and M. coracobrachialis are supplied by the musculocutaneous nerve. M. brachialis receives its principal innervation from this nerve, but is supplied also by a small branch of the radial nerve.

M. coracobrachialis

Origin. — From the coracoid process of the scapula in common with the short head of M. biceps brachii.

Insertion. — On the medial surface of the distal two-fifths of the humerus between M. brachialis and M. triceps, caput medialis.

Remarks. — In *Sigmodon* and *Oryzomys* this muscle is made up of only one slip, which probably represents the fused middle and long parts of the primitive muscle (as interpreted by Wood, 1867:45). Insertion of this slip is similar in all four genera, but extends a bit more proximad in *Peromyscus* (on distal half of medial surface of the humerus).

In *Neotoma* and *Peromyscus* there is another slip of this muscle which passes directly from the coracoid process to the humerus and inserts proximal to the tendons of M. teres major and M. latissimus dorsi. The musculocutaneous nerve passes between this part and the long slip of the muscle. Among the Myomorpha this short part has been described only in *Cricetus* and *Cricetomys* (Parsons, 1896:169, 184). Its presence in other groups of mammals has long been established (Wood, 1867; Parsons, 1894; Hill, 1937; Bryant, 1945).

In *Neotoma* and *Peromyscus* the long part of this muscle is considerably more robust than in *Sigmodon.* In *Oryzomys* it is very thin, not more than two-thirds as thick as in *Sigmodon.*

M. biceps brachii

Origin. — Short head: from the coracoid process by a tendon common to it and to M. coracobrachialis. Long head: from the superior lip of the glenoid fossa of the scapula.

Insertion. — Onto the tuberosity of the radius and the brachial ridge of the ulna.

Remarks. — The short head of this muscle is intimately fused with M. coracobrachialis in the first third of its length. The fleshy fibers of the two muscles arise from opposite sides of the common tendon like vanes from the shaft of a feather. The two heads of the biceps remain distinct almost to their insertion. A weak lacertus fibrosus is developed in *Sigmodon, Oryzomys,* and *Peromyscus.* This structure in *Neotoma* is quite strongly developed, and a considerable number of the muscle fibers pass directly into the aponeurosis.

The insertional tendon in *Sigmodon* splits shortly before inserting, one part going to the radius, the other inserting medial to M. brachialis on the proximal half of the brachial ridge of the ulna. Thus, the brachialis tendon passes between the two branches of the biceps tendon. This is also true in *Oryzomys,* but in *Neotoma* and *Peromyscus* insertion is only on the tuberosity of the radius, and the entire tendon passes lateral to that of M. brachialis.

M. brachialis

Origin. — By two heads: (1) from the lateral and posterior aspects of the neck of the humerus; and (2) from the anteromedial surface of the humerus below the deltoid ridge, with a few fibers arising in the angle between the craniomedial side of the ridge and the shaft of the humerus.

Insertion. — On the brachial ridge of the ulna.

Remarks. — The two heads of this muscle are very nearly continuous, especially in *Neotoma* and *Peromyscus.* In these two genera origin of the short head is confined to a narrow area along a line projected directly distad from the deltoid ridge. In *Sigmodon* and *Oryzomys,* however, this head arises almost entirely medial to that line, and the most lateral fibers take origin from the anteromedial surface of the deltoid ridge.

Flexor Group of the Forearm
(Figs. 8, 12, 13)

The muscles of this group are supplied by the median and ulnar nerves. The ulnar nerve supplies M. flexor carpi ulnaris and M. epitrochleoanconeus. The median nerve supplies the remaining muscles of the group. In many mammals the ulnar head of M. flexor digitorum profundus is supplied by a branch of the ulnar nerve, but I have not been able to demonstrate this in the forms studied. Instead, this part is supplied by a rather large branch of the median nerve.

M. epitrochleoanconeus (*M. anconeus* Howell, 1926)

Origin. — From the medial epicondylar process of the humerus.

Insertion. — On the ventromedial aspect of the olecranon.

Remarks. — (see also p. 73.) This small but distinct muscle is present in all four genera. Howell (1926) described it as M. anconeus and stated that it is innervated by the radial nerve. In all specimens which I dissected innervation was by a small branch of the ulnar nerve (Hill, 1937; Leche, 1900; McMurrich, 1903).

M. flexor carpi ulnaris

Origin. — By two heads: (1) from the medial surface of the olecranon and proximal fourth of the ulna, and (2) from the medial epicondyle.

Insertion. — On the pisiform bone.

Remarks. — The humeral head of this muscle is quite small and inserts on the aponeurosis of the deep surface of the ulnar head. It lies in a V-shaped cleft between the caudal surface of M. palmaris longus and the lateral surface of M. flexor digitorum profundus. In *Sigmodon* this head of the muscle is entirely discrete until it merges with the ulnar head. In *Neotoma* and *Peromyscus* it is fused for about half its length with the two muscles between which it lies. The humeral head is not present in *Oryzomys*.

M. palmaris longus

Origin. — From the distal part of the medial epicondyle.

Insertion. — On the radial side of the thumb, the falciform bone, and the proximal borders of the thenar and hypothenar pads.

Remarks. — Near the middle of the forearm the tendon splits into two parts. The radial division, about one-third the size of the other, passes over the falciform bone to insert around the radial side of the thenar pad and to send a small slip to the first phalanx of the thumb. The larger ulnar slip of the tendon broadens as it approaches the carpal region and inserts on the ulnar half of the falciform and into the proximal borders of the thenar and hypothenar pads. Fibers of this tendon continue into the hand to form the superficial palmar aponeurosis which attaches near the bases of the three ulnar digits.

In *Neotoma* and *Peromyscus* the proximal third of this muscle is fused with M. flexor digitorum sublimis, M. flexor digitorum profundus, and the

ulnar head of M. flexor carpi ulnaris. In these two forms the divisions of the tendon are of nearly equal size, and the palmar aponeurosis is more strongly developed. In *Oryzomys* the tendon passes predominantly to the ulnar side of the hand. The radial division consists of only a few fibers.

M. flexor carpi ulnaris

Origin. — From the medial epicondyle and from the fascia of the medial surface of M. pronator teres.

Insertion. — On the base of the third metacarpal.

Remarks. — The insertion of this muscle was found to be the same in all specimens dissected. Howell (1926) placed this insertion on the base of the second metacarpal in *Neotoma*.

M. pronator teres

Origin. — From the medial epicondyle and from an aponeurosis common to this muscle and M. flexor carpi radialis.

Insertion. — On the craniomedial surface of the middle third of the radius.

Remarks. — In *Peromyscus* insertion is restricted to the second fifth of the radius; in *Oryzomys* attachment is to the second fourth of the radius. Insertion in *Neotoma* covers approximately the middle half of the radius.

M. flexor digitorum sublimus

Origin. — From the medial epicondyle, deep to M. flexor carpi ulnaris and M. palmaris longus.

Insertion. — By three distinct tendons into the base of the second phalanx of each of the three middle digits.

Remarks. — In *Peromyscus* the bundles of fibers which give rise to each of the three tendons have a greater degree of individuality than in the other three genera, in which they fuse into a single muscular belly. Except for this minor difference, there is little variation among the four genera.

Insertion of the tendons of this muscle is accomplished in the same manner as is the insertion of the short flexor tendons of the foot (see M. flexor digitorum brevis of the foot, p. 110).

M. flexor digitorum profundus

Origin. — By three heads: (1 and 2) from the medial epicondyle, (3) from the medial aspect of the proximal two-thirds of the radius and from the second and third fourths of the ulna.

Insertion. — By tendons on the distal phalanges of each of the five digits.

Remarks. — The first head of this muscle lies deep to M. palmaris longus between that muscle and M. flexor carpi radialis, partly superficial to the latter. The second head is the smallest of the three; it lies deep to M. flexor digitorum sublimus, directly on the ulnar side of the first head. The tendons of these two heads join to form a common tendon

at the level of the junction of the third and distal fourths of the forearm. The third head appears to represent the fused ulnar and radial heads which are found in many rodents (Windle, 1890; Hill, 1937). This head ends in a broad, strong tendon which is joined just proximal to the end of the radius by the common tendon of the other two heads. In the palmar region the common tendon of all three heads divides into four tendons which pass to the four medial digits. The tendon which passes to the pollex arises from the middle of the volar surface of the main tendon just before its division and passes deep to the lumbrical muscle of the second digit as it crosses to the pollex.

The arrangement of the tendons in *Neotoma* and *Peromyscus* differs from that in *Sigmodon*. In the former two genera the tendon of the small central head, lying at first dorsomedial to that of the larger condylar head, crosses the latter and merges with the tendon of the radioulnar head on its radial side, a few millimeters proximolateral to the point where the condylar head joins the principal tendon. As was mentioned above, the two epicondylar heads in *Sigmodon* form a common tendon before fusing with the tendon of the radioulnar head. In *Oryzomys* the tendons of the two epicondylar heads join the radial border of the radioulnar head as in *Sigmodon*, but although they lie close together, they are not fused with each other before doing so.

M. pronator quadratus

Origin. — From the radial surface of most of the distal three-fifths of the ulna.

Insertion. — On the adjacent surface of the radius.

Remarks. — The fibers of the proximal third of this muscle run obliquely proximad; those of the middle third pass directly across the long axis of the forearm; and those of the distal third pass obliquely distad.

In *Peromyscus* this muscle is somewhat reduced; it is restricted to the third and fourth fifths of the forearm. In *Neotoma* and *Oryzomys* it is essentially similar to that in *Sigmodon*.

Flexor Group of the Manus
(Fig. 14)

Innervations of the intrinsic muscles of the hand were not determined.

The works of Cunningham (1882), McMurrich (1903), and certain other anatomists have contributed much to the knowledge of the phylogeny and homologies of the muscles of the hand. There are still many questions, however, which have not been answered. This is particularly true of the muscles of the fifth digit in the genera under consideration here. There are six discrete muscular slips intrinsic to the manus, which insert on the fifth digit. Three of these, M. adductor digiti quinti, the fourth lumbrical, and the last volar interosseus muscle can be identified with a considerable degree of certainty, but the applicability of the names here assigned to the other three slips is admittedly open to question. For this reason, it should be emphasized that the names M. abductor digiti quinti, M. flexor digiti

quinti brevis, and M. opponens digiti quinti are used here in a topographical sense and do not necessarily imply my belief that the muscles concerned are homologous with those of the same name in man. There has been much confusion in regard to the proper terminology of these muscles, and most of the names have been applied to different muscles by one author or another. An attempt has been made to point out the different terms which have been used for each muscle.

M. abductor pollicis brevis

Origin. — From the distal border of the falciform bone.

Insertion. — On the radial side of the first metacarpal.

Remarks. — The fibers of this muscle pass almost directly radiad to their insertion. In *Neotoma* and *Oryzomys* insertion is on the metacarpal and first phalanx.

M. flexor pollicis brevis

Origin. — From the base of the thenar pad and from the ulnar end of the falciform bone, superficial to M. flexor digiti quinti.

Insertion. — On the base of the distal phalanx of the thumb.

Remarks. — There is almost no variation among the four genera.

M. adductor pollicis

Origin. — From the common deep palmar ligament between the scapholunar bone and the base of the second metacarpal (see Mm. interossei).

Insertion. — On the ulnar side of the base of the first phalanx of the pollex.

Remarks. — This muscle is similar in all four genera.

M. adductor digiti secundi

Origin. — From the proximal two-thirds of the raphe between the adjacent interosseus muscles of the third and fourth digits.

Insertion. — On the ulnar side of the base of the first phalanx of the second digit.

Remarks. — This muscle varies little among the four genera. It is easily overlooked, or it may be confused with the interossei unless one observes closely its relationship to the nerve which passes between it and the interossei.

M. abductor digiti quinti

Origin. — From the cartilage in the base of the hypothenar pad, directly superficial to the pisiform bone.

Insertion. — On the distal third of the fascia of the ulnar surface of the opponens digiti quinti, on the ulnar side of the base of the first phalanx of the digit, and with M. flexor digiti quinti on the vestige of the perforated tendon of the digit.

Remarks. — The relationships of this muscle are such that it is functionally almost a direct continuation of the fibers of the ulnar part of the palmaris longus tendon.

In some specimens of *Peromyscus* the muscle divides into two slips at the insertion. One of these inserts on the ulnar surface of the opponens digiti quinti; the other joins M. flexor digiti quinti brevis just before that muscle inserts. Except for this variation the muscle is similar in all four genera.

M. flexor digiti quinti brevis

Origin. — From the ulnar end of the falciform bone.

Insertion. — On the vestigial part of the flexor perforatus tendon of the fifth digit (similar to that described under M. flexor digitorum brevis of the foot) and, secondarily through this, on the base of the second phalanx.

Remarks. — This muscle has been referred to as "flexor brevis digitorum manus" (Parsons, 1896), "adducteur du cinquieme doigt" (Alezais, 1900), "palmaris brevis" (Leche, 1900), and "flexor brevis minimi digiti" (McMurrich, 1903). McMurrich used the last term in connection with the opossum, the cat, and the mouse (*Mus musculus*). His remarks (1903: 478-79, 489-90) make it obvious that he considered this the homologue of the human M. flexor digiti quinti brevis. This muscle has similar relationships in all four genera.

M. adductor digiti quinti

Origin. — From the common deep palmar tendon and from the proximal third of the raphe between the adjacent interosseus muscles of the third and fourth digits.

Insertion. — On the radial side of the base of the first phalanx of the fifth digit.

Remarks. — This muscle lies on the surface of the interossei but is separated from them by the deep branch of the ulnar nerve. There seems to be some variation in the relative development of this muscle, but it is so thin that accurate comparisons would be difficult to make.

Parsons (1896) said that this muscle was present in *Cricetomys*, *Microtus*, and "possibly in *Cricetus*." It is also present in *Mus musculus* (McMurrich, 1903) and in the Norway rat, although Greene (1935) did not describe it under this name. I believe that this is the muscle which Greene called M. flexor digiti quinti brevis. Her descriptions of the muscles of the fifth digit are not only inconsistent with the relationships shown in her illustration of them, but the figure and the descriptions also fail to agree with the muscles in the forefeet of several specimens of the Norway rat which I have dissected. In these latter specimens the muscles differed only slightly from those in the four genera under consideration here.

M. opponens digiti quinti

Origin. — From the distoradial aspect of the pisiform.

Insertion. — On the two sesamoid bones of the fifth metacarpophalangeal joint.

Remarks. — Parsons (1894, 1896) called this muscle "M. flexor brevis minimi digiti" and considered it to be the ulnar slip of the interosseus layer. This disposition of the muscle has also been made by various other

authors (e.g., Alezais, 1900; Bryant, 1945). McMurrich (1903), however, showed that only one slip of the epineural muscles of the mammalian manus from which the interosseus muscles are derived inserts on the fifth digit. This slip is described under the interossei. The other muscles inserting on this digit are all derived from the hyponeural layers. None of them should, therefore, be included in the interosseus series.

Sigmodon is the only one of the four genera in which this muscle is inserted into the two sesamoids. In the other three genera attachment is only to the ulnar sesamoid.

Mm. lumbricales

Origin. — From the palmar surface of the tendon of M. flexor digitorum profundus and from the sides of its branches after it divides into its terminal slips.

Insertion. — On the borders of the tendons of M. extensor digitorum longus of the second to fifth digits.

Remarks. — The tendons of these muscles are closely bound to the metacarpophalangeal joints of the respective digits and appear to insert on them. The tendons, however, continue through the dense fibrous tissue around the joints and pass dorsad on the radial sides of the first phalanges to join the tendons of the extensor digitorum longus immediately proximal to the joints between the first and second phalanges.

The first lumbrical muscle is considerably reduced in *Sigmodon.* In some specimens no trace of it was found; however, it might have been overlooked. This muscle is somewhat reduced in *Oryzomys*, also, but in the other two forms all four muscles are about equally developed.

Mm. interossei

Of these muscles, I have been able to identify only seven — one to the radial side of the fifth digit and two to each of the second to fourth digits. The origin of all is from the distal border of a common deep palmar tendon which is attached on the ulnar side to the base of the pisiform bone and on the radial side, to the base of the first metacarpal. Proximally, the tendon is attached to the scapholunar, the triangular, and the hamate bones. It lies in contact with the palmar surfaces of the proximal ends of the metacarpals, but is not attached to them. The adductors of the first and fifth digits also arise from this tendon.

If an interosseus muscle to the thumb is present, I have not been able to distinguish it from M. adductor pollicis. Parsons (1896:173) stated that "in all the animals examined, except *Georychus* and *Bathyergus* there were eight interossei, the inner of which formed the flexor brevis minimi digiti [= my opponens]." This corresponds with my findings when disposition of the ulnar slip to the fifth digit is made in the manner described above.

M. palmaris brevis

Origin. — From the ulnar end of the falciform bone and the adjacent margin of the base of the thenar pad.

Insertion. — Into the deep side of the base of the hypothenar pad and into the fascia of the ulnar side of the hand.

Remarks. — In some specimens there is also a small group of fibers extending from the radial border of the thenar pad into the fascia over the region of the first metacarpal. This appears to be the part referred to by McMurrich (1903) as "palmaris brevis radialis." The main part of the palmaris brevis is rather well developed in all four genera studied. It lies in the heavy connective tissue of the palm and is usually removed when the pads are stripped off. This may be why many workers have overlooked the muscle.

Muscles of the Pelvic Girdle and Limb

Extensor System

Iliacus Group
(Figs. 16C, D)

These muscles are innervated by branches of the femoral nerve. In many mammals the posterior fibers of M. pectineus receive a branch from the obturator nerve. I was not able to demonstrate any obturator innervation of the pectineus in any of the specimens dissected during this study.

M. iliacus

Origin. — From the iliac fossa by fleshy fibers and by small tendons from the transverse processes of the last two lumbar vertebrae.

Insertion. — By a tendon on the shaft of the femur, just below the lesser trochanter, for a distance of about 6 or 7 mm.

Remarks. — The insertional tendon of this muscle is continuous with that of M. psoas major, which inserts on the lesser trochanter. In *Neotoma* the insertion of M. iliacus is relatively only about one-half the width of the insertion in *Sigmodon*; in *Peromyscus* it is even narrower.

The differentiation of M. iliacus from M. psoas major is usually somewhat greater in *Sigmodon* and *Oryzomys* than in the other two genera. This varies in different individuals, however, and seems not to be of significance.

M. psoas major

Origin. — From the bodies of all the lumbar vertebrae and the extreme anterior end of the first sacral vertebra.

Insertion. — By tendon on the lesser trochanter of the femur.

Remarks. — In the posterior lumbar region the psoas major and the iliacus muscles are separable only with difficulty, and their insertional tendons are continuous. In *Peromyscus*, *Neotoma*, and *Oryzomys* few, if any, fibers of this muscle arise from the first lumbar vertebra.

M. pectineus

Origin. — From the inferior border of the pelvis, directly ventral to the acetabulum.

Insertion. — Along a line on the caudomedial surface of the femur, from a point where the crest of the lesser trochanter blends with the shaft, to the middle of the femur.

Gluteal Group
(Figs. 15; 16B, C, D)

The muscles of this group are arranged in two layers. Typically, the gluteus maximus, tensor fasciae latae, femorococcygeus, and tenuissimus make up the superficial layer; the deep layer comprises the gluteus medius, gluteus minimus, and pyriformis. In many rodents, including those described here, the tensor fasciae latae and gluteus maximus form a continuous muscular sheet which has been designated as M. gluteus superficialis by some authors (Howell, 1926).

Innervation of M. tensor fasciae latae, M. gluteus medius, M. gluteus minimus, and M. pyriformis is by the superior gluteal nerve; M. gluteus maximus and M. femorococcygeus are supplied by the inferior gluteal nerve. M. tenuissimus receives a separate branch directly from the common peroneal nerve.

M. tensor fasciae latae

Origin. — From the lumbodorsal fascia at the level of the last lumbar and first two sacral vertebrae and from the spine and cranial half of the inferior border of the ilium.

Insertion. — The fibers arising from the inferior border of the ilium insert on the fascia of the medial surface of the quadriceps femoris about half way to the knee; those which take origin from the spine of the ilium and the lumbodorsal fascia insert on the fascia of the anterior and lateral surfaces of the thigh along a line extending from about 1 cm. proximal to the knee, on the anterior border, dorsocaudad to the distal end of the lateral ridge of the femur.

Remarks. — The posterior border of this muscle is continuous with the anterior border of the gluteus maximus. Parsons (1896) believed that the medial part of this muscle represents M. sartorius, but, as Howell (1926) and Hill (1937) pointed out, this part is innervated only by the superior gluteal nerve and must, therefore, belong to the gluteal complex.

Variation of this muscle is only slight among the forms studied. In *Peromyscus* insertion does not extend so far distad on the thigh.

M. gluteus maximus (*M. gluteus superficialis* Howell, 1926, part)

Origin. — From the dorsal fascia in the region of the second to fourth sacral vertebrae.

Insertion. — On the craniolateral border of the lateral ridge of the femur.

Remarks. — The nerve to this muscle enters its deep surface immediately caudal to the head of the femur. The fibers of the anterior border are continuous with those of the posterior border of M. tensor fasciae latae and pass caudolaterad to insert on the most distal part of the lateral

ridge. The fibers of the caudal border pass laterad and slightly craniad over the greater trochanter to the posterior lip of the lateral crest. This muscle is similar in all four genera.

M. femorococcygeus (*M. biceps anticus* Howell, 1926)

Origin. — From the spine of the fourth sacral vertebra and the interspinous ligament between this vertebra and the first caudal vertebra.

Insertion. — On the distal half of the lateral border of the patella and onto the lateral surface of the capsule of the knee joint.

Remarks. — The application of the term "M. femorococcygeus" here corresponds to the usage of Leche (1883). Various authors have used "M. biceps anticus" and "M. caudofemoralis" to designate this muscle. It is, however, a member of the gluteal complex, not related to M. biceps femoris. The term "M. caudofemoralis" should be restricted to a muscle of the flexor system (Appleton, 1928; Hill, 1937).

In *Sigmodon* this is a well-developed muscle completely differentiated from the gluteus maximus. There is no indication of fusion with M. biceps femoris, from which it is separated by the posterior femoral cutaneous nerve which passes between the two muscles. The origin is entirely covered by M. semitendinosus. In its proximal half the muscle lies between M. gluteus maximus and M. biceps femoris. At the level of the lateral femoral crest it lies on the posterolateral surface of M. adductor magnus, and its distal part is in contact anteriorly with M. vastus lateralis, superficial to M. caudofemoralis.

In *Neotoma* origin is from the spines of the first two caudal vertebrae. In this genus the muscle is not so strongly developed, but has the same relationships as in *Sigmodon*. In *Peromyscus* origin is from the spine of the first caudal vertebra. The origin in *Oryzomys* is from the interspinous ligament between the last sacral and first caudal vertebrae.

Insertion of the femorococcygeus in *Peromyscus* is on the posterolateral surface of the femur below the lateral ridge and onto the lateral epicondyle proximomedial to the origin of the lateral head of M. gastrocnemius. In *Oryzomys* some fibers insert on the lateral epicondyle, but most pass to the capsule of the knee joint.

According to Appleton (1928), the primitive insertion of this muscle is on the proximal half of the femur. As Hill (1937) pointed out, insertion on the patella and distal part of the femur must, then, be considered a secondary extension of the muscle. From this standpoint the relationships of this muscle in *Peromyscus* must be considered the most primitive among the four genera under consideration. *Sigmodon* and *Neotoma* would be considered the most advanced in this respect, and *Oryzomys* would occupy an intermediate position.

M. tenuissimus

This muscle is not present in *Sigmodon* and *Oryzomys*. The following description applies only to *Neotoma* and *Peromyscus*.

Origin. — From the deep fascia of the sacral region immediately posterior to the origin of M. gluteus maximus, between this muscle and M. femorococcygeus.

Insertion. — On the fascia of the lateral surface of the calf just distal to the posterior border of M. biceps femoris.

Remarks. — This muscle passes superficial to the posterior femoral cutaneous nerve and M. caudofemoralis, and deep to M. femorococcygeus and M. biceps femoris. Innervation is by a branch of the common peroneal nerve.

M. gluteus medius

Origin. — From the deep layer of the lumbosacral fascia, lateral to the last two lumbar and the first two sacral vertebrae, and from the superior crest, spine, gluteal fossa, and anterior part of the inferior margin of the ilium.

Insertion. — On the greater trochanter and a roughened area on the posterolateral surface of the femur just lateral to the intertrochanteric crest, extending distad to the level of the lateral crest.

Remarks. — The gluteus medius is composed of three poorly differentiated parts. The dorsolateral part includes the fibers which arise from the lumbodorsal fascia. These fibers converge caudoventrad, pass over the proximal end of the femur to its caudal surface, and insert proximal to the insertion of M. adductor magnus. This fascicle was identified by Howell (1926) as M. gluteus maximus. The second superficial element comprises those fibers which take origin from the superior iliac spine, the anterior part of the gluteal fossa, and the anterior half of the ventral margin of the ilium. These fibers terminate in a short, broad tendon which attaches to the caudolateral surface of the greater trochanter. The deep part of the muscle arises from the posterior two-thirds of the gluteal fossa and inserts by tendon on the proximomedial part of the greater trochanter. This insertion is continuous with that of M. pyriformis.

In *Sigmodon* the origin of the dorsal superficial part of the gluteus medius extends onto the superficial aponeurosis of M. longissimus anterior to the spine of the ilium, as far as the level of the interval between the spines of the fourth and fifth lumbar vertebrae, thus forming a "gluteal tongue" apparently similar to that found in many ungulates. To the best of my knowledge, such an extension of the gluteus medius has been reported among the rodents only in *Cuniculus paca* (Slijper, 1946). In *Peromyscus* there is a slight indication of this gluteal extension, but none was found in *Neotoma* and *Oryzomys*. In *Oryzomys* the muscle is shorter and broader, relatively, than in the other genera.

M. pyriformis

Origin. — From the ends and ventral surfaces of the transverse processes of the second and third sacral vertebrae.

Insertion. — Principally on the medial border of the tendon of the deep part of M. gluteus medius; a few fibers insert directly on the medial aspect of the greater trochanter.

Remarks. — Although this muscle is closely associated with M. gluteus medius, it is easily distinguishable, especially near the origin. A branch of the superior gluteal nerve passes dorsad between the two muscles. In

Neotoma this muscle is hardly differentiated from the deep part of M. gluteus medius, and only the branch of the superior gluteal nerve serves to separate them. In *Peromyscus* differentiation of M. pyriformis from M. gluteus medius is as great as in *Oryzomys* and *Sigmodon*.

M. gluteus minimus

Origin. — From the posterior part of the gluteal fossa deep to M. pyriformis and M. gluteus medius, from the lateral crest of the ilium, and from the lateral part of the inferior iliac surface as far posteriad as the femoral tubercle.

Insertion. — On the cranial and medial parts of the greater trochanter.

Remarks. — The present interpretation of M. gluteus minimus agrees with that of Greene (1935) and of Hill (1937). The fibers which take origin from the lateral crest and the inferior iliac surface probably represent the scansorius muscle, but in the genera studied they are continuous with that part of the gluteus minimus which arises from the superior surface of the ilium. Howell (1926, 1932) placed under this name only the ventrolateral part of the muscle and included the remainder of the muscle in his "M. gemellus superior." Alezais (1900) correctly identified the dorsal part (his "portion sciatique du petit fessier") and called the lateral part M. scansorius. This much is correct, but he also included in his gluteus minimus the deep part of M. gluteus medius (his "portion iliaque du petit fessier"). Consequently, he was led to conclude that the scansorius was separate from the gluteus minimus and that the pyriformis was closely related to it.

The gluteus minimus is separated from the gluteus medius by the superior gluteal nerve and vessels. In the four genera studied the adjacent borders of M. gluteus minimus and M. gemellus superior cannot be separated with certainty in many individuals unless the thigh is in a position of nearly complete flexion. These two muscles can be distinguished, however, by tracing their innervations since the gemellus superior is supplied by a branch of the tibial nerve, and the gluteus minimus is supplied by the superior gluteal nerve.

In *Neotoma* and *Peromyscus* there is a group of fibers which arises from the inferior margin of the ilium by an aponeurosis beneath those fibers which take origin from the iliac fossa and inserts on the ventrolateral border of the tendon of this latter part (Howell, 1926:73, and Fig. 16, p. 71). This element is represented only by a small number of fibers in *Sigmodon* and *Oryzomys* and might easily be overlooked.

Quadriceps Femoris Group
(Figs. 10A; 15; 16A, C, D)

The femoral nerve provides the innervation for the muscles of this group. M. sartorius, which would be included here, is absent in the forms studied.

M. rectus femoris

Origin. — By straight and reflected heads from the ventral aspect of the femoral tubercle of the ilium and from the dorsocranial border of the acetabulum, respectively.

Insertion. — On the proximal aspect of the patella.

Remarks. — In *Sigmodon* and *Oryzomys* the two heads of this muscle are quite distinct, more so than in the other two genera. The muscle fibers arise from the posterior border of the tendon of the reflected head and from the medial surface of the tendon after the two heads fuse. The tendon of the reflected head forms the principal axis of the muscle. The straight head, a loosely constituted bundle of fibers, joins the reflected head 3 to 4 mm. from its origin, and the two heads form an angle of about 30 degrees.

In *Peromyscus* the straight head forms the main axis of origin. The muscle fibers arise almost directly from the femoral tubercle, and it is the reflected head which joins this at an angle (Fig. 16A). In *Neotoma* the relations of the two heads are intermediate between the condition in *Sigmodon* and that in *Peromyscus*.

M. vastus lateralis

Origin. — From the anterior aspect of the greater trochanter and from the anterior side of the lateral ridge of the femur.

Insertion. — On the fascia of the distal part of M. rectus femoris and on the dorsolateral border of the patella.

Remarks. — Topographical relationships are similar in all four genera. The muscle is most strongly developed in *Oryzomys* and least developed in *Peromyscus*. This muscle covers the entire lateral surface of the thigh anterior to the femur, with some of the fibers passing around the anterior border to lie on the medial surface of the thigh.

M. vastus medialis

Origin. — From the craniomedial surface of the proximal two-fifths of the shaft of the femur.

Insertion. — On the proximomedial aspect of the patella and on the medial surface of M. rectus femoris.

Remarks. — Distally, this becomes a flattened band lying on the medial surface of the thigh. At the insertion this muscle is quite distinct from M. vastus intermedius and lies superficial to its medial border.

In *Neotoma* this muscle is broader at the insertion and inserts on the patella, the upper part of the patellar ligament, and on the lower part of the rectus femoris tendon.

M. vastus intermedius

Origin. — From the anterior face of the shaft of the femur below the level of the lateral crest.

Insertion. — Into the proximal aspect of the patella, deep to the tendons of M. rectus femoris and M. vastus lateralis.

Remarks. — This muscle is not completely separable from M. vastus medialis except at the insertion. No M. articularis genu is differentiated.

Tibial Extensor Group
(Figs. 15A, B, C; 17A, B, C)

The tibial extensor muscles are supplied by the deep peroneal nerve. Hill (1937) included only the extensor digitorum longus, extensor hallucis longus, and tibialis anterior in this group. On the basis of evidence discussed below, I have placed the short extensors of the digits in this group rather than in the peroneal group, where Hill placed them.

M. extensor digitorum longus

Origin. – From the lateral epicondyle of the femur, immediately medial to the attachment of the fibular ligament.

Insertion. — On the dorsal surfaces of the bases of the terminal phalanges of the second to fifth digits.

Remarks. — The fleshy fibers insert on an aponeurosis which develops on the medial surface of this muscle. This aponeurosis condenses distad to form four tendons which pass beneath the transverse crural ligament to the dorsum of the foot. As they pass beneath this ligament, the tendons are separated from those of M. tibialis anterior and M. extensor hallucis longus by a fibrous partition. Upon reaching the dorsum of the foot, the tendons pass through a ligamentous trochlea which attaches to the calcaneus (Keith, 1894; Hill, 1937). As the tendons emerge from this trochlea, they diverge, passing to the four lateral digits. The medial tendon passes directly to the second digit. The tendons to the third and fourth digits are rather closely associated and are held together by the heavy fascia of the foot. The most lateral tendon has the most complex relationships. The major part of the tendon passes directly to the fifth digit, but as it passes across the distal two-thirds of the metacarpal region, it gives rise along its medial border to a heavy aponeurotic sheet which passes obliquely distomediad across the foot deep to the other extensor tendons, to insert around the bases of the three middle digits.

In *Neotoma* the tendons to the third and fourth digits are more closely associated, appearing as one tendon until they separate a short distance proximal to their passage into the digits. The aponeurotic sheet from the tendon of the fourth digit is not so strongly developed.

In *Oryzomys* the tendons on the dorsum of the foot are almost completely fused into a broad, fan-shaped sheet which inserts on all five digits. The tendon to the middle toe alone has retained its individuality, but even that is closely adherent to the common aponeurosis. This condition is foreshadowed in *Sigmodon*, where the tendons are still distinguishable but are bound together by the heavy fascia of the foot.

The relationships of the tendons in *Peromyscus* are much the same as in *Neotoma*.

M. extensor hallucis longus

Origin. — From the lateral intermuscular septum and the immediately adjacent part of the interosseus membrane at the level of the middle of the leg.

Insertion. — On the bases of both phalanges of the hallux.

Remarks. — The thin tendon of this muscle accompanies that of M. tibialis anterior beneath the transverse crural ligament. In *Sigmodon* this muscle lies deep to, and between, M. extensor digitorum longus and M. tibialis anterior. In *Neotoma* this muscle arises from the interosseus membrane and the adjacent surface of the tibia on the same level as in *Sigmodon*; here, the muscle lies deep to M. tibialis anterior and is not in contact with the lateral intermuscular septum. The relationships in *Peromyscus* are the same as in *Neotoma*, except that the origin is more from the tibia. In *Oryzomys* the origin is restricted to the intermuscular septum. Thus, the relationships in *Sigmodon* are intermediate between those in *Oryzomys*, on one hand, and those in *Peromyscus* and *Neotoma*, on the other.

M. tibialis anterior

Origin. — From the lip of the lateral condyle and the upper part of the lateral fossa of the tibia.

Insertion. — On the medioplantar aspect of the medial cuneiform bone.

Remarks. — Immediately before it inserts, the tendon passes deep to a ligament which connects the tibial sesamoid bone with the base of the first metatarsal. Where this ligament passes over the medial cuneiform, it contains a small sesamoid bone. This ligament is present in *Oryzomys* and *Peromyscus* also, but not in *Neotoma*.

Mm. extensores breves

Origin. — From the dorsal aspect of the distal part of the calcaneus.

Insertion. — On the bases of the second phalanges of the second and third digits.

Remarks. — These two small muscles lie deep to the long extensor tendons with which their tendons appear to fuse in many instances. The medial muscle lies partly deep to the lateral one.

Ruge (1878) concluded that these muscles are derived from the peroneal group, although they receive their innervation from the deep peroneal nerve rather than from the superficial peroneal nerve which supplies the peroneal muscles. This discrepancy is not necessarily significant, however, as Ruge also demonstrated that the peroneal muscles may be associated with branches from both rami of the common peroneal nerve. Indeed, this situation exists in the pocket gophers in which the peroneus longus is innervated by a branch from the deep ramus (Hill, 1937).

A different light is thrown on the question of the derivation of the short extensors, however, by a condition found almost constantly in the four genera studied here. Two very small tendinous slips detach themselves from the posterior side of the long extensor tendon just before it divides into its four principal branches. These small slips accompany the other

tendons of the muscle onto the dorsum of the foot and, after passing through the trochlea, merge with the fascia of the dorsal surface of the short extensors. This suggests strongly that these muscles primitively were slips of M. extensor digitorum longus, which have gained a secondary origin from the calcaneus. Since I have found these same conditions in certain other rodents, I believe that the concept of the derivation of the short extensors from the peroneal musculature, at least among the rodents, must be discarded. This opinion also does away with the necessity of making allowances for the difference in innervation of the peroneal muscles and the short extensors.

Peroneal Group
(Figs. 15A, B, C; 17B, C; 18H)

A branch given off by the common peroneal nerve just before it divides into its superficial and deep rami supplies the innervation of M. peroneus longus. The remaining peroneal muscles are supplied by branches of the superficial ramus.

M. peroneus longus

Origin. — From the peroneal process of the fibula and from the proximal half of the septum between the peroneal muscles and the extensor digitorum longus.

Insertion. — On the medial cuneiform and the base of the first metatarsal.

Remarks. — The fibers are attached in pennate manner onto the tendon which forms the deep margin of the muscle. The tendon passes under the lateral malleolus and over a groove in the trochlear process of the calcaneus, turns under the tarsus in a groove in the cuboid, and passes across the tarsus deep to the flexor tendons.

The general relations of this muscle are similar in all four genera. Howell's statement that insertion is on the ectocuneiform in *Neotoma* is not applicable to the specimens of that genus which I dissected.

M. peroneus brevis

Origin. — From the cranial border of the fibula, the intermuscular septum, and the distal part of the interosseus membrane.

Insertion. — On the base of the fifth metatarsal.

Remarks. — This is the largest of the peronei. Its heavy tendon passes under the lateral malleolus with those of the other peronei. Except for very minor differences in degree of development, this muscle is similar in all four genera.

M. peroneus digiti quarti

Origin. — From the craniolateral border of the middle third of the free part of the fibula below the origin of M. peroneus digiti quinti.

Insertion. — On the base of the terminal phalanx of the fourth digit.

Remarks. — The tendon, after emerging onto the dorsum of the foot, passes along the groove between the fourth and fifth metatarsals. General relationships are similar in all four genera. The muscle is almost equally developed in *Sigmodon* and *Oryzomys*; it is somewhat weaker in *Neotoma* and is even thinner in *Peromyscus*.

M. peroneus digiti quinti

Origin. — From the craniolateral aspect of the proximal third of the free part of the fibula, superficial to M. peroneus brevis.

Insertion. — On the terminal phalanx of the fifth digit.

Remarks. — This muscle passes deep between M. peroneus digiti quarti and M. peroneus brevis. The thin tendon passes under the lateral malleolus and then along the fifth metatarsal to the digit. Similar relationships are found in all four genera, but the muscle is strongest in *Sigmodon* and *Oryzomys*, less so in *Neotoma*, and weakest in *Peromyscus*.

Flexor System

Adductor Group
(Figs. 10A; 15B, C, D; 16C, D)

Hill (1937:124), discussing the adductor muscles, stated:

> In man the nerve to the gracilis passes between adductor longus and adductor brevis, the latter lying caudal to the nerve. The branch of the obturator nerve supplying adductor magnus passes between that muscle and adductor brevis, the latter muscle being situated medially and cranially in respect to the nerve. In all the rodents examined, including *Dipodomys*, *Rattus*, and *Neotoma*, ... there are muscles with topographical relationships to these nerves similar to those described above. These muscles agree with the respective muscles in man in their origins, their relations to one another, and their relations to neighboring muscles. Consequently, in spite of differences in size and insertion, I conclude that the muscles which exhibit these similar relationships are homologous with the respective muscles in man.

In all the rodents which I have examined the topographical relationships of these muscles are consistently similar to those described by Hill, and I am led to accept his identification as correct.

M. gracilis, pars anterior

Origin. — From the ventral border of the pubis, entirely deep to the origin of the adductor longus.

Insertion. — On the medial crest of the tibia, about 1 cm. from the proximal end.

Remarks. — In *Neotoma*, *Peromyscus*, and *Oryzomys* this muscle is broader at the origin than it is in *Sigmodon*. In these three genera the origin extends posterior to the caudal border of M. adductor longus and is not completely covered by that muscle. In *Peromyscus* and *Neotoma* the insertion is somewhat more proximal than in *Sigmodon*. In this last respect *Oryzomys* resembles *Sigmodon*.

M. gracilis, pars posterior

Origin. — From the posterior border of the ventral end of the descending ramus of the ischium.

Insertion. — Into a small fossa on the craniomedial surface of the tibia, deep to the anterior part.

Remarks. — This part is narrowly triangular and lies on the medial surface of M. semimembranosus. It passes deep to the anterior part near the middle of the thigh, then contracts immediately to a small round tendon which continues independently to its insertion.

In *Neotoma* the muscular part of this slip is relatively narrower than in *Sigmodon*, but the tendon is broader and flat, being only about two-thirds as long as the tendinous part in *Sigmodon*. In the latter genus insertion of the posterior part of the gracilis is deep to the anterior half of the tendon of the anterior part. In *Neotoma* and *Peromyscus* insertion of the posterior part is directly deep to the insertion of the anterior part. In no case did I find the two parts fused as Howell (1926) reported them to be in *Neotoma*.

In *Oryzomys* the posterior part of the gracilis is remarkably developed. Arising from the inferior ischial tuberosity and the ventral half of the posterior border of the descending ramus of the ischium, it fans out to a width of about 12 mm. (in contrast to a width of 2 to 3 mm. in *Sigmodon* of equivalent size). The fibers of the anterior fifth of the muscle insert as in *Sigmodon*. Those of the posterior four-fifths of the muscle end abruptly, about half the distance from the pubis to the crest of the tibia, on a dense fascia which covers the medial surface of M. semitendinosus. These fibers insert in such a manner that they appear to be tucked back under themselves. The heavy fascia into which these fibers insert attaches along the tibial crest and merges with the crural fascia on the posterior aspect of the leg. From a medial view this muscle has the appearance of a broad muscle which has been almost bisected from the posterior border and the distal parts of the cut fibers have been stripped away (Fig. 16C).

M. adductor longus

Origin. — From the ventral border of the pubis, caudal to M. pectineus and medial (superficial) to the origin of M. gracilis anterior.

Insertion. — On a small roughened area near the middle of the caudomedial surface of the femur.

Remarks. — This is by far the smallest of the three adductors. The fibers converge rapidly from the origin to end in a small tendon, the length of which is about one-half that of the fleshy part of the muscle. Relations of this muscle are similar in all four genera.

M. adductor brevis (*M. adductor magnus* Howell, 1926)

Origin. — From the cranial two-thirds or three-fifths of the ventral border of the pubis, deep to M. adductor longus and M. gracilis anterior.

Insertion. — On the caudal surface of the femur below the level of the distal end of the gluteal crest, on the medial surface of the capsule of the knee joint, and on the patellar ligament.

Remarks. — The part inserting on the capsule of the knee joint encloses the distal part of M. caudofemoralis. Between it and the part which inserts on the shaft of the femur there is a hiatus through which the femoral artery passes. Howell (1926) considered this muscle to be M. adductor magnus and stated that the medial part of it was innervated by the sciatic nerve. I cannot agree with this statement of the innervation, since I have found no evidence whatsoever that any nerve but the obturator supplies this muscle.

Hill (1937) has given in detail the reasons that this muscle should be considered homologous with the human adductor brevis. In its course this muscle lies caudal and lateral to M. adductor longus, craniomedial to M. adductor magnus, medial to the insertional end of M. caudofemoralis, and cranial to M. semimembranosus. Its relationships are generally similar in all four genera.

M. adductor magnus (*M. adductor brevis* Howell, 1926)

Origin. — From the lateral surface of the posterior part of the pubis and from the ventral ischial tuberosity.

Insertion. — On the entire posterior border and surface of the gluteal crest of the femur.

Remarks. — There is no indication of differentiation of this muscle into an adductor minimus and an adductor magnus proprius. Innervation of this muscle is only by the obturator nerve. The element which may be homologous with the sciatic part of the adductor magnus in man in present as a discrete muscle (see M. caudofemoralis p. 100).

In *Neotoma* the origin of this muscle extends farther anterior along the ventral border of the pubis. With this exception the muscle is similar in all forms.

M. obturator externus

Origin. — From the margin of bone (ischium and pubis) around the obturator foramen and from the external surface of the obturator membrane.

Insertion. — Into the trochanteric fossa, deep (medial) to the insertion of the gemelli and the internal obturator muscle.

Remarks. — There are no differences of importance among the forms studied.

Ischiotrochanteric Group
(Figs. 10A; 15B, C, D)

A small branch from the tibial component of the sciatic nerve supplies the gemelli and quadratus femoris. M. obturator internus is supplied by a special nerve which arises from the plexus.

M. obturator internus

Origin. — From the pelvic surface of the ischium, dorsal and posterior to the obturator foramen, and from the dorsoposterior half of the pelvic surface of the obturator membrane.

Insertion. — Into the trochanteric fossa of the femur.

Remarks. — The muscle fibers insert on an aponeurosis which develops on the medial surface of the muscle. This converges dorsocraniad to form a broad, strong tendon which turns laterad over the dorsal margin of the ischium. Immediately after it crosses the ischium this tendon receives, on its anterior and posterior margins, the fibers of M. gemellus superior and M. gemellus inferior, respectively.

In *Neotoma* this muscle arises from almost the same area of the ischium, but only a few fibers take origin from the obturator membrane. In *Peromyscus* the muscle is more extensive than in any of the other genera. Here it arises from the entire margin of the obturator foramen, including the pubic part, and from the entire medial surface of the obturator membrane. *Oryzomys* has the origin restricted to that part of the ischium posterior to the spine and dorsal to the obturator foramen. This muscle is developed in *Sigmodon* and *Neotoma* to an extent intermediate between its development in *Peromyscus* and *Oryzomys*.

M. gemellus superior (not *M. gemellus superior* Howell, 1926)

Origin. — From the dorsal surface of the ischium immediately caudal to the level of the posterior border of the acetabulum.

Insertion. — On the cranial border of the tendon of M. obturator internus and into the trochanteric fossa.

Remarks. — According to Hill (1937): "The muscle described under this name in *Neotoma* and *Dipodomys* by Howell (1926, 1932), while apparently homologous to the muscle so designated in the cat by Reighard and Jennings (1930), is probably not homologous to that in man, judging from its relationships and from the fact that there is another muscle with the attachments and relations of gemellus superior." That muscle which Howell identified in the wood rat as gemellus superior is what I have described as the sciatic, or posterior, part of M. gluteus minimus (*q.v.*), and there is, as Hill stated, another muscle which corresponds exactly with the gemellus superior of man. In all four genera studied this muscle was found to have the relationships described above for *Sigmodon*.

M. gemellus inferior

Origin. — Along the superior ramus of the ischium, posterior to the level at which the tendon of M. obturator internus crosses it, as far caudad as the superior tuberosity.

Insertion. — On the posterior border of the tendon of M. obturator internus. A few fibers insert directly into the trochanteric fossa.

Remarks. — Except for possible small variations in amount of development, this muscle is similar in all four genera.

M. quadratus femoris

Origin. — From the lateral surface of the superior ramus of the ischium, from the superior tuberosity deep to M. biceps femoris, and from the dorsal half of the inferior ramus of the ischium.

Insertion. — On the lesser trochanter of the femur.

Remarks. — The dorsal fibers of this muscle arise by tendon, the ventral fibers directly, whereas at the insertional end the opposite is true (Hill, 1937). In *Sigmodon* this muscle inserts directly on the end of the lesser trochanter and does not extend onto the adjacent part of the femur. The relations of this muscle in *Neotoma* are similar at the origin, but the insertion extends well onto the posterior surface of the trochanter. This situation is also found in *Peromyscus,* in which the muscle appears to be more strongly developed than in the other three forms. In *Oryzomys* the insertion is restricted to the tip of the trochanter as in *Sigmodon.*

Hamstring Group
(Figs. 15A, B, C, D; 16B, C, D)

These muscles receive their innervation from a branch of the tibial nerve. This branch passes deep to M. caudofemoralis, sending a twig to that muscle, then branches to supply the remaining muscles of the group.

M. caudofemoralis (*M. semimembranosus anticus* Howell, 1926)

Origin. — From the spines and interspinous ligament of the last sacral and first caudal vertebrae, immediately deep to the origin of M. femorococcygeus.

Insertion. — On the medial epicondylar ridge of the femur immediately above the origin of the medial head of M. gastrocnemius.

Remarks. — This muscle passes dorsal to the perineal nerve and to the nerve to the hamstring muscles. Innervation is by the most proximal branch of the latter nerve. Near the middle of the thigh the muscle passes deep (medial) to the common peroneal and tibial nerves, paralleling the anterior border of M. semimembranosus.

There has been much uncertainty among various workers in mammalian comparative myology in regard to the identity or homologies of this muscle. In the discussion which follows, a review of the opinions of some authors is given, and certain suggestions are made which may lead to a better understanding of its relationships, especially among the rodents.

Leche (1883) described a M. caudofemoralis in *Tupaia,* which takes origin from the transverse process of the second caudal vertebra and the ligament between this and the third caudal vertebra. Insertion of this muscle is on the lateral border of the femur distal to the gluteal crest, passing around distally to the posterior surface of the femur. The insertional part of this muscle is pierced by the popliteal artery, so that there are two insertional slips, one of which attaches to the medial surface of the lateral condyle, the other to the inner surface of the medial condyle distal to the insertion of M. adductor magnus. The muscle is overlain by M. femorococcygeus, M. tenuissimus, M. biceps femoris, and the sciatic nerve. Deep to the muscle lie M. ischiococcygeus, M. gemellus, and M. adductor magnus. In *Macroscelides* Leche found a muscle which takes origin from the ischial tuberosity and inserts on the lateral condyle of the femur but otherwise has the same relationships as the caudofemoralis of *Tupaia.* Leche considered this muscle homologous with the caudofemoralis in *Tupaia.*

Among the lipotyphlous insectivores, Leche (1883; 1900) described a "M. praesemimembranosus" which arises (*Talpa, Crocidura)* from the vicinity of the ischial tuberosity, posterior to M. quadratus femoris, and inserts on the medial condyle of the femur. This muscle has essentially the same topographical relationships as the caudofemoralis of the menotyphlous insectivores.

Appleton (1928) presented evidence demonstrating that Leche's (1883) caudofemoralis and praesemimembranosus muscles are actually homologous. Appleton (1928:390-91) pointed out that the acquisition of an ischial origin by the caudofemoralis is a matter of rather common occurrence among many groups of mammals. He also said:

> ...distal attachments on the shaft of the femur [of caudofemoralis and praesemimembranosus, Leche, 1883] present relations to neighboring muscle attachments which are very much alike (cf. Leche's Figs. 60, 63, with Fig. 5, *supra*). It may be further pointed out that the relations already established for Menotyphla between M. caudofemoralis and nerves, viz. Nn. tibialis and peronaeus, surae dorsalis and surae ventralis (p. 387), and to the nerves to the hamstring muscles (semitend., semimembr. and biceps), are identical with those presented by M. praesemimembranosus in *Erinaceus* and *Talpa*, and Leche's figures show that the same may be said for M. praesemimembranosus in certain other Lipotyphlous Insectivora (cf. *Chrysochloris*, Fig. 93, with *Erinaceus*, Fig. 75, Leche, 1883). The muscle thus identified in Lipotyphla as M. caudofemoralis (Leche's praesemimembranosus) differs from that of *Tupaia* in just those features which are incidental to the transference of its origin to the tuber ischii, as in Macroscelides. For example, the nerve to the dorsal head of M. flexor cruris caput dorsale does not pass ventrally to it.... The conclusions of Leche have been found to require modification. The "praesemimembranosus" of that author has been identified with his "caudofemoralis," and the latter name has been adopted for use throughout Insectivora (and mammals generally,...). The lipotyphlous praesemimembranosus of Leche has been found to differ from the muscle so named in the cat (cf. Fig. 12 I) and from the "ischiocondyloideus" of various Primates (with which muscles it was compared by Leche, 1883, p. 95), inasmuch as these are parts of the semimembranosus musculature, situated medially to the nerves to Mm. biceps and semitendinosus and medially also to M. caudofemoralis in such Carnivora and Primates as possess it (e.g. *Lutra*, Fig. 7, and *Lemur*, Appleton, 1922: 301).

I have not had available any specimens to verify Appleton's statement that both a caudofemoralis and a presemimembranosus are present in *Lutra* and *Lemur*. In the weasel, *Mustela frenata*, however, I have found that two such muscles are present. One of these takes origin from the anterior part of the tuberosity of the ischium and inserts on the lateral condyle of the femur. In its course down the thigh this muscle passes dorsal to the nerve to the hamstring muscles, deep to the tenuissimus muscle, and deep to the sciatic nerve. Thus, its relationships are almost exactly the same as those of Leche's caudofemoralis in *Macroscelides*. The other muscle arises from the ischium, deep and posterior to the origin of the caudofemoralis. Its insertion is on the medial condyle and distal part of the medial surface of the shaft of the femur, distal and medial to the insertion of the adductor. This muscle passes ventral to the nerve to the hamstring muscles and ventral to the popliteal artery. It lies medial also to M. caudofemoralis. This muscle has all the typical relationships of the presemimembranosus, as that term was applied by Appleton (1922, 1928) in *Lutra* and *Lemur*.

Hill (1934) reported a peculiar situation which he discovered in the thigh of a specimen of the squirrel, *Sciurus griseus*. Hill's description of this was:

In the specimen dissected, the muscle arose by tendinous and fleshy fibers from the ischial bone and, by a slender tendon... from the transverse process of the first caudal vertebra. The tendon crossed superficial to the nerve to the hamstring muscles, while the part of the muscle arising from the ischium lay medial and deep to the nerve.... This relation may be considered a stage intermediate between the typical position of the caudofemoralis and that of the so-called presemimembranosus muscle.

It may be concluded that muscles do, in rare instances, change their topographical relations to nerves, and that the caudofemoralis and the presemimembranosus are homologous muscles.

Whatever the merits of Hill's analysis of this situation in the squirrels, his conclusions cannot be accepted as applicable to mammals in general. This is obvious since the caudofemoralis and a presemimembranosus have been shown to exist side by side in certain mammals (see above). There is, however, the possibility that a different interpretation of the relationships described by Hill might lead to a closer approach to the solution of the problems involved. I have found that the situation described by Hill in *Sciurus griseus* and by Alezais (1900) in *Sciurus vulgaris* also occurs in the red squirrel, *Tamiasciurus hudsonicus*. I have examined this region in both *Tamiasciurus hudsonicus* and *Sciurus vulgaris*. Hill's description of the relationships is accurate but lacking in detail; thus, for the sake of clarity, a complete description is given here, although it repeats some of Hill's remarks. This description is made directly from a specimen of *Sciurus vulgaris*. Many of the fibers of the muscle mass in question arise from the anterior part of the ischial tuberosity by a short, strong tendon. From the anterior border of this tendon, 3 to 4 mm. from the point of origin, another tendon passes craniodorsad, curving up to attach to the transverse process of the first caudal vertebra (Fig. 15D), forming an arcade through which passes the main trunk of the nerve to M. biceps femoris, M. semimembranosus, and M. semitendinosus (ischial head).

The ventrolateral border of the caudal half of the latter tendon gives rise to muscle fibers which, with those which arise from the ischium, make up a rather large muscle mass that passes toward the knee. These fibers pass ventromedial to M. tenuissimus and the sciatic nerve. Slightly below the middle of the thigh, this mass divides into two parts. The lateral part inserts on the posterolateral aspect of the distal half of the femur and onto the lateral condyle. This part passes lateral to the popliteal artery. The medial part passes medial to the popliteal artery to insert on the distal 1 cm. of the medial surface of the femur and on the medial condyle. In addition to the passage of the popliteal artery between them, these two slips are further separated by M. adductor brevis which inserts on nearly all the area of the femur intervening between the insertion of the two slips. A factor which may be very significant in these relationships is disclosed when one follows the plane of separation of these two terminal slips proximad. They separate along what appears to be a distinct fascial plane. As the ischium is approached a heavy aponeurosis develops on that surface of the medial part which is in contact with the lateral part. This aponeurotic plane continues directly to the ischial tuberosity. Many of the fibers of the lateral part of the muscle mass take origin from the surface of the proximal 10 to 12 mm. of this aponeurosis. All of the fibers which insert laterally arise either from the tendon which attaches to the caudal vertebra or from the surface of the aponeurosis of the fibers which take their origin from the ischium. It may be significant also that all of the fibers which arise directly from the ischium insert medially on the femur.

The relationships just described suggest that it is not a question here of the caudofemoralis muscle shifting its origin from the vertebra dorsal to the nerve of the hamstring muscles to a position on the ischium ventral to that nerve, as Hill thought, but that it is rather a situation wherein two discrete muscles have begun to fuse. If the description of the caudofemoralis and presemimembranosus in the weasel is recalled, it will be seen immediately that the lateral and medial muscle masses in *Sciurus vulgaris*, when separated completely, have relationships identical with those of M. caudofemoralis and M. presemimembranosus, respectively.

In squirrels other than *Sciurus griseus*, S. *vulgaris*, and *Tamiasciurus hudsonicus* there is present a muscle which divides terminally to send one slip to the lateral condyle and one to the medial condyle of the femur, just as has been described above. Origin of this muscle, however, is only from the ischium. Nearly all of the lateral fibers arise from an internal aponeurosis which is directly continuous with the tendon by which the medial fibers arise from the ischium. This situation is thus similar to that found in *S. vulgaris*, except that the tendon from the caudal vertebrae has been lost, and the transferal of the origin of this part from a position dorsal to the nerve of the hamstring muscles to a position ventral to that nerve is complete.

From a consideration of the relationships which have thus far been described, it would not be difficult to accept the suggested hypothesis that this muscle in the squirrels actually represents a compound muscle formed by the fusion of M. caudofemoralis and M. presemimembranosus. There are, however, certain facts not yet mentioned which do not exactly fit into this concept. One of these concerns the manner in which the parts of the muscle mass are innervated. In the weasel the caudofemoralis is supplied by the first branch of the trunk which, after passing deep to M. caudofemoralis, supplies the hamstring muscles, sending a separate branch to each. That muscle, which I have called M. presemimembranosus, is supplied in the weasel by a branch of the same twig which supplies M. semimembranosus, a fact which supports the identification of this muscle as a presemimembranosus. If the presemimembranosus were to fuse with the caudofemoralis, would it not be expected to retain the nerve supply which comes from the branch to M. semimembranosus? The muscle mass described in the squirrels receives only one nerve, and that one arises from the trunk of the nerve to the hamstring muscles exactly as does the nerve to the typical M. caudofemoralis. There are, therefore, only the following alternatives: one is to throw out the suggested concept of fusion of the two muscles; the other is to go even further and postulate that, with the fusion of the two muscles, the nerve fibers supplying them have become consolidated into a single trunk. Of course, these nerve fibers derive originally from the same trunk, and such a consolidation can hardly be said to be impossible.

Another drawback to the acceptance of the "fusion hypothesis" lies in the relationships of the caudofemoralis in the insectivores, in which it was originally described by Leche. In *Tupaia* it has the caudal origin which I have considered as typical, but divides distally to insert on both the lateral and medial condyles of the femur. In *Macroscelides* insertion is only on the lateral aspect of the femur. In the lipotyphlous insectivores, however, insertion is only on the medial condyle of the femur. Does this

mean that insertion, whether it be on the lateral or medial condyle, lateral or medial to the popliteal artery, or both, is of no significance? At present the most logical answer to this question is in the affirmative. Is it not possible, however, that even among the insectivores there is a derived condition, or conditions, in which the muscles have already gone through the stage of fusion and have lost one or the other of the origins and insertions, the one which has been lost differing in the different insectivores?

The relationships which are presented by the "caudofemoralis" in the muroids differ from any yet described in this discussion. In those forms which I have examined this muscle takes origin from the caudal vertebrae or from the ischium, in either case dorsal to the nerve to the hamstring muscles, and inserts on the medial aspect of the distal part of the femur and on the medial condyle. As it passes down the thigh the topographical relationships are similar to those of the typical caudofemoralis. Thus, the muroids have a single muscle which has the original relationships of a typical caudofemoralis and the insertional relationships of the presemimembranosus, at least insofar as that muscle is demonstrated by the presemimembranosus of the weasel. In line with the "fusion concept" this could be explained by assuming that the dorsal head of the fused muscle and the medial insertion of the fused muscle have been retained.

A series of schematic diagrams has been prepared showing the possible progression of changes which may have led to the various relationships which I have discussed above. The hypothetical primitive condition is exemplified by the weasel (Fig. 16B-1). The stage of fusion of the two muscles is represented by Figure 16B-2, which is taken from the condition seen in *Sciurus griseus*, *S. vulgaris*, and *Tamiasciurus hudsonicus*. From this stage, it is simple to arrive at the condition which is shown in Figure 16B-3 and which can be found in most squirrels other than those just named. Figure 16B-4 represents the condition found in muroids and would be attained by loss of the ischial head, which is ventral to the nerve, and loss of the lateral insertion.

I do not urge acceptance of the suggestions which have been made above. These comments have been presented only in order to emphasize the difficulties of interpretation which are presented by available evidence and to show that there is a great need for study of this area of the thigh of mammals in as many forms as possible before final conclusions may be drawn. The suggestions which have been made are justifiable at present only as working hypotheses upon which further investigation of the problem may be based.

M. semitendinosus

Origin. — By two heads: (1) by aponeurosis from the spines and interspinous ligaments of the last sacral and first two caudal vertebrae, and (2) from the dorsocaudal part of the superior tuberosity of the ischium.

Insertion. — On the middle of the medial ridge of the tibia.

Remarks. — The two heads fuse shortly below the level of the origin of the ischial head. At the point of fusion there is a distinct tendinous inscription in all the forms studied. Forster (1918) found this tendinous inscription in many mammals and considered it to represent the insertion

of the dorsal head upon the ischial part. He believed, however, that the dorsal head represents an element of the gluteal complex. Appleton (1928) concurred in the interpretation of the tendinous inscription, but showed that the dorsal head, rather than being a part of the gluteal complex, actually is homologous with the reptilian M. flexor cruris dorsale. In discussing the manner of insertion of this part, Appleton (1928:422) said: "Now there are indications that the characteristic mammalian mode of linkage is still in a state of flux, at any rate in Marsupialia, Rodentia, and perhaps Carnivora. In certain members of these orders, M. flexor cruris caput dorsale is inserted laterally near the biceps, whereas usually in mammals it is inserted near semitendinosus, or is implanted on that muscle by a tendinous intersection." In the four genera studied this dorsal element not only inserts onto the ischial part of M. semitendinosus but also attaches to the surface of the posterior border of M. biceps femoris. Thus, the semitendinosus and the biceps are connected at this level by the tendinous inscription, which makes it appear as if a part of the fibers of M. biceps femoris arose from the anterior border of the semitendinosus.

Relationships of the semitendinosus at the origin are similar in all four genera. At the insertion the anterior fibers lie deep (lateral) to the anterior part of M. gracilis in *Sigmodon*, *Neotoma*, and *Peromyscus*. In *Oryzomys*, however, the insertion is entirely distal to that of M. gracilis anterior. A very dense fascia covers the medial surface of the muscle in *Oryzomys*, and it is on this fascia that most of the fibers of M. gracilis posterior insert.

M. semimembranosus

Origin. — From a roughly triangular area on the lateral surface of the inferior ramus of the ischium, ventral to the area of origin of M. biceps femoris and the ischial head of M. semitendinosus and caudal to the origin of M. obturator externus.

Insertion. — Along the medial border of the anterior crest of the tibia for a distance of about 5 to 6 mm. immediately below the epiphyseal line and on the distal part of the tibial collateral ligament.

Remarks. — There are only minor variations in this muscle. In *Neotoma* the origin is more from the caudal border of the ischium. In *Oryzomys* insertion is entirely superficial to the tibial collateral ligament, whereas in the other three genera many of the fibers pass deep to this structure.

M. biceps femoris

Origin. — From the dorsal part of the superior tuberosity of the ischium.

Insertion. — On the lateral condyle and proximal three-fourths of the lateral aspect of the tibia.

Remarks. — The tendinous intersection which represents the insertion of the caudal head of M. semitendinosus on the ischial part of that muscle is continued into the posterior border of the biceps (see M. semitendinosus, above).

From the origin the fibers of this muscle fan out to cover most of the lateral aspect of the thigh, posterior to the femur. Aside from differences

in relative development, there is little variation of the biceps among the four genera. This muscle is most robust in *Oryzomys*, least so in *Peromyscus*; *Sigmodon* and *Neotoma* occupy intermediate positions in this respect.

Flexor Group of the Leg
(Figs. 15A, B, C; 17A, B; 18A, B, C, D, F, G)

These muscles are supplied by branches of the tibial nerve.

M. gastrocnemius

Origin. — Medial head: from the caudal surface of the medial epicondyle of the femur. Lateral head: from the caudal surface of the lateral epicondyle of the femur and from the crural fascia deep to the insertion of the anterior fibers of M. biceps femoris.

Insertion. — On the caudodorsal surface of the calcaneus.

Remarks. — A well-developed sesamoid bone is present in the tendon of origin of each head. The distal one-fifth to one-fourth of the two heads of this muscle are fused. As the common terminal tendon of this muscle passes toward the heel it is twisted, as in many other mammals (Hill, 1937; Parsons, 1894).

The fibers which make up the anterolateral border of the lateral head in *Sigmodon* and *Oryzomys* arise from the deep surface of the crural fascia just medial to the anterior border of M. biceps femoris as that muscle crosses the crus. The small band of fibers arising thus lies lateral to the common peroneal nerve as the nerve crosses the lateral surface of the main part of the lateral head of the gastrocnemius. *Neotoma* and *Peromyscus* do not have this slip.

The three parts of the lateral head of the gastrocnemius which Howell (1926) described in *Neotoma* are also present in *Sigmodon*, *Peromyscus*, and *Oryzomys*, with essentially the same relationships. The gastrocnemius of *Sigmodon* and of *Oryzomys* is very large in relation to that of *Neotoma* and *Peromyscus*.

The medial head of this muscle is nearly equal in bulk to that of the lateral head, M. soleus, and M. plantaris combined.

There is a close relationship of the lateral head with M. plantaris in all four genera in that these two muscles have a common tendon of origin and are fused in their proximal parts. This fusion is greatest in *Neotoma* and *Peromyscus*, less in *Sigmodon*, and least in *Oryzomys*.

M. plantaris

Origin. — From the lateral epicondyle of the femur just medial to the origin of the lateral head of M. gastrocnemius and partly in common with that muscle.

Insertion. — Principally into the three middle digits, with some fibers contributing to the superficial plantar aponeurosis.

Remarks. — The plantaris tendon joins that of M. gastrocnemius, lying first on the anterior side of it. As the latter tendon twists, the plantaris

tendon is carried with it around its medial side and is thus posterior to the gastrocnemius tendon at the level of the calcaneus.

After passing under the calcaneus to the plantar region, the plantaris tendon divides into two layers. The thin, superficial layer continues distad as the superficial plantar aponeurosis and inserts into the bases of the pads which lie at the bases of the three middle digits and into those digits themselves. This aponeurosis is joined near the middle of the foot by a thin tendinous slip from M. flexor digitorum tibialis. This slip merges inseparably with the plantar aponeurosis, but its fibers may be traced to the second digit.

The superficial plantar aponeurosis in *Neotoma* is more strongly developed than in *Sigmodon*, and slips of it pass toward all five digits. These slips insert primarily into the bases of the distal plantar tubercles. The tendon from M. flexor digitorum tibialis which joins the plantar aponeurosis is much stronger than in *Sigmodon*. In the wood rat this element makes up at least as much of the aponeurosis as does the superficial division of the plantaris tendon. In *Peromyscus* the plantar aponeurosis is similar to that in *Neotoma* and sends slips to all five digits. This structure in *Oryzomys* is very thin and narrow and receives no slip from M. flexor digitorum tibialis. In this genus the aponeurosis does not reach the digits but is lost in the dense connective tissue beneath the distal parts of the metatarsals.

The main part of the plantaris tendon, after the superficial segment splits off, continues into the foot and becomes fleshy again. For description of this part, see M. flexor digitorum brevis (p. 110).

M. soleus

Origin. — By a short tendon from the caudolateral surface of the head of the fibula.

Insertion. — With the gastrocnemius muscle on the calcaneus.

Remarks. — In *Sigmodon* this muscle is tendinous for the first sixth of its length; in *Neotoma* and *Peromyscus* the first third is tendinous. In *Oryzomys* the proximal half of the muscle is tendinous.

M. popliteus

Origin. — By a thin tendon from the lateral condyle of the femur immediately anterior to the attachment of the tibial collateral ligament and distal to the origin of M. extensor digitorum longus.

Insertion. — On the medial surface of the proximal two-fifths of the tibia and on the fascia of M. flexor tibialis.

Remarks. — The tendon of origin passes caudad around the lateral condyle and gives rise to muscular fibers as soon as it reaches the popliteal space. The proximal fibers pass directly mediad to their insertion. The fibers of the distal border which insert on the surface of M. flexor tibialis often appear to be continuous with that muscle.

The popliteus varies little among the four genera studied. In *Neotoma* the insertion does not extend so far distad as in the other genera.

M. flexor digitorum tibialis

Origin. — From the medial ridge of the tibia in its third sixth and from the adjacent fascia of M. tibialis posterior.

Insertion. — Principally on the base of the first plantar tubercle which lies superficial to the base of the first metatarsal. A small slip continues onto the sole of the foot to join the medial side of the superficial part of the plantaris tendon.

Remarks. — The tendon of this muscle passes across the medial malleolus in company with the tendon of M. tibialis posterior. Among the forms studied there is considerable variation in the relations of this tendon in the foot. In *Neotoma* the main part of the tendon passes onto the plantar surface to join the superficial plantar aponeurosis, but a small slip separates from the main tendon and passes along the medial side of the foot to insert on the hallux. Howell's (1926:83) statement that the broader part of this tendon joins "the superficial tendon of the flexor fibularis" is obviously a *lapsus calami*, since the flexor fibularis has no superficial tendon and since he stated on the same page that the superficial plantar aponeurosis "might with equal propriety be said to have its relationship rather with the flexor digitorum longus [= my flexor digitorum tibialis]."

M. flexor digitorum tibialis is somewhat larger in *Neotoma* and *Peromyscus* than in *Sigmodon*. In *Oryzomys* this muscle is much reduced and arises, not from the tibia, but rather from the deep surface of the heavy fascia which separates the deep muscles of the posterior compartment from the superficial muscles. In *Peromyscus* the relationships of this muscle are very nearly the same as in *Neotoma*. In *Oryzomys* the tendon passes directly to the proximomedial border of the medial plantar tubercle, where it inserts. There is no branch to the plantar aponeurosis or to the hallux.

The insertional relationships of the tendon of this muscle were shown by Dobson (1882) to be extremely variable among the mammals. In rodents he found two general types of insertion. One of these, which might be termed the hystricomorph type, concerns the union of the flexor tibialis tendon with that of the flexor fibularis in the foot. The other type, which occurs widely among the myomorphs and sciuromorphs, concerns insertion or union with the superficial plantar aponeurosis or attachment to the first digit. Dobson stated that the flexor digitorum fibularis tendon and the tendon of flexor digitorum tibialis are always separate in the foot of the Myomorpha. Parsons (1896:182), however, recorded the union of these two tendons in *Rhizomys*. Greene (1935) reported a similar situation in the Norway rat, but in the several specimens of this species which I have dissected, the flexor tibialis tendon passes into the foot as in *Neotoma* and has the same relationships as in the latter genus, except that in *Rattus* this tendon forms the entire superficial plantar aponeurosis since there is no superficial division of the plantaris tendon. These relationships were correctly described for the Norway rat by Alezais (1900).

M. tibialis posterior

Origin. — From the proximal two-thirds of the crest of the tibia, from a small adjacent area of the caudal fossa, and from the deep surface of the heavy fascia between this muscle and M. flexor digitorum tibialis.

Insertion. — On the medial tarsal bone (os tarsale mediale Hill, 1937).

Remarks. — The muscle fibers insert on the tendon which develops on the posterior border of the distal half of the fleshy part of the muscle. Distally, the tendon passes over the medial malleolus with that of M. flexor digitorum tibialis, to which it lies anterior. In the tarsal region the tendon passes deep to the deltoid ligament before inserting. Insertion is similar in all four genera. The muscle, in general, appears to be relatively larger in *Neotoma* and *Peromyscus* than in *Sigmodon* and *Oryzomys*.

M. flexor digitorum fibularis

Origin. — From the mediocaudal aspect of the head and corresponding surface of the fibula along its entire length, from the interosseus membrane and entire interosseus crest of the tibia, and from most of the caudal fossa of the tibia.

Insertion. — By five tendons into the terminal phalanges of the five digits.

Remarks. — The fibers of this muscle join a heavy central tendon in a complex manner. Proximally, the tibial and fibular parts of the muscle are more or less discrete, and it might be said that the muscle arises by two heads. The heavy tendon passes under the medial malleolus to the sole of the foot. Beneath the metatarsal region it divides into the five slips which pass into the digits.

In *Neotoma* and *Peromyscus* the Mm. flexores breves accessorii (*q. v.*) arise from the plantar surface of the tendon just before it divides. In all four forms the lumbricales take origin from the clefts between the terminal branches of the tendon. In no case was a quadratus plantae found, nor did this tendon have any direct relationship with that of M. flexor digitorum tibialis.

The flexor fibularis is not so strongly developed in *Peromyscus* as in the other three genera, and the fleshy part of the muscle is restricted to the proximal two-thirds of the leg in contrast to the condition in the other genera, where there are muscle fibers inserting on the tendon as far distad as the end of the tibia.

M. quadratus plantae

The muscle described under this name by Howell (1926) is actually the M. abductor ossis metatarsi quinti. No true quadratus plantae occurs in any of the four genera with which this publication is concerned.

Flexor Group of the Pes
(Figs. 18E, F, G, H)

The flexor muscles of the foot are supplied by the lateral and medial branches of the tibial nerve. Except in specific cases, no attempt was made to ascertain the specific innervation of the various muscles.

M. flexor digitorum brevis

Origin. — From the surface of the deep division of the plantaris tendon in the sole of the foot.

Insertion. — Ultimately into the bases of the second phalanges of the three middle digits (see Remarks).

Remarks. — It is perhaps just as correct to say that this muscle arises as a direct fleshy continuation of the plantaris tendon. The muscle fibers arise from the superficial and lateral surfaces of the tendon which, by the time the level of the mid-metatarsal region is reached, is represented only by the thin aponeurosis on the dorsal surface of the muscle. The muscle divides into three terminal slips which insert by thin round tendons on the plantar aspect of ligamentous rings which surround the tendons of the flexor digitorum fibularis at the level of the metatarsophalangeal joints of the second, third, and fourth digits. The dorsal parts of these rings appear to be cartilaginous and are wider and thicker than the ventral parts (Fig. 18E). This cartilaginous part acts as a bearing which slides in the groove between the two sesamoids of the metatarsophalangeal joint. From the distal aspect of these rings two small, round tendons, one on each side of the long flexor tendon, pass distad to insert on the respective sides of the base of the second phalanx of the digit. From the ring which surrounds the long flexor tendon of the second digit there is, in most specimens, only one tendon passing to the second phalanx; this is on the medial side. In a few individuals a very small tendon is present on the lateral side as well. Although no flexor brevis tendon passes to the fifth digit in *Sigmodon*, there is a ligamentous ring corresponding to those on which the short flexor tendons insert in the other digits. A tendon connecting the ring with the base of the second phalanx is present only on the lateral side. In at least some specimens part of the fibers of M. flexor digiti quinti brevis have shifted their insertion from the lateral sesamoid to the lateral aspect of this ring.

To the best of my knowledge, only Parsons (1894:266) has previously recorded these fibrous loops or rings around the tendons of the perforating flexors. In his description of the perforated slips of M. flexor digitorum sublimus of the manus he stated: "Just before the perforation there is usually a strong fibrous loop, which passes under the perforating tendon and comes in contact with the sesamoid bones in front of the metacarpophalangeal joints; this is especially well marked in *Coelogenys*." Parsons also noted that this loop in the fifth digit of *Coelogenys* "was entirely unconnected with the flexor sublimus." He suggested that this shows a stage in the gradual suppression of the flexor sublimus tendon to the fifth digit, which I believe to be true also of the similar condition described above for *Sigmodon*. Parsons found these loops in the foot as well as in the hand; he stated (1894:292): "In many cases a loop is given off from the deep surface of each tendon [of flexor digitorum brevis] before it is perforated; this loop embraces the long flexor tendon as in the anterior extremity."

In *Neotoma* and *Peromyscus* there are four terminal slips of M. flexor digitorum brevis which attach to the four lateral digits. *Oryzomys* usually has only three, as is true of *Sigmodon*, but in the left foot of one specimen

there was a fourth well-developed tendon to the fifth digit. In the right foot of this same individual only three slips were present. In all specimens of *Oryzomys* which I dissected the ligamentous ring was present around the long flexor tendon to the fifth digit, regardless of the absence of a short flexor tendon to that digit.

Mm. flexores breves accessorii

These muscles are present only in *Neotoma* and *Peromyscus*.

Origin. — From the plantar surface of the tendon of M. flexor digitorum fibularis in the mid-region of the foot, separate from, and proximal to, the lumbricales.

Insertion. — On the dorsal sides of the three lateral tendons of M. flexor digitorum brevis, just proximal to their insertions.

Remarks. — Various authors have noted these muscles. Greene (1935: 83, Fig. 101) showed two such muscles in the foot of the rat (*R. norvegicus*) and labeled them "lumbricales," although a complete set of these latter muscles is present with typical relationships. Reighard and Jennings (1930:213-14) described six "lumbricales" in the cat, of which three have the same relationships as those described here in *Neotoma* and *Peromyscus*. McMurrich (1907:423-24) described four such muscles in the mouse (*Mus musculus*). He also noted the discrepancy in the identification of these muscles in the cat as lumbricales by Reighard and Jennings and demonstrated that the lumbricales and the muscles here called accessory short flexors have been derived from different primitive layers (from his "flexor brevis medius superficialis" and "flexor brevis superficialis stratum profundum," respectively). For this reason, McMurrich considered the assignment of these muscles to the lumbricales series as improper. Hill (1937) correctly placed these muscles with the flexor digitorum brevis, stating: "In squirrels, the short flexors are in two layers; the superficial slips [my M. flexor digitorum brevis] fuse with the plantaris tendon completely; the deep layer [my flexores breves accessorii] consists of two muscles which arise from the long flexor tendon (much as in mouse and cat, McMurrich, 1907). These insert on tendons of plantaris which attach to second and third digits."

Bryant (1945) apparently failed to appreciate that the flexor brevis proper is completely fused with the plantaris tendon and described the muscles here called flexores breves accessorii as the flexores digitorum breves. It is easily understood that the flexor digitorum brevis might not be seen in the squirrels. By examination of specimens of *Tamias striatus* and *Tamiasciurus hudsonicus* I have found this muscle to be represented by a small number of fibers on the superficial surface of the plantaris tendons to the second, third, and fourth digits in the former species and represented by only two or three fiber bundles on the medial side of the plantaris tendon to the third digit in the latter species. The flexores breves accessorii, by contrast, are rather well developed in these forms.

In view of the fact that these muscles are present in widely separated groups with consistent relationships and also because their derivation has been shown to be distinct from the derivation of the lumbricales, I believe

they are deserving of a specific designation and propose the term Mm. flexores breves accessorii. The lateral muscle is innervated by a branch from the medial common digital division of the lateral plantar nerve. The two medial muscles receive their innervation from terminal filaments of the branch of the medial plantar nerve which serves the flexor digitorum brevis.

M. abductor hallucis brevis

Origin. — From the medial side of the plantar surface of the navicular (scaphoid).

Insertion. — On the medial sesamoid bone beneath the metatarsophalangeal joint of the first digit.

Remarks. — This is the most medial of the intrinsic foot muscles. There is little variation among the forms studied.

M. abductor ossis metatarsi quinti (*M. quadratus plantae* Howell, 1926)

Origin. — By a short tendon from the medial side of the plantar surface of the proximal end of the calcaneus, deep to the plantaris tendon.

Insertion. — On the lateral side of the base of the fifth metatarsal.

Remarks. — The broad tendon of origin passes obliquely distolaterad across the calcaneus; muscle fibers develop in the tendon as it approaches the lateral border of the calcaneus. In *Neotoma* and *Peromyscus* the origin extends well up onto the medial surface of the calcaneus. The muscle is best developed in *Neotoma*; in *Peromyscus* it is mostly tendinous although not apparently reduced in bulk. In *Oryzomys* origin is restricted to the plantar surface of the calcaneus, as in *Sigmodon*.

According to McMurrich (1907), this muscle and M. abductor digiti quinti are both derived from the reptilian "abductor V."

M. abductor digiti quinti

Origin. — From the distal end of the calcaneus by a heavy tendon which is common to this muscle and M. flexor digiti quinti brevis, from a sesamoid bone which lies in that tendon as it passes beneath the medial side of the base of the fifth metatarsal, and from the lateral surface of M. flexor digiti quinti brevis for most of its length.

Insertion. — On the lateral sesamoid bone of the metatarsophalangeal joint of the fifth digit.

Remarks. — This muscle lies on the lateral side of M. flexor digiti quinti brevis. The fleshy belly is well developed, but is separable from the flexor only with difficulty. The insertion is similar in all four genera, but certain peculiarities in the manner of origin are shown by each genus. In many specimens of *Neotoma* origin is similar to that in *Sigmodon*, but in other individuals it is only from the sesamoid bone beneath the medial side of the fifth metatarsal and from the lateral surface of the flexor digiti quinti. In these latter individuals the tendon from the calcaneus is reduced to a thin aponeurosis, and the sesamoid bone is attached by ligament to the ventral surface of the cuboid bone. In *Peromyscus*, in which there is no sesamoid bone, the muscle arises directly from the calcaneus and cuboid

bones; it is very slender and attenuated. In *Oryzomys* the fleshy fibers take origin from the sesamoid bone and the surface of the flexor digiti quinti; the sesamoid bone is attached to the calcaneus by a strong tendon, but no fibers of the tendon continue directly into the muscle as they do in *Sigmodon*.

M. flexor hallucis brevis

I am not certain of the status of this muscle in the four genera which were studied. Howell described a muscle by this name in *Neotoma*, but I believe his muscle to be M. adductor hallucis, for reasons which are given below in the discussion of that muscle. McMurrich (1907) found only two intrinsic foot muscles inserting on the hallux in the mouse (*Mus musculus*). One of these, which arises from the navicular and inserts on the medial sesamoid bone of the first metatarsophalangeal joint, McMurrich considered to be derived from the "flexor brevis superficialis" layer. Its homologue in *Sigmodon* is described above as M. abductor hallucis. The other was identified by McMurrich as M. adductor hallucis. He found no fibers of the interosseus layer which inserted on the hallux, although the medial interosseus muscle of the second digit takes its origin from the first metatarsal.

In all the specimens of *Neotoma* and *Peromyscus* there were only two intrinsic foot muscles which inserted on the hallux, and they seemed to correspond to those described by McMurrich. In *Oryzomys*, however, there is a third slip which appears to be the M. flexor hallucis brevis. This arises from the common deep plantar tendon (see M. adductor hallucis) beneath the base of the first metatarsal, immediately medial to the origin of the medial interosseus muscle of the second digit. As it passes along the plantar surface of the first metatarsal, the slip is in contact laterally with the interosseus of the second digit and superficiomedially with M. abductor hallucis. Insertion is on the lateral sesamoid of the metatarsophalangeal joint. These relationships are almost exactly the same as those of M. flexor hallucis brevis in the squirrels (Bryant, 1945).

In *Sigmodon* there is a thin tendon, apparently without muscle fibers, which has these same relationships and thus appears to be a vestigial M. flexor hallucis brevis. No muscle slip or tendon with these relationships was found in either *Neotoma* or *Peromyscus*, but there is a possibility that this muscle is fused with M. adductor hallucis (p. 114).

M. flexor digiti quinti brevis

Origin. — From the distal aspect of the sesamoid bone which lies just beneath the medial part of the base of the fifth metatarsal and which is attached to the distal end of the calcaneus by a heavy tendon.

Insertion. — Into the medial sesamoid bone of the fifth metatarsophalangeal joint.

Remarks. — This muscle is very closely united with M. abductor digiti quinti, and many of the fibers of the latter muscle arise from its lateral surface. In *Peromyscus* there is no sesamoid in the tendon from the calcaneus, and origin of the muscle is thus directly from the calcaneus. This muscle probably represents the interosseus muscle of the fifth digit.

M. adductor hallucis

Origin. — From the mediodistal border of the deep palmar tendon, superficial to the origin of the medial interosseus muscle of the second digit.

Insertion. — On the lateral side of the base of the first phalanx of the hallux and on the lateral side of the lateral sesamoid bone of the joint.

Remarks. — The deep palmar tendon, or aponeurosis, from which this muscle takes origin also gives rise to the medial interossei. It is attached medially to the base of the first metatarsal and to the medial cuneiform bone; proximally, it attaches to the navicular; laterally, it ends on a strong ligament which passes from the distal end of the calcaneus and from the navicular to a well-developed lateral process near the proximal end of the third metatarsal.

The general relationships of this muscle are similar in all four forms. In *Neotoma*, however, it has the appearance of a compound muscle. The fibers are divided into medial and lateral groups by a longitudinal fascial plane, and many of the fibers insert on this internal fascia. Howell (1926) reported that this muscle (his M. flexor hallucis) seemed to occur in two divisions. I have not seen any specimens in which this was true, nor any in which fibers of this slip inserted on the medial sesamoid, as Howell described. In my specimens the only muscle attaching to the medial sesamoid was M. abductor hallucis. Nevertheless, the character of the adductor hallucis in my specimens is such that it is possible that the mass represents two muscles fused into a single unit. The medial part of this muscle could represent M. flexor hallucis brevis.

In *Peromyscus* the muscle is so small that I have not been able to discover its internal structure.

My reasons for considering this muscle to be M. adductor hallucis rather than M. flexor hallucis brevis are: (1) the presence in *Oryzomys* of a muscle, in addition to M. adductor hallucis, which has the proper relationships for a M. flexor hallucis brevis; (2) the muscle arises and lies for most of its length superficial to the medial interosseus muscle of the first digit; (3) innervation is from the lateral plantar nerve.

M. adductor digiti secundi

Origin. — From the raphe between the interossei of the third digit.

Insertion. — On the ventrolateral aspect of the base of the first phalanx of the second digit.

Remarks. — This very thin slip is present in all four genera. In *Neotoma* and *Peromyscus* origin seems to extend somewhat farther distad than in *Sigmodon* and *Oryzomys*.

M. adductor digiti quinti

Origin. — From the proximal three-fifths of the raphe between the two interossei of the third digit.

Insertion. — On the ventromedial part of the base of the first phalanx of the fifth digit.

Remarks. — This muscle appears to be more strongly developed in *Neotoma* and *Peromyscus* than in the other two genera. In the former genera origin extends along the raphe to a point immediately proximal to the sesamoids. In *Oryzomys* relationships are similar to those in *Sigmodon*.

Mm. lumbricales

Origin. — From the ventral surface of the tendon of M. flexor digitorum fibularis and from within the angles formed by the terminal divisions of this tendon.

Insertion. — On the medial border of the extensor digitorum longus tendons of the four lateral digits, just proximal to the ends of the first phalanges of the digits.

Remarks. — Four lumbricales with typical relationships are present in all four genera. Reference has already been made above to the Mm. flexores breves accessorii, which might be confused with the lumbricales.

Mm. interossei

There are only six of these muscles, two to each of the three middle digits, unless the short flexors of the hallux and the fifth digit be assigned to this group. Each appears to be made up of two elements, or groups of fibers, as is shown in Figure 18H. The medial element of the medial muscle of the second digit in *Sigmodon* and *Oryzomys* arises from the plantar surface of the first metatarsal. The lateral element of this muscle, both elements of the lateral muscle of the second digit, both muscles of the third digit, and the medial element of the medial muscle of the fourth digit arise from the distal margin of the deep palmar tendon which was described above (see under M. adductor hallucis). The lateral element of the medial muscle of the fourth digit and both elements of the lateral muscle to this digit take origin from the sesamoid in the flexor digiti quinti-abductor digiti quinti tendon.

In *Peromyscus* and *Neotoma* the tendons by which these muscles arise are not fused. Their borders are united by a fascia, but the separate tendons have not lost their identity. In these forms the medial element of the medial muscle of the second digit arises from the first metatarsal as in the other two genera. The lateral element of this muscle, both elements of the lateral muscle of the second digit, and the medial element of the medial muscle of the third digit arise by a common tendon directly from the navicular. The lateral element of the medial muscle of the third digit, all of the lateral muscle of this digit, and the medial element of the medial muscle of the fourth digit take origin by common tendon from the cuboid. The remaining elements of the interossei arise from the sesamoid in the tendon of the abductor and flexor of the fifth digit in *Neotoma* and by direct continuation of this tendon in *Peromyscus*, since the sesamoid is not developed in the latter genus.

DISCUSSION AND CONCLUSIONS

This section is most appropriately divided into two parts. The first part deals with conclusions pertaining to myological problems; the second part concerns the intergeneric relationships.

Myological Problems

The conclusions which pertain particularly to myological problems have already been discussed under the headings of the individual muscles to which they apply in the four genera studied. Only those conclusions having a more general application are repeated here.

The "M. longus atlantis" of Howell (1926) and Bryant (1945) is an integral part of the dorsal intertransverse system; the use of that term is not appropriate.

In the rodents there are elements of the lateral intertransverse series associated with M. scalenus, as was suggested by Hill (1937:112).

The direct continuity of M. serratus posterior inferior and M. obliquus abdominis internus, found in many rodents, is a secondarily derived condition.

M. sternocostalis is a derivative of the external oblique layer of thoracoabdominal muscles (Hill, 1937:113).

The muscle designated by Howell (1926), Mossman, Lawlah, and Bradley (1932), and also in this paper, as M. sphincter ani externus may not be strictly homologous with the muscle so designated in man. There is a need for a comprehensive study of the perineal muscles of the mammals.

M. dorsoepitrochlearis is apparently derived from M. triceps; vestiges of its primitive attachment to the humerus remain in *Neotoma* (Hill, 1937:116).

The muscle designated in this paper as M. opponens digiti quinti does not belong with the interosseus muscles, where it has been placed by various authors, but should be grouped with the more superficial hypothenar muscles.

M. pyriformis appears to be derived directly from M. gluteus medius.

Mm. extensores breves of the pes are probably derived, at least in the rodents, from M. extensor digitorum longus rather than from Mm. peronei.

The conclusions of Hill (1937:124) with regard to the identification of M. adductor magnus and M. adductor brevis in the rodents are correct.

The muscles designated here as Mm. flexores breves accessorii are discrete elements which occur in several widely separated groups and are not a part of the lumbrical series.

Intergeneric Relationships

In order to establish a basis for the conclusions which have been drawn from the observations recorded in the previous section, one fundamental assumption has been made, namely, that similarities among the genera in the relationships of corresponding muscles are a result of "heritage" from a common ancestral stock. I believe this to be a reasonable procedure in this particular situation since all the genera concerned are within a single

subfamily. It would not, perhaps, be a good basis in more comprehensive taxonomic groups and may be challengeable even in this case. As Hill (1937:159) concluded, however: "Although great modifications of attachment occur in the muscular system of mammals, 'heritage' exerts a great influence on the muscular system.... The evidences of relationship drawn from the muscular system, while important within families, are too complex to be of much importance in more comprehensive groups."

A. H. Miller (1937:58-59) was faced with almost the same problems which are inherent in the present interpretation. His procedure and the reasons for it are quite pertinent.

> The inequality in values of these ... characters cannot be too greatly stressed. Some characters involve parts that evidently are capable of rapid evolutionary change, such, for example, as muscle bulk [excluded from consideration in the present study; see p. 14]; there is even some doubt as to the degree to which this is hereditary. Many characters may be classed as of current adaptive value (cenotelic) but these may be, nevertheless, distinctly useful and reliable in showing the relationships of lesser taxonomic groups. Adaptations may be of current survival value and yet have great antiquity. Still other characters seem to have no special adaptive value at present. The stress that should be placed upon them is largely a matter of personal opinion. Some such characters are of great antiquity but others may recently have been swept into the genetic complex of the species linked to an adaptive character that perhaps was purely functional in nature. Characters, currently nonadaptive, and equally manifested in several distinct species, must of course be of decided antiquity (paleotelic). If one classifies characters as to value there almost inevitably is injected to a noticeable degree the investigator's personal theory and bias as a means of arranging the facts. This procedure often departs too completely from the inductive method.
>
> When a large number of characters is available, sheer quantity should point out the resemblances and differences and, to a degree, the genetic relationships of the genera. I propose, therefore, to treat all characters in equal fashion to begin with and then modify, where necessary, the conclusions drawn on this basis through consideration of the values of the characters.

Although I fail to appreciate just what necessity should cause Miller to modify his conclusions "through a consideration of the values of the characters" after he had rejected this procedure in the previous paragraph, I am in substantial agreement as regards the objectivity which may be attained by treating all characters equally. Even the segregation of characters into adaptive and nonadaptive categories, or a classification based on current survival value, is, in my opinion, a highly subjective approach. I do not believe that the present state of knowledge will allow this approach to be used with any appreciable degree of certainty. It appears to me that success in such an attempt would require much greater insight into the relationship of structure and function, into the basis of habitat preferences (or restrictions), and into many more phenomena than is possible at present.

I have proceeded, therefore, to consider the data at hand on the assumption that "heritage" is the most important factor accounting for similarities in structure and relationships of muscles, and that when all the skeletal muscles are considered, the resulting arrangement will give a better indication of the genetic affinities of the genera than would be the case if attempts were made to weigh the individual characters. In other words, I consider the number of corresponding muscles which have similar form

and relationships in two genera to be an index of the proximity of genetic relationship. The greater the number of myological characters common to the two forms, the closer their genetic relationship is considered.

If, then, the number of muscles with similar relationships in each possible combination of two of the four genera is determined, an idea will be gained of the proximity of each genus to each of the other three genera. The figures given below do not include a group of 65 muscles which occur in all four genera and which do not present any noticeable differences in any of the genera. Neither do they include a group of 46 muscles which have different relationships or attachments in one or more genera, but with differences so slight that I cannot be certain that they are significant. These 111 muscles, having similar or very nearly similar relationships in all four genera, offer no evidence of relative proximity of genetic relationship of any two of the four genera, and have, therefore, been rejected from consideration here.

There remain 70 muscles with similar relationships in *Sigmodon* and *Oryzomys*, 71 in *Neotoma* and *Peromyscus*, but only 6 in *Sigmodon* and *Neotoma*, 7 in *Sigmodon* and *Peromyscus*, 8 in *Neotoma* and *Oryzomys*, and 10 in *Peromyscus* and *Oryzomys*. It is evident from these figures that *Sigmodon* and *Oryzomys* are relatively much more closely related than either of these genera is to *Peromyscus* or *Neotoma*. Similarly, *Neotoma* and *Peromyscus* appear to be related to approximately the same extent as are *Sigmodon* and *Oryzomys*.

When a list of the 70 muscles which are similar in *Sigmodon* and *Oryzomys* is compared with a list of the 71 which are similar in *Neotoma* and *Peromyscus*, 54 muscles, or approximately three-fourths of them, are found to be included in both lists. That is to say, these 54 muscles have similar relationships in each pair of genera, but the relationships in one pair are different from those of the corresponding muscles in the other pair. This pattern may be of considerable significance, since it does not appear to me that it would be found if each of the four genera had differentiated independently from the common stock of the subfamily. Rather, it seems to indicate that there were first two lines of descent from that common stock, one line characterized by, among other characters, relationships of these muscles as exemplified by the *Sigmodon-Oryzomys* complex; the other line characterized by the relationships of the corresponding muscles as seen in the *Neotoma-Peromyscus* complex. Adaptive differentiation within each of these secondary lines may then have given rise to the genera as we see them at present.

Such a concept of the phyletic lines and intergeneric relationships of these genera is not in conformity with the opinions now held by certain taxonomists. Indeed, it is directly opposed to some of them. Hershkovitz (1944), basing his conclusions almost entirely upon dental characters, denied any very close relationship between the oryzomyine group and the sigmodont groups. Several earlier taxonomists compared certain of the oryzomyine group (*Nectomys*, *Sigmodontomys*) with members of the sigmodont group (*Holochilus* and *Sigmodon*, respectively) and placed them rather close together in their classifications. Hershkovitz (1944:19) dismissed this as "due, at least partly, to a confounding of the remarkable

extent of parallelism in the external characters of these two forms with a similar degree of genetic affinity...." It might well be asked how it was determined that this similarity in external characters was parallelism.

If the evidence presented in this paper is actually an indication of the true genetic relationships of the genera concerned, then it is obvious that the differences in dental pattern between *Oryzomys* and *Sigmodon* and between *Neotoma* and *Peromyscus* are of relatively recent development and show an independent tendency in each phyletic line toward the development of a prismatic pattern from the tuberculate pattern in the teeth. Hershkovitz (1944:16) himself pointed out that "the enamel pattern, just as any other character composed of numerous structural details, is replete with instances of individual, local, and geographic variations." Ellerman (1941:328) based his key to the cricetine genera on dental characters, but was careful to indicate that it "...is in many places much more average than absolute, and probably can be broken down; this is chiefly owing to the fact that although such forms as *Neotoma*, *Sigmodon* and *Oryzomys*, representing three extremes, are very widely separated dentally, there are a host of subsidiary genera which have intergrading dental characters; in fact some genera start life in one section, and in the adult appear to develop a dental pattern not distinguishable from that of another section." The quotations and my own remarks are given merely to emphasize the opinion that it is a questionable procedure to rely almost exclusively on dental characters in arranging genera, especially in such a group as the Cricetinae, and that re-examination of this group in the light of evidence to be obtained from more thorough morphological study is definitely in order.

The remaining muscles fall into several categories, as shown in Table II. These appear to afford no further clues to the solution of the problem at hand, with a few possible exceptions. To be sure, for the sake of consistency, the similarities which exist between the various combinations of genera must be considered as indicative of common ancestry, but there is no pattern to indicate the relative time level of this common ancestry. For example, the muscles in category IIIa and IIIb of Table II may be considered.

This pattern could be derived in several different ways. (1) The muscle relationships common to the two genera might be the primitive relationships which characterized the common ancestor of all four genera, whereas the corresponding muscles in each of the other two genera have taken on new relationships. (2) The muscle relationships common to the two genera might be secondary or derived relationships which characterized a secondary stock, and the relationships of the corresponding muscles in one of the other two genera might be the primitive relationships, although the remaining genus presents an independently derived condition. (3) The muscle relationships common to the two genera might be those of a derived stock, as in (2), whereas the relationships of the corresponding muscles in the other two genera might be independently derived from those of the original stock or from a secondary common stock. There are still other ways in which such a pattern could have been developed which are just as obvious as those presented. There appears to be no manner of

TABLE II

Comparison of Muscles in the Four Genera

I. Muscles similar in all four genera, or differing to insignificant degree	
a. Similar in all four genera	65
b. Differing only insignificantly	46
II. Muscles similar in *Sigmodon* and *Oryzomys*, similar in *Neotoma* and *Peromyscus*, but with difference between the pairs	54
III. Muscles similar in two genera, but different in each other genus	
a. Similar in *Sigmodon* and *Oryzomys*, different in *Neotoma* and *Peromyscus*	9
b. Similar in *Neotoma* and *Peromyscus*, different in *Sigmodon* and *Oryzomys*	12
c. Similar in *Sigmodon* and *Neotoma*, different in *Peromyscus* and *Oryzomys*	1
d. Similar in *Neotoma* and *Oryzomys*, different in *Sigmodon* and *Peromyscus*	0
e. Similar in *Peromyscus* and *Oryzomys*, different in *Neotoma* and *Sigmodon*	3
f. Similar in *Sigmodon* and *Peromyscus*, different in *Neotoma* and *Oryzomys*	3
IV. Muscles similar in three genera, different in one	
a. Similar in *Sigmodon*, *Neotoma*, and *Peromyscus*, different in *Oryzomys*	1
b. Similar in *Sigmodon*, *Peromyscus*, and *Oryzomys*, different in *Neotoma*	3
c. Similar in *Sigmodon*, *Neotoma*, and *Oryzomys*, different in *Peromyscus*	4
d. Similar in *Neotoma*, *Peromyscus*, and *Oryzomys*, different in *Sigmodon*	4
V. Muscles different in all four genera	12
VI. Muscles present only in *Sigmodon*	1
VII. Muscles not compared	10
Total number of muscles examined	228

determining which of these possibilities is responsible for the pattern set by any one muscle. There may, however, be some significance in the number of muscles in each division of category III in Table II.

If the four genera treated here evolved independently from the common ancestral stock, it seems to me that each possible combination of two genera would have approximately the same number of muscles in this category, since the first possibility outlined above would be the only one applicable to the situation. On the other hand, if any two of the genera were derived more recently from a single secondary line resulting from the earlier division of the common stock of the subfamily, it might be expected that these two would have some muscles owing their similarities to each of the possibilities given. Thus, such a pair would have more muscles falling into this category than would two genera not having a secondary

common ancestry. Although the number of muscles in this category is small, a glance at the table will show that *Sigmodon* and *Oryzomys*, as well as *Neotoma* and *Peromyscus*, follow this pattern, but that no other combinations of two genera do so.

The most simple explanation for the pattern of similarities and differences set by the muscles of category IV in Table II is that the primitive relationships of the various muscles have been retained by three of the genera and have undergone some change in the other genus. This appears to be a distinct probability in most of the cases. There is, however, no sure way of ascertaining this.

The remaining groups of muscles in Table II offer no evidence to aid in determining generic interrelationships.

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FIGURES

FIGURE I

A. Lateral view of the superficial muscles of the masticatory group in *Sigmodon*.

B. Lateral view of the deeper muscles of the masticatory group in *Sigmodon*.

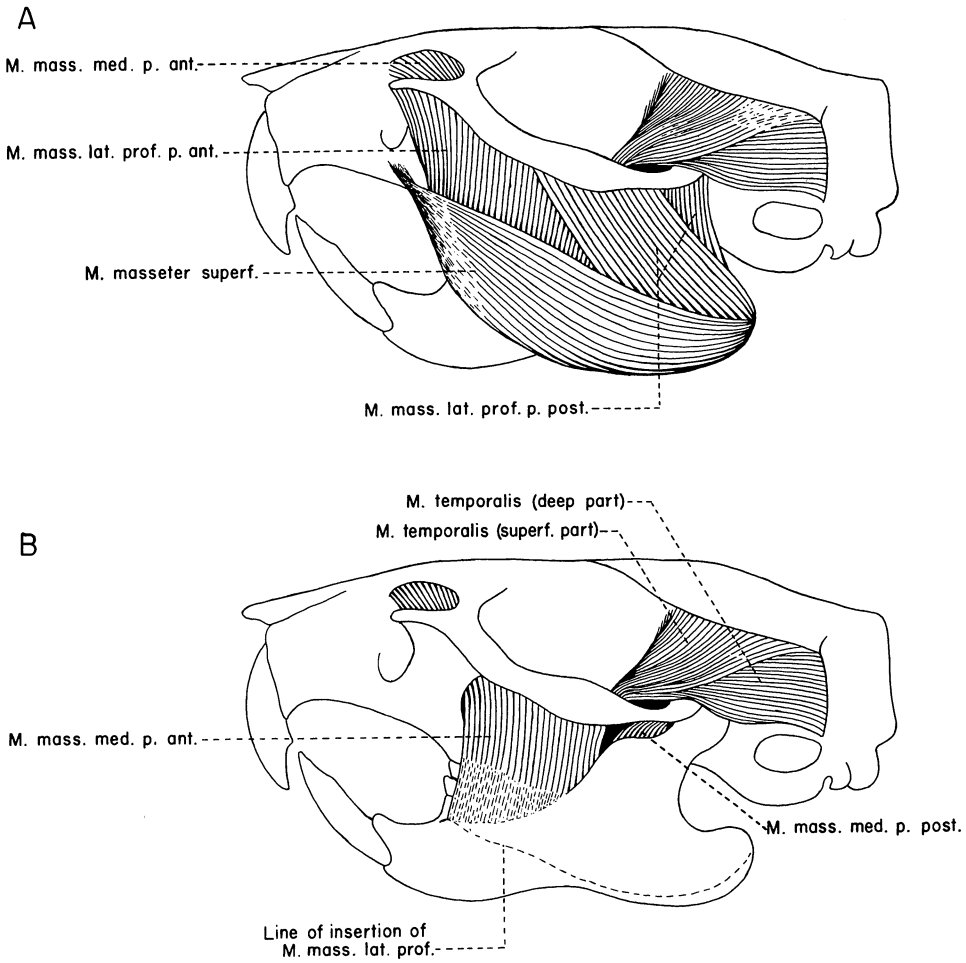

A
M. mass. med. p. ant.
M. mass. lat. prof. p. ant.
M. masseter superf.
M. mass. lat. prof. p. post.
B
M. temporalis (deep part)
M. temporalis (superf. part)
M. mass. med. p. ant.
M. mass. med. p. post.
Line of insertion of
M. mass. lat. prof.

Fig. 1

FIGURE 2

Lateral view of the superficial facial muscles in *Sigmodon*.

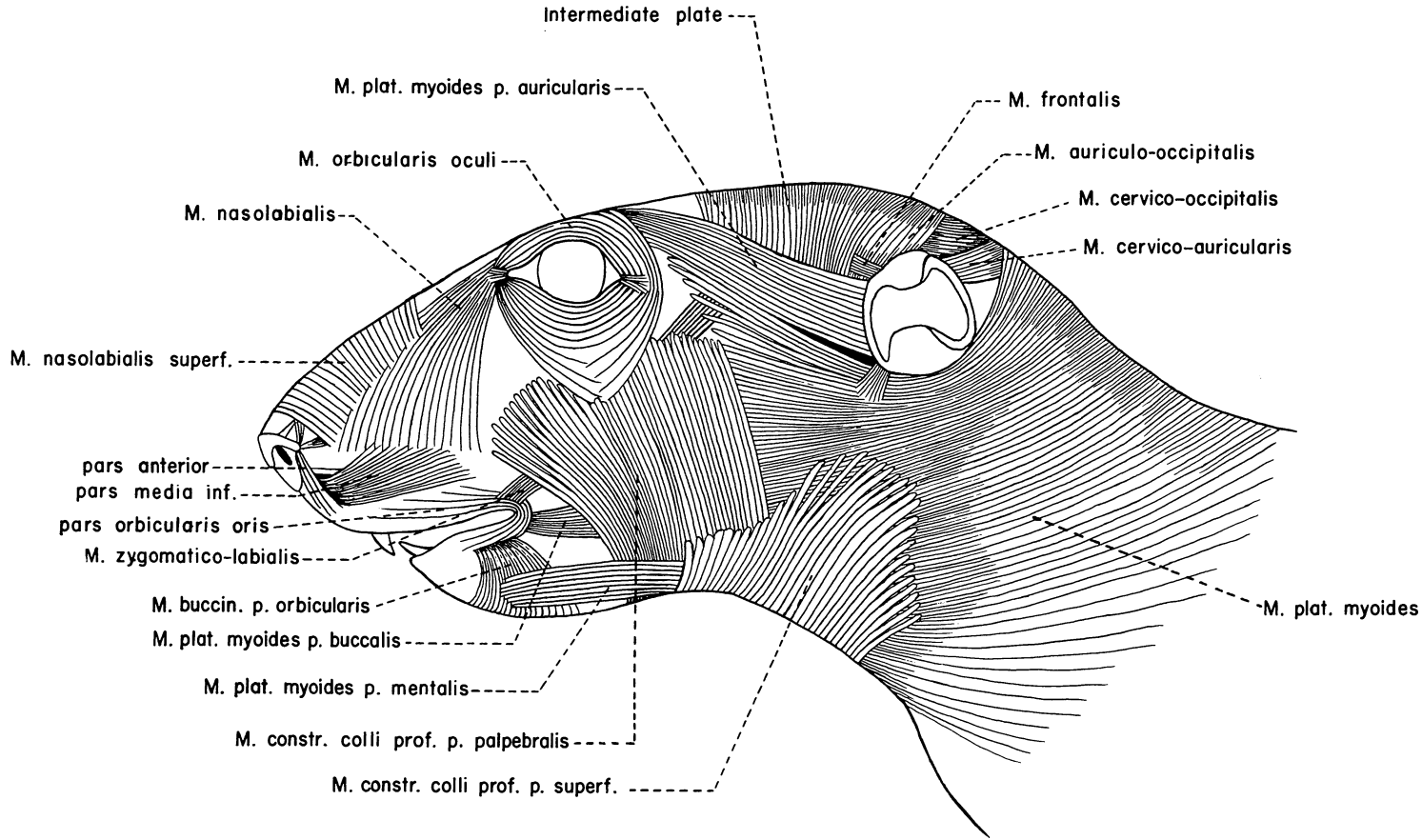

Intermediate plate
M. plat. myoides p. auricularis
M. orbicularis oculi
M. nasolabialis
M. nasolabialis superf.
pars anterior
pars media inf.
pars orbicularis oris
M. zygomatico-labialis
M. buccin. p. orbicularis
M. plat. myoides p. buccalis
M. plat. myoides p. mentalis
M. constr. colli prof. p. palpebralis
M. constr. colli prof. p. superf.
M. frontalis
M. auriculo-occipitalis
M. cervico-occipitalis
M. cervico-auricularis
M. plat. myoides

Fig. 2

FIGURE 3

Dorsal view of some of the superficial facial muscles in *Sigmodon*, with the M. platysma myoides removed.

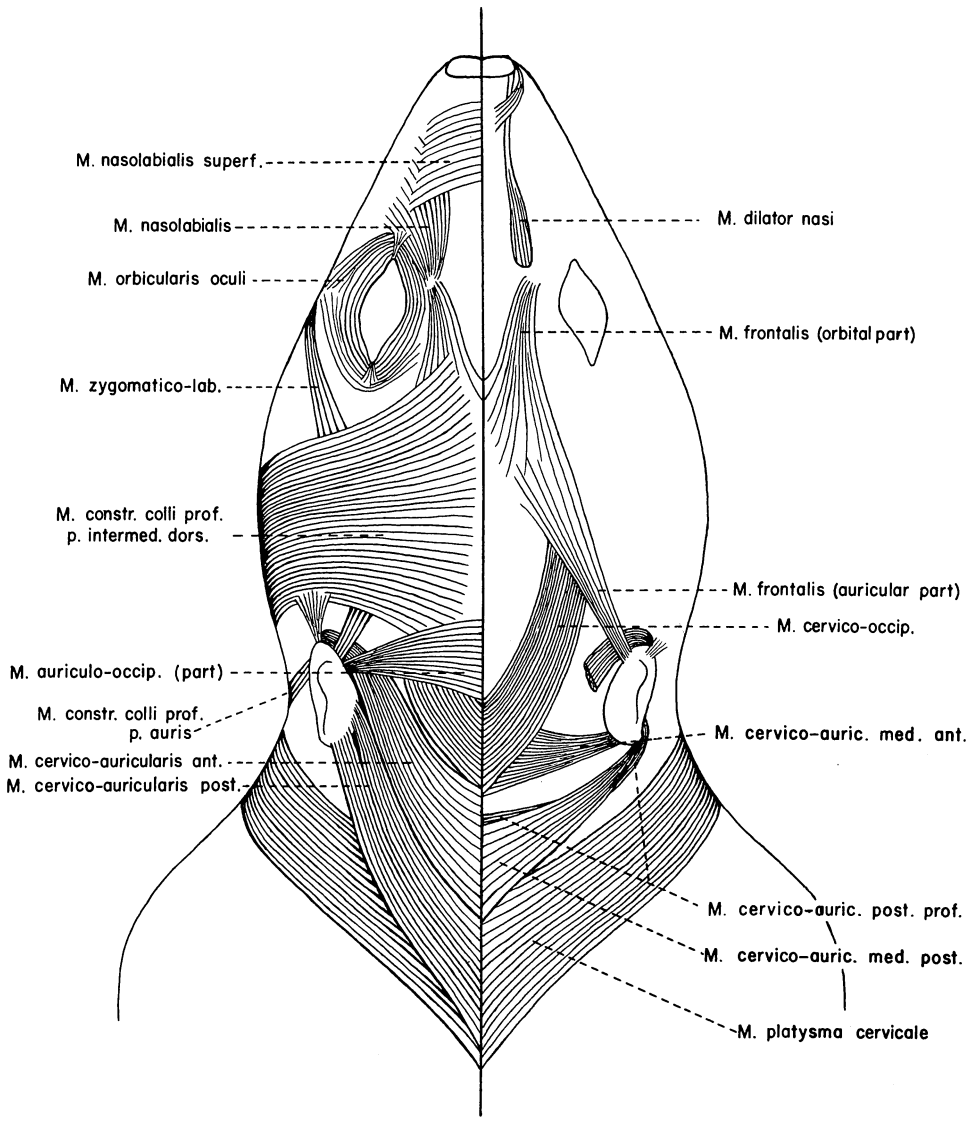

M. nasolabialis superf.
M. nasolabialis
M. orbicularis oculi
M. zygomatico-lab.
M. constr. colli prof.
p. intermed. dors.
M. auriculo-occip. (part)
M. constr. colli prof.
p. auris
M. cervico-auricularis ant.
M. cervico-auricularis post.
M. dilator nasi
M. frontalis (orbital part)
M. frontalis (auricular part)
M. cervico-occip.
M. cervico-auric. med. ant.
M. cervico-auric. post. prof.
M. cervico-auric. med. post.
M. platysma cervicale

Fig. 3

FIGURE 4

A. Lateral view of the superficial facial muscles of the rostrum in *Sigmodon*, with M. nasolabialis superficialis and M. nasolabialis removed.

B. Lateral view of the same, with pars media inferior and M. maxillo-labialis removed.

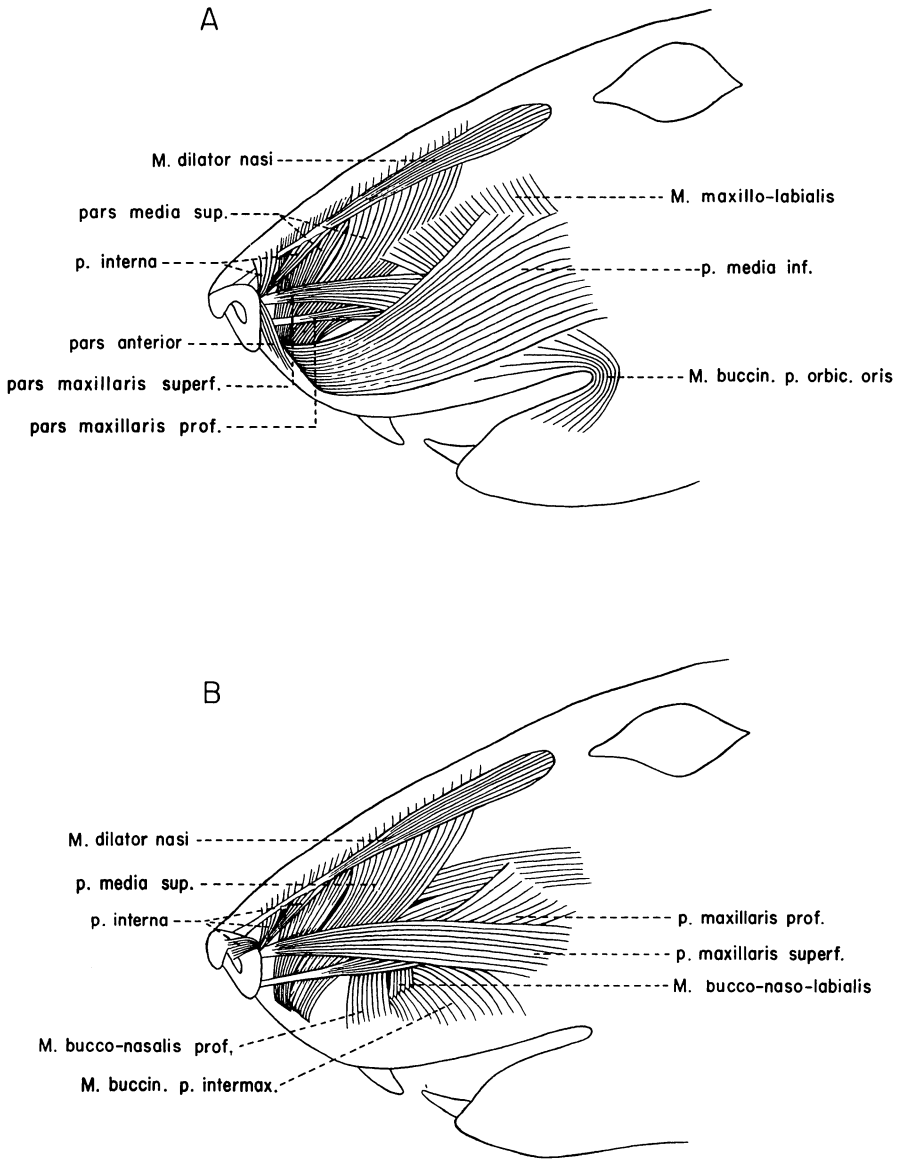

A
M. dilator nasi
pars media sup.
p. interna
pars anterior
pars maxillaris superf.
pars maxillaris prof.
M. maxillo-labialis
p. media inf.
M. buccin. p. orbic. oris
B
M. dilator nasi
p. media sup.
p. interna
M. bucco-nasalis prof.
M. buccin. p. intermax.
p. maxillaris prof.
p. maxillaris superf.
M. bucco-naso-labialis

Fig. 4

FIGURE 5

Lateral views of M. buccinatorius and associated muscles in (A) *Sigmodon*, (B) *Oryzomys*, (C) *Peromyscus*, and (D) *Neotoma*.

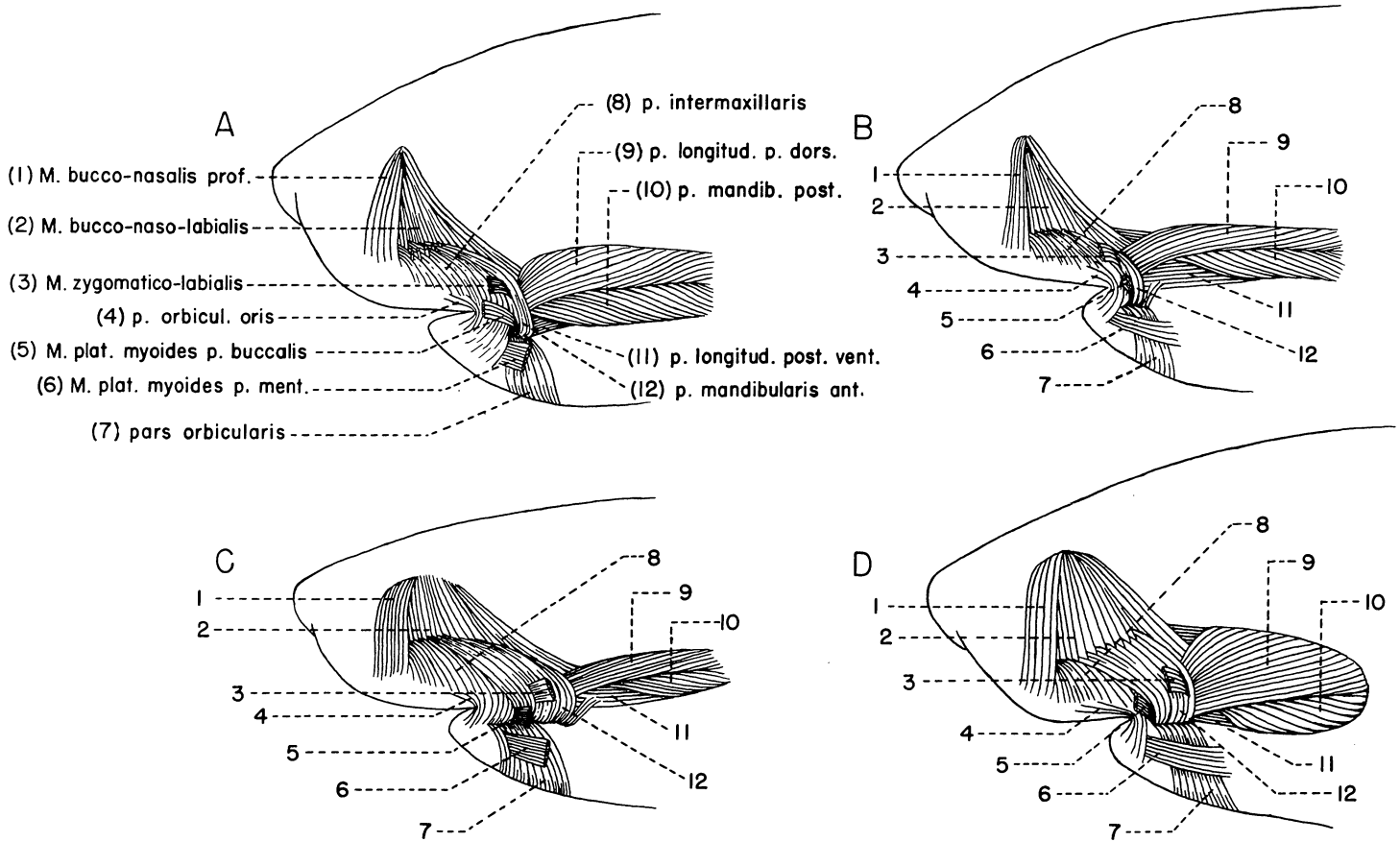

A
(1) M. bucco-nasalis prof.
(2) M. bucco-naso-labialis
(3) M. zygomatico-labialis
(4) p. orbicul. oris
(5) M. plat. myoides p. buccalis
(6) M. plat. myoides p. ment.
(7) pars orbicularis
(8) p. intermaxillaris
(9) p. longitud. p. dors.
(10) p. mandib. post.
(11) p. longitud. post. vent.
(12) p. mandibularis ant.
B
C
D

Fig. 5

FIGURE 6

A. Comparison of M. digastricus in *Neotoma* and *Sigmodon*. The digastric muscle of *Neotoma* is shown above and that of *Sigmodon* is shown below.

B. Ventral view of the submandibular region in *Sigmodon*. Lower half of figure shows superficial structures; upper half has M. transversus mandibulae, M. mylohyoideus, and M. stylohyoideus removed.

C. Ventral view of the submandibular region in *Sigmodon*, showing deeper levels. Upper half of figure shows the deepest level.

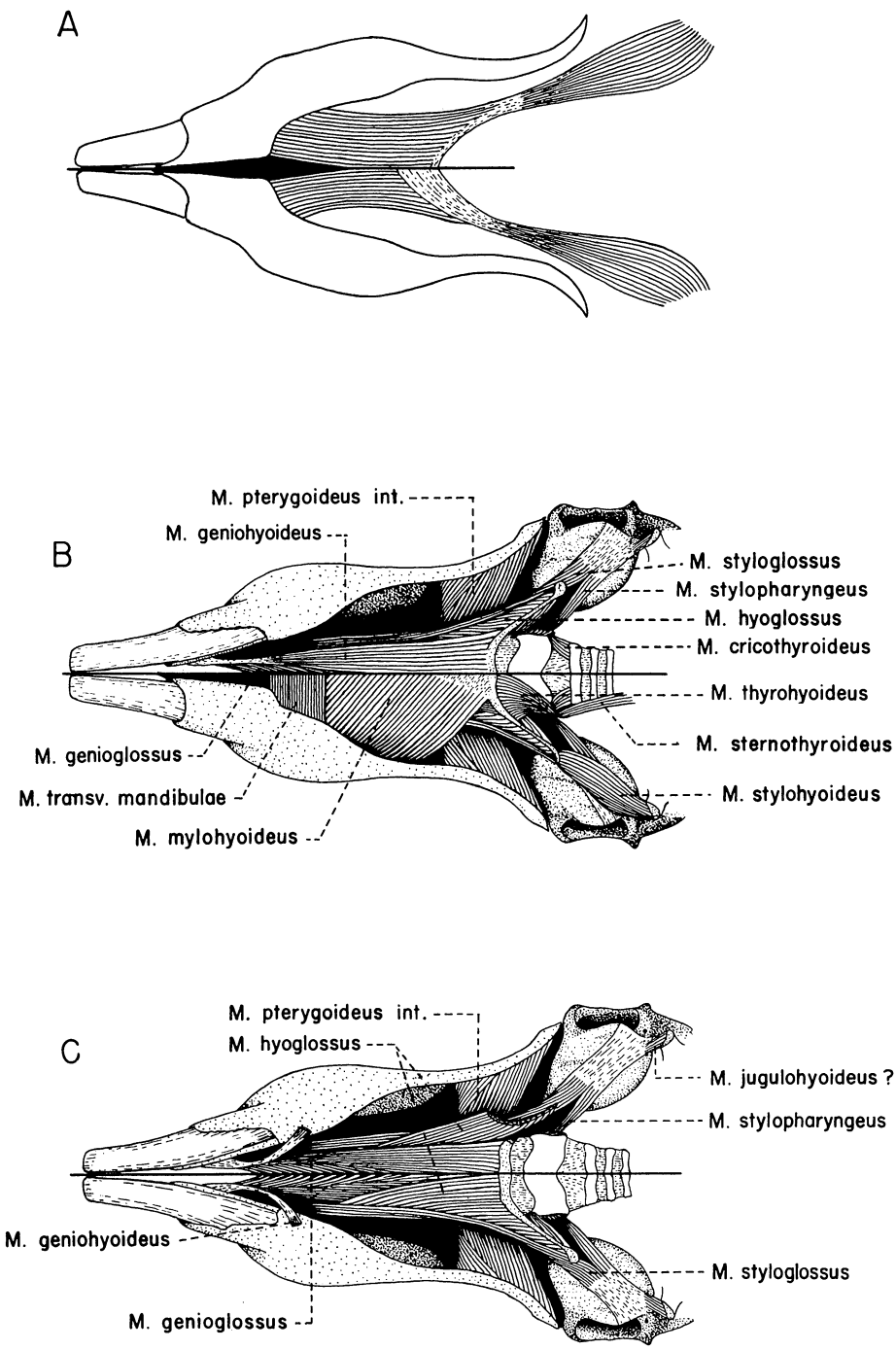

A
B
M. pterygoideus int.
M. geniohyoideus
M. styloglossus
M. stylopharyngeus
M. hyoglossus
M. cricothyroideus
M. thyrohyoideus
M. sternothyroideus
M. stylohyoideus
M. genioglossus
M. transv. mandibulae
M. mylohyoideus
C
M. pterygoideus int.
M. hyoglossus
M. jugulohyoideus ?
M. stylopharyngeus
M. geniohyoideus
M. styloglossus
M. genioglossus

Fig. 6

FIGURE 7

A. Lateral view of the intrinsic back muscles in *Sigmodon*.

B. Schematic representation of M. longissimus.

C. Schematic representation of M. iliocostalis.

D. Schematic representation of M. semispinalis dorsi.

E. Sketch of the shorter fascicles of the transversospinal and intertransverse systems in the lower thoracic region.

F. Schematic representation of M. semispinalis capitis and M. longissimus capitis.

G. Schematic representation of M. longissimus cervicis.

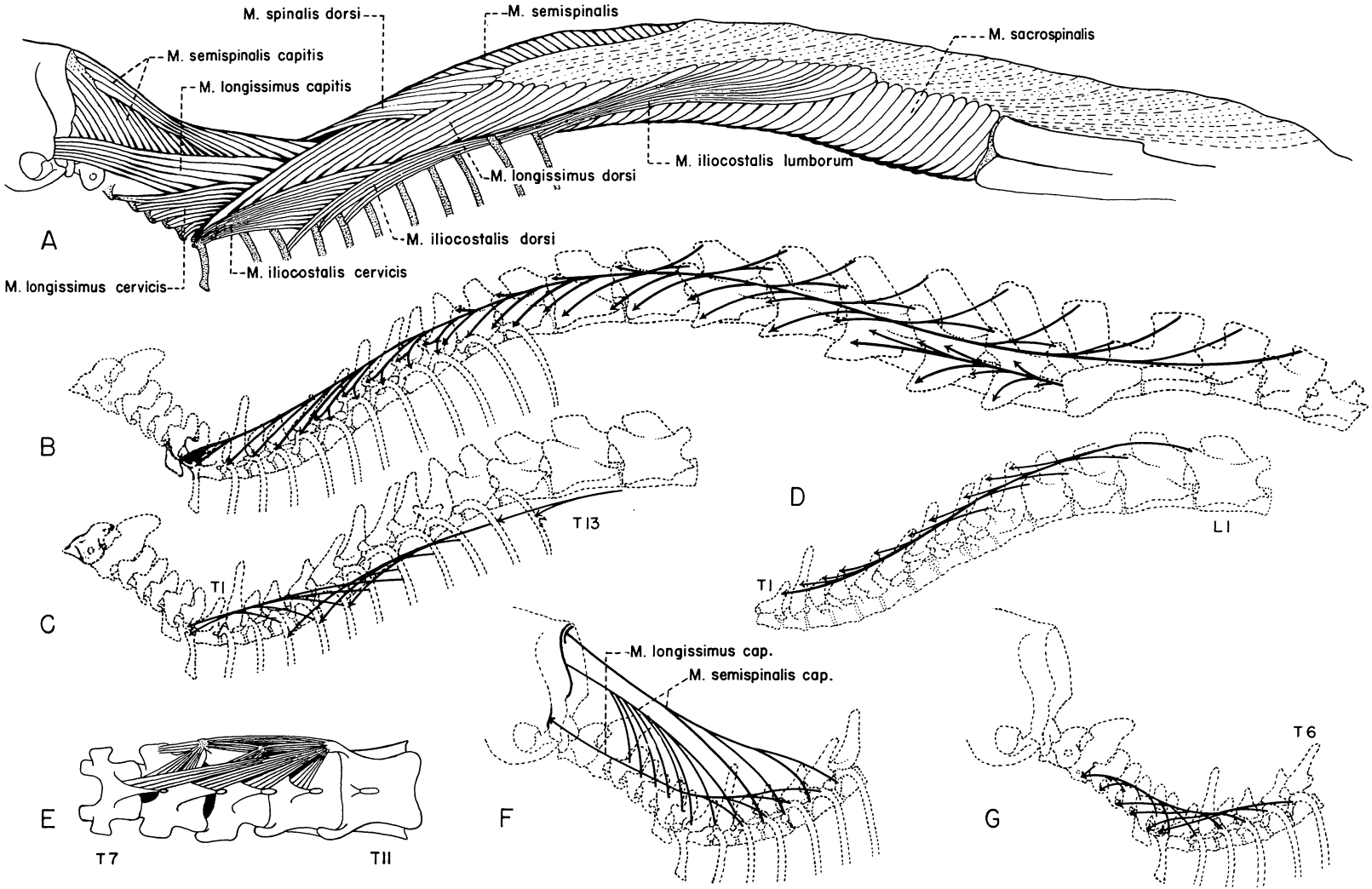

M. spinalis dorsi
M. semispinalis
M. sacrospinalis
M. semispinalis capitis
M. longissimus capitis
M. iliocostalis lumborum
M. longissimus dorsi
A
M. iliocostalis dorsi
M. iliocostalis cervicis
M. longissimus cervicis
B
T13
D
L1
T1
C
T1
M. longissimus cap.
M. semispinalis cap.
T6
E
F
G
T7
T11

Fig. 7

FIGURE 8

Ventral view of anterior half of *Sigmodon*. Superficial structures on the left, deeper on the right. Inset shows insertion of M. pectoralis abdominalis and M. cutaneus maximus.

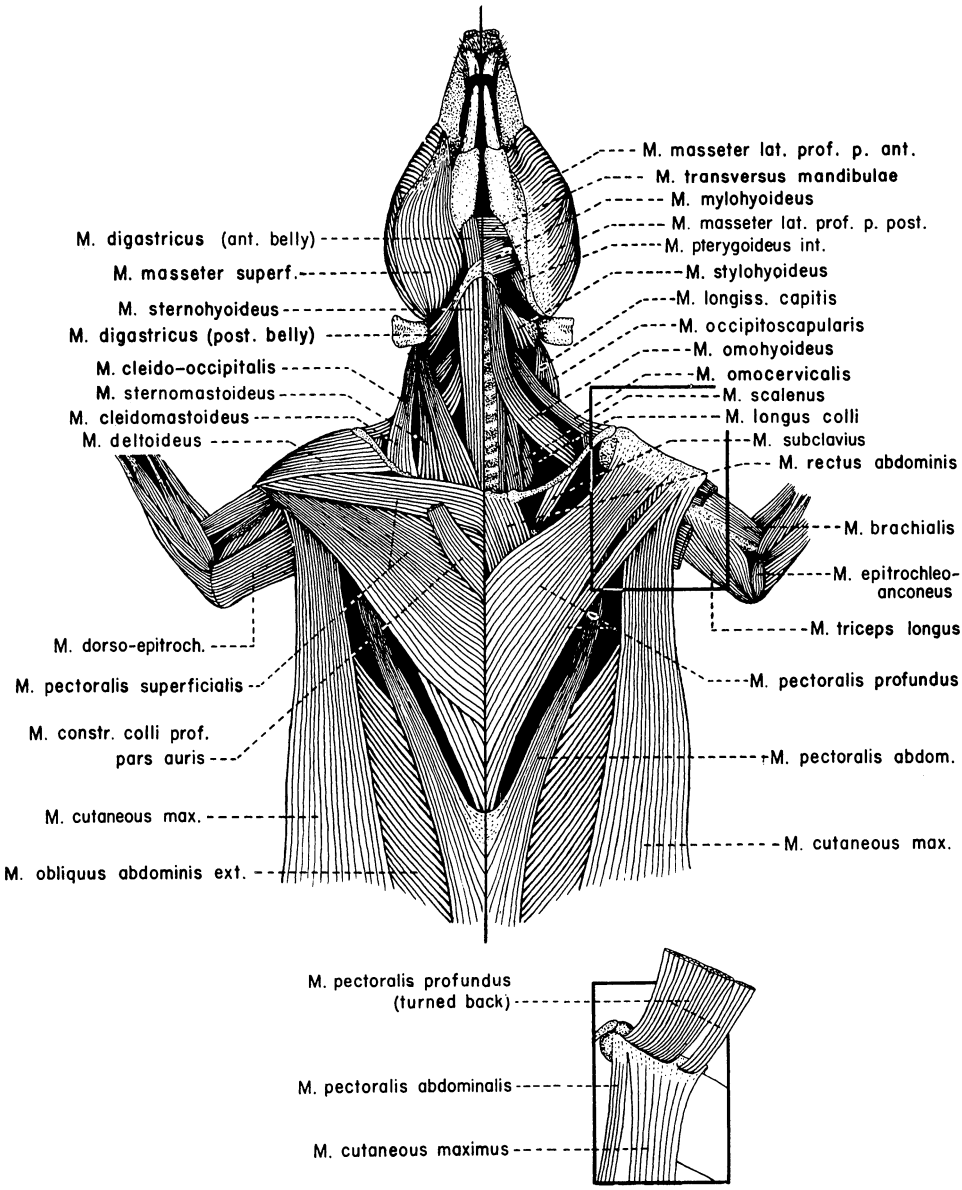
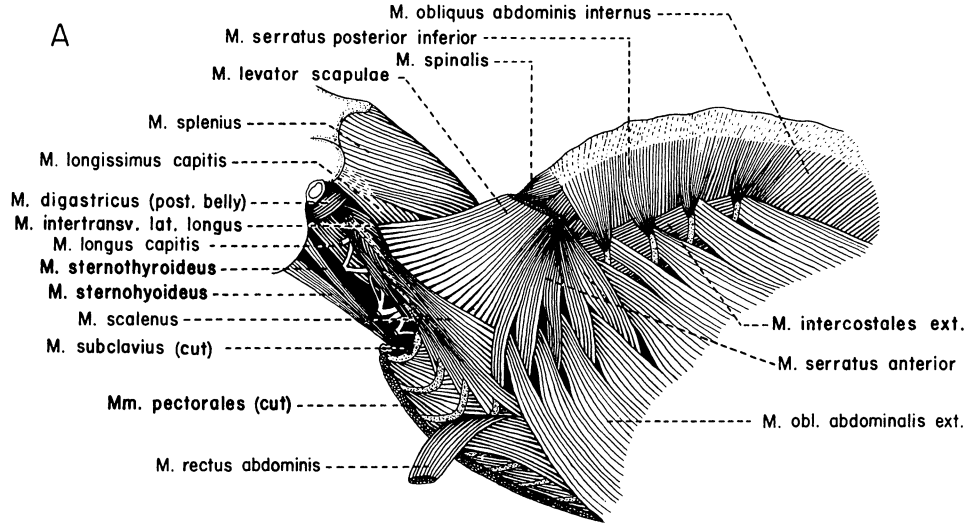

M. masseter lat. prof. p. ant.
M. transversus mandibulae
M. mylohyoideus
M. masseter lat. prof. p. post.
M. pterygoideus int.
M. digastricus (ant. belly)
M. masseter superf.
M. stylohyoideus
M. sternohyoideus
M. longiss. capitis
M. digastricus (post. belly)
M. occipitoscapularis
M. omohyoideus
M. cleido-occipitalis
M. omocervicalis
M. sternomastoideus
M. scalenus
M. cleidomastoideus
M. longus colli
M. deltoideus
M. subclavius
M. rectus abdominis
M. brachialis
M. epitrochleo-anconeus
M. triceps longus
M. dorso-epitroch.
M. pectoralis superficialis
M. pectoralis profundus
M. constr. colli prof. pars auris
M. pectoralis abdom.
M. cutaneous max.
M. cutaneous max.
M. obliquus abdominis ext.
M. pectoralis profundus (turned back)
M. pectoralis abdominalis
M. cutaneous maximus

Fig. 8

FIGURE 9

A. Lateral view of neck and thorax of *Sigmodon*, with scapula removed.

B. Sketch showing the relationships of Mm. obliquus abdominis externus and internus to the inguinal ligament.


A
M. obliquus abdominis internus
M. serratus posterior inferior
M. spinalis
M. levator scapulae
M. splenius
M. longissimus capitis
M. digastricus (post. belly)
M. intertransv. lat. longus
M. longus capitis
M. sternothyroideus
M. sternohyoideus
M. scalenus
M. subclavius (cut)
Mm. pectorales (cut)
M. rectus abdominis
M. intercostales ext.
M. serratus anterior
M. obl. abdominalis ext.

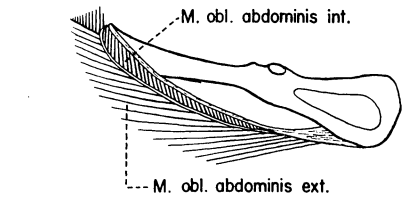

B
M. obl. abdominis int.
M. obl. abdominis ext.

Fig. 9

FIGURE 10

A. Ventral view of the perineal region in *Sigmodon*. The ischium is turned laterad to show structures on its pelvic side.

B. Lateral view of the structure associated with the urethra, anus, and penis in *Sigmodon*.

C. Ventral view of the structure associated with the urethra, anus, and penis in *Sigmodon*.

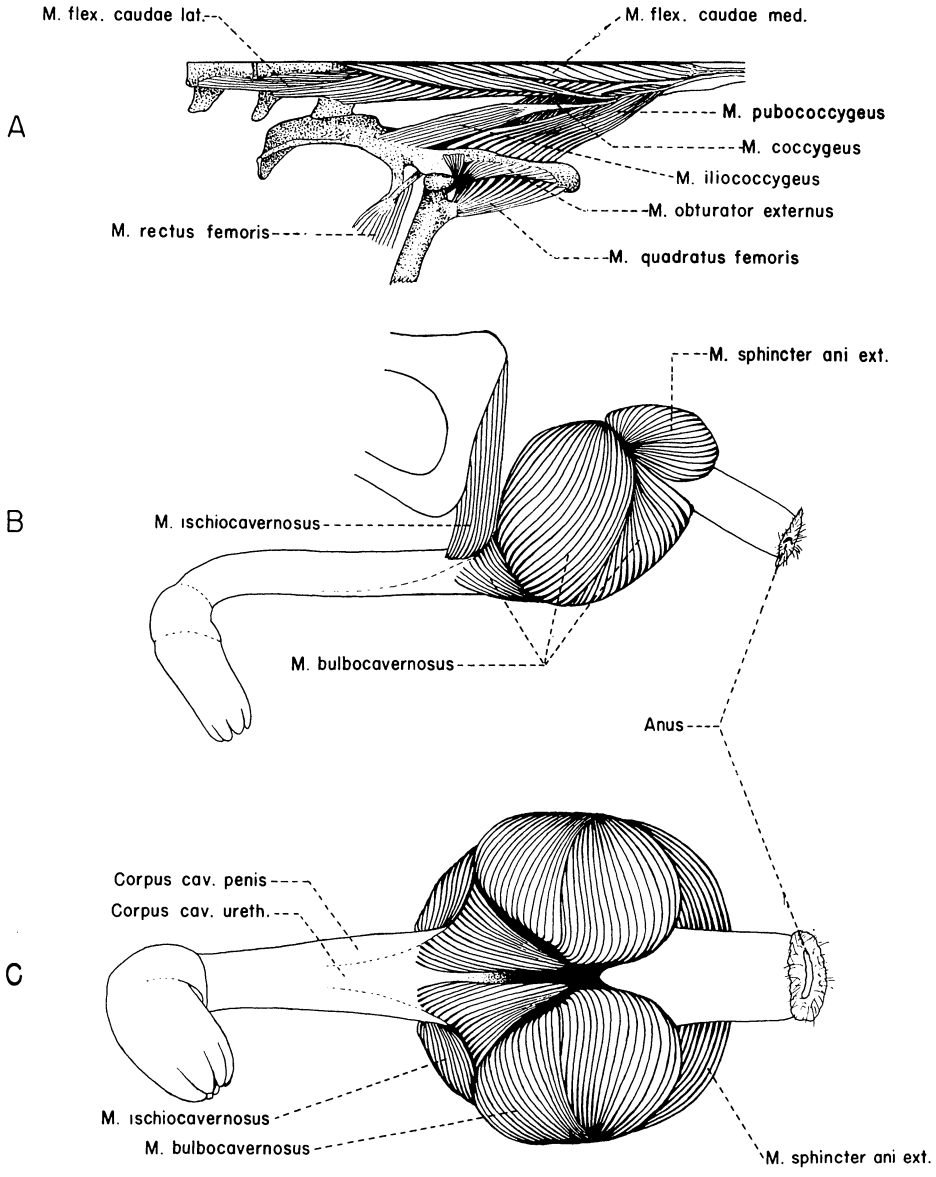

A
M. flex. caudae lat.
M. flex. caudae med.
M. pubococcygeus
M. coccygeus
M. iliococcygeus
M. obturator externus
M. quadratus femoris
M. rectus femoris
B
M. sphincter ani ext.
M. ischiocavernosus
M. bulbocavernosus
Anus
C
Corpus cav. penis
Corpus cav. ureth.
M. ischiocavernosus
M. bulbocavernosus
M. sphincter ani ext.

Fig. 10

FIGURE 11

Dorsal view of the anterior part of the body of *Sigmodon.* Superficial structures are shown on the left, deeper structures on the right.

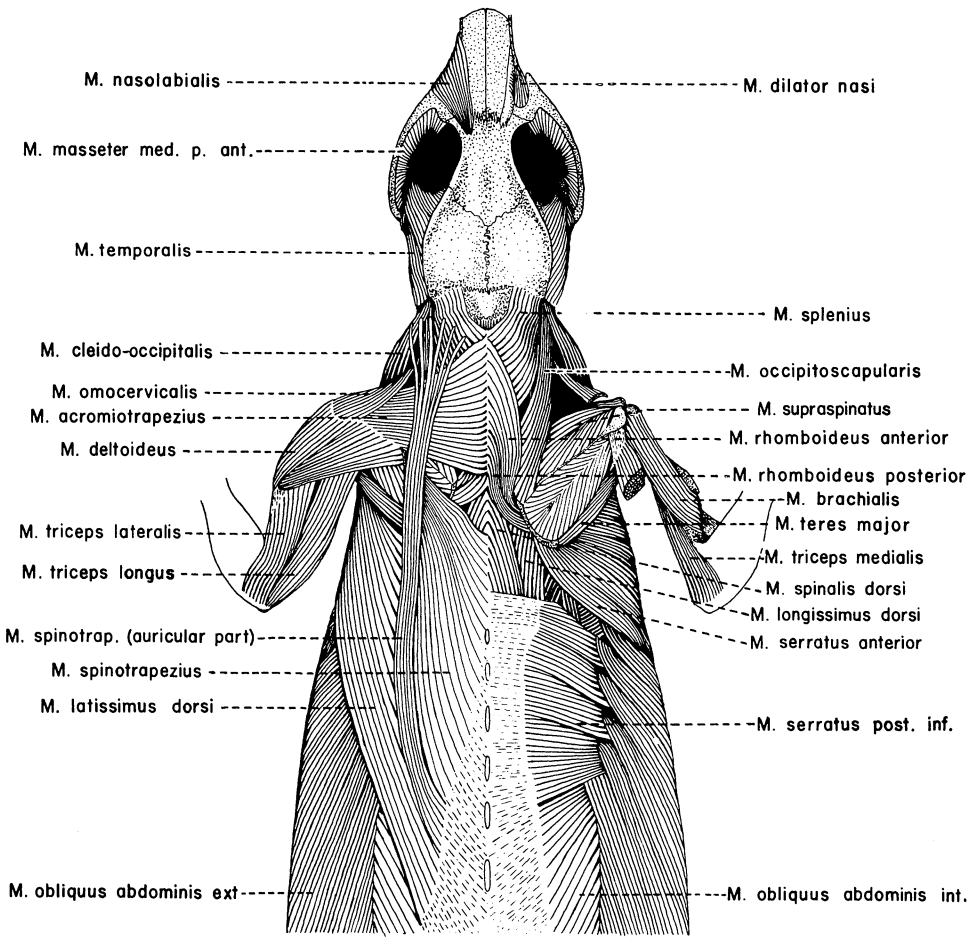

M. nasolabialis
M. dilator nasi
M. masseter med. p. ant.
M. temporalis
M. splenius
M. cleido-occipitalis
M. occipitoscapularis
M. omocervicalis
M. supraspinatus
M. acromiotrapezius
M. rhomboideus anterior
M. deltoideus
M. rhomboideus posterior
M. brachialis
M. teres major
M. triceps lateralis
M. triceps medialis
M. triceps longus
M. spinalis dorsi
M. longissimus dorsi
M. spinotrap. (auricular part)
M. serratus anterior
M. spinotrapezius
M. latissimus dorsi
M. serratus post. inf.
M. obliquus abdominis ext
M. obliquus abdominis int.

Fig. 11

FIGURE 12

A. Lateral view of the anterior limb of *Sigmodon.*

B. Lateral view of the anterior limb of *Sigmodon,* with many of the superficial muscles removed.

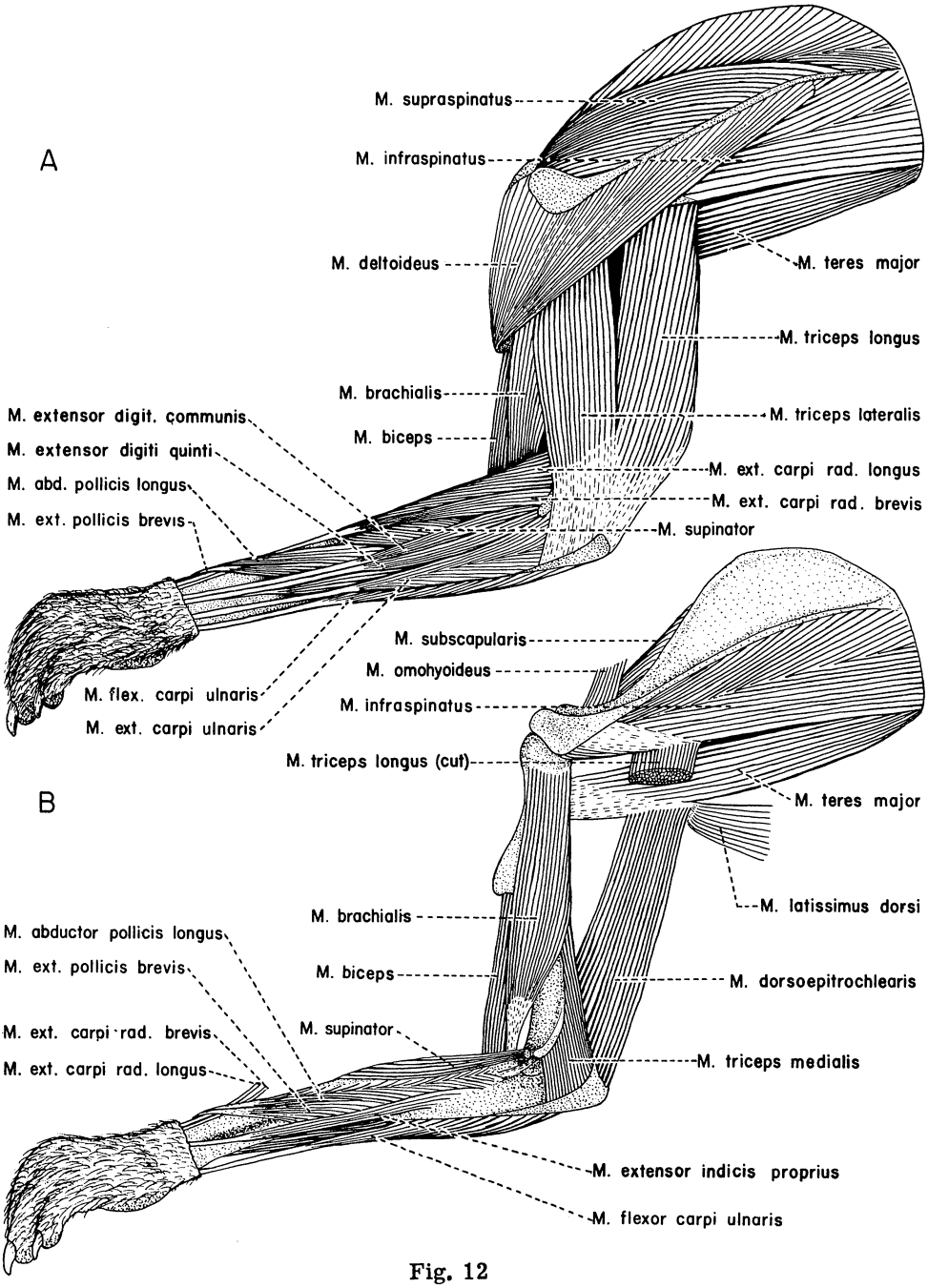

A
M. supraspinatus
M. infraspinatus
M. deltoideus
M. teres major
M. triceps longus
M. brachialis
M. triceps lateralis
M. extensor digit. communis
M. biceps
M. extensor digiti quinti
M. ext. carpi rad. longus
M. abd. pollicis longus
M. ext. carpi rad. brevis
M. ext. pollicis brevis
M. supinator
M. subscapularis
M. omohyoideus
M. infraspinatus
M. flex. carpi ulnaris
M. ext. carpi ulnaris
M. triceps longus (cut)
B
M. teres major
M. latissimus dorsi
M. brachialis
M. abductor pollicis longus
M. ext. pollicis brevis
M. biceps
M. dorsoepitrochlearis
M. ext. carpi rad. brevis
M. supinator
M. ext. carpi rad. longus
M. triceps medialis
M. extensor indicis proprius
M. flexor carpi ulnaris

Fig. 12

FIGURE 13

A. Medial view of the anterior limb of *Sigmodon.*

B. Medial view of the forearm of *Sigmodon*, with many of the more superficial muscles removed.

C. Sketch showing the manner in which the three heads of M. flexor digitorum profundus unite to form a common tendon in (1) *Sigmodon,* (2) *Neotoma.*

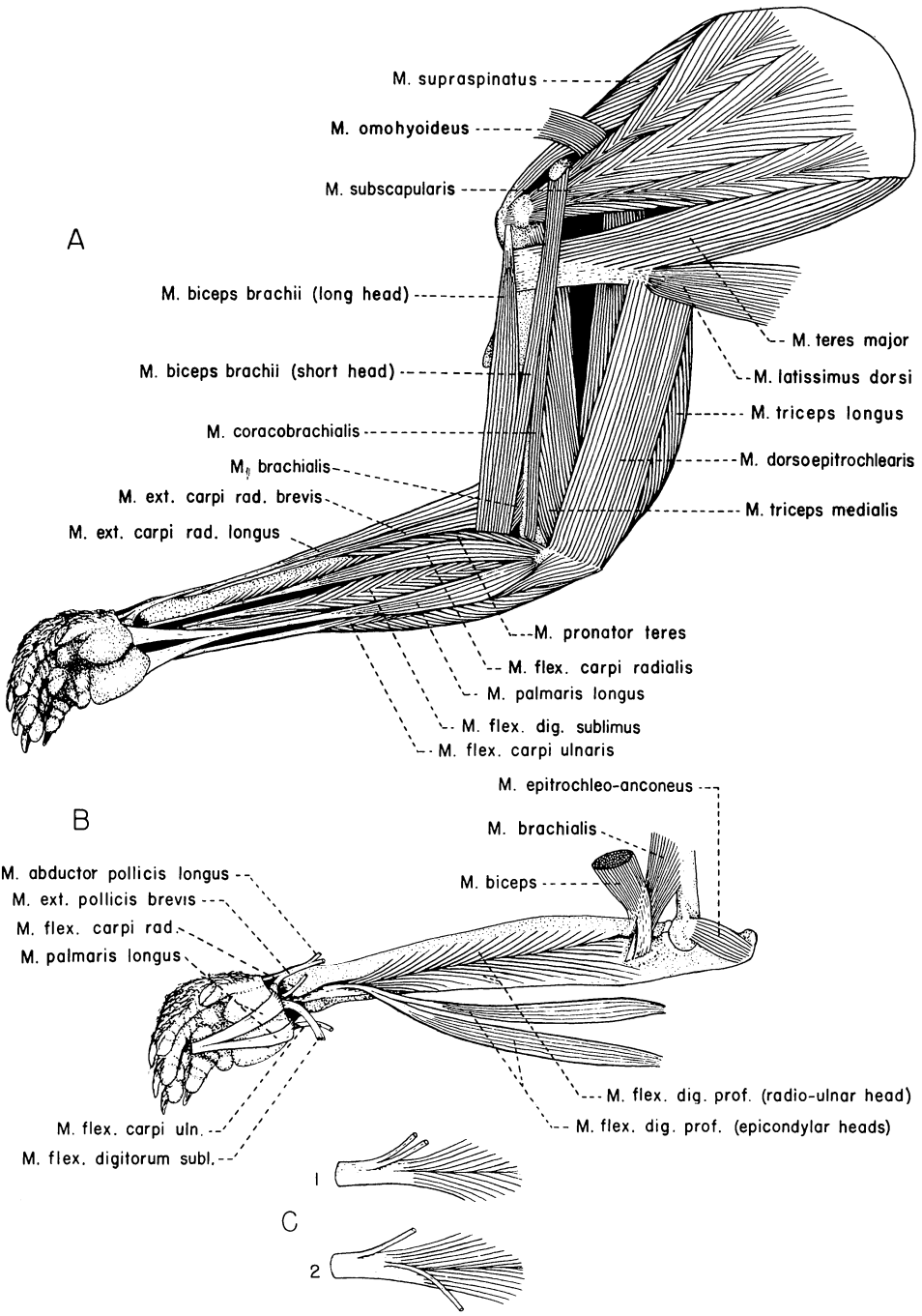

A
M. supraspinatus
M. omohyoideus
M. subscapularis
M. biceps brachii (long head)
M. biceps brachii (short head)
M. coracobrachialis
M. brachialis
M. ext. carpi rad. brevis
M. ext. carpi rad. longus
M. teres major
M. latissimus dorsi
M. triceps longus
M. dorsoepitrochlearis
M. triceps medialis
M. pronator teres
M. flex. carpi radialis
M. palmaris longus
M. flex. dig. sublimus
M. flex. carpi ulnaris
B
M. epitrochleo-anconeus
M. brachialis
M. biceps
M. abductor pollicis longus
M. ext. pollicis brevis
M. flex. carpi rad.
M. palmaris longus
M. flex. dig. prof. (radio-ulnar head)
M. flex. dig. prof. (epicondylar heads)
M. flex. carpi uln.
M. flex. digitorum subl.
C
1
2

Fig. 13

FIGURE 14

A. Sketch of left manus of *Sigmodon*, showing some of the more superficial structures.

B. Sketch of the left manus of *Sigmodon*, after removal of the tendon of M. palmaris longus.

C. Dissected view of the same, to show origins of some of the short flexor muscles.

D. The deep palmar muscles in *Sigmodon*.

E. The dorsum of the manus of *Sigmodon*, showing the relationships of the tendons.

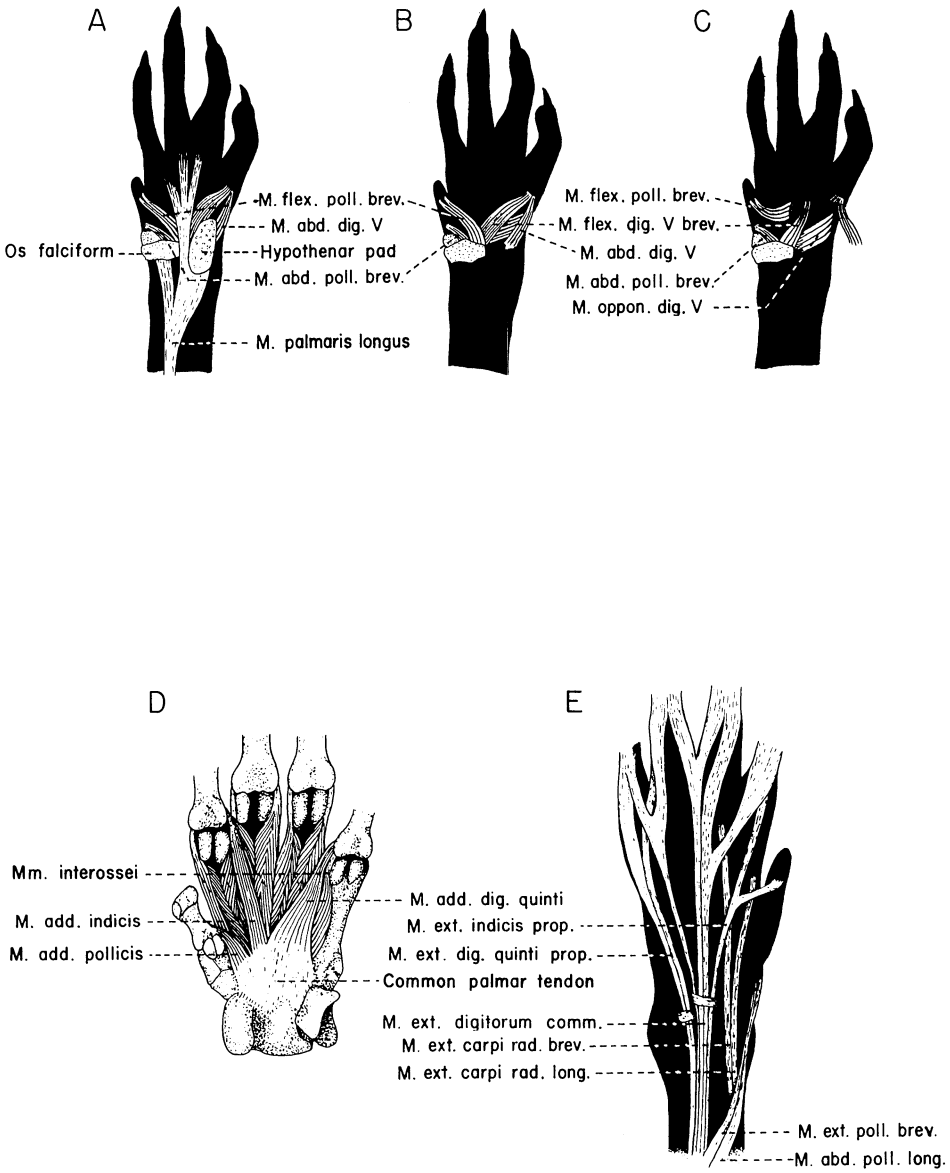

A
B
C
M. flex. poll. brev.
M. abd. dig. V
Os falciform
Hypothenar pad
M. abd. poll. brev.
M. palmaris longus
M. flex. poll. brev.
M. flex. dig. V brev.
M. abd. dig. V
M. abd. poll. brev.
M. oppon. dig. V
D
E
Mm. interossei
M. add. indicis
M. add. pollicis
M. add. dig. quinti
M. ext. indicis prop.
M. ext. dig. quinti prop.
Common palmar tendon
M. ext. digitorum comm.
M. ext. carpi rad. brev.
M. ext. carpi rad. long.
M. ext. poll. brev.
M. abd. poll. long.

Fig. 14

FIGURE 15

A, B, and C. Progressively deeper views of the lateral aspect of the posterior limb of *Sigmodon.*

D. Lateral view of the thigh of *Sciurus vulgaris* (level of dissection equivalent to B) showing the relationships of M. caudofemoralis? and M. presemimembranosus?

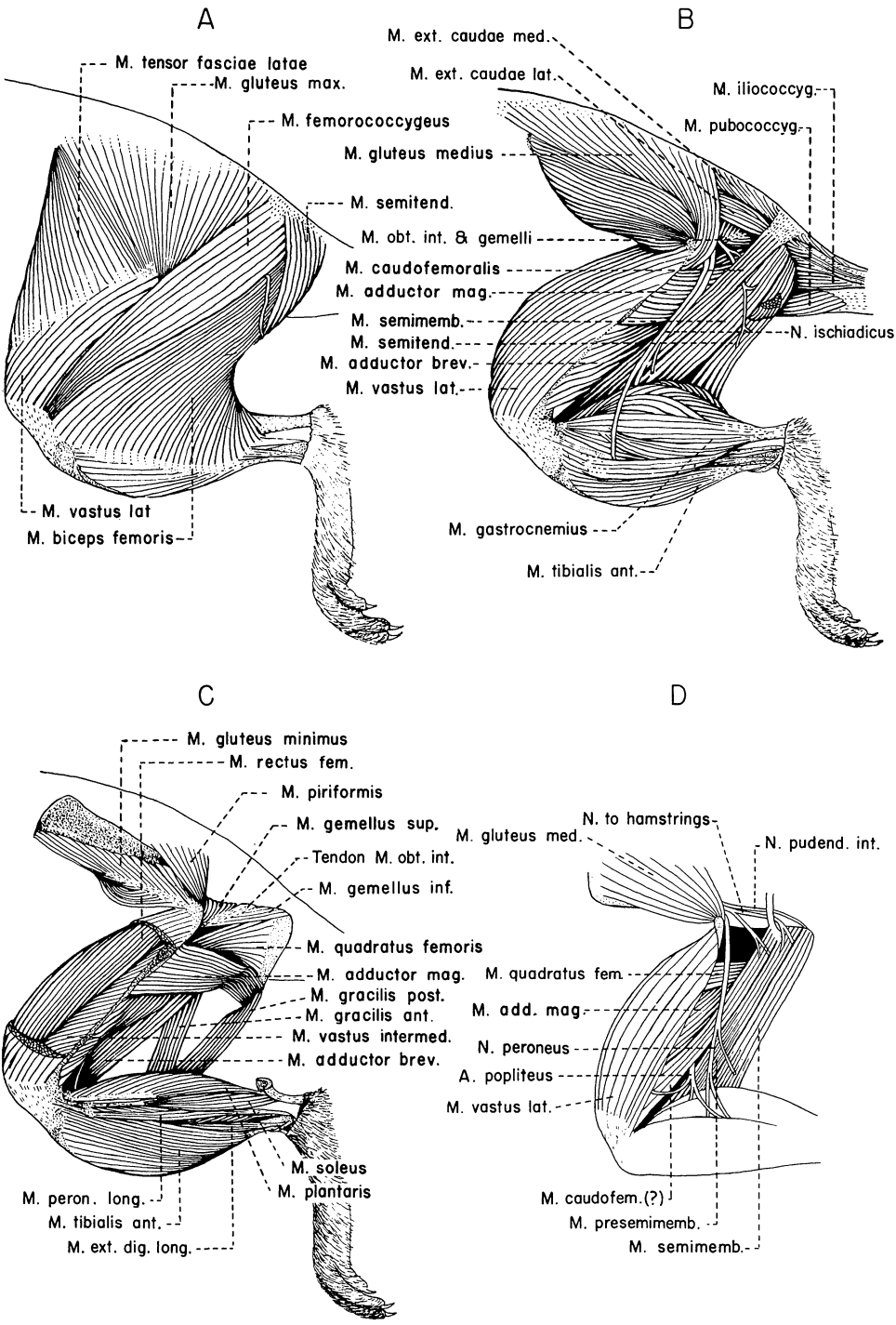

A
M. tensor fasciae latae
M. gluteus max.
M. femorococcygeus
M. gluteus medius
M. semitend.
M. obt. int. & gemelli
M. caudofemoralis
M. adductor mag.
M. semimemb.
M. semitend.
M. adductor brev.
M. vastus lat.
M. vastus lat
M. biceps femoris
B
M. ext. caudae med.
M. ext. caudae lat.
M. iliococcyg.
M. pubococcyg.
N. ischiadicus
M. gastrocnemius
M. tibialis ant.
C
M. gluteus minimus
M. rectus fem.
M. piriformis
M. gemellus sup.
Tendon M. obt. int.
M. gemellus inf.
M. quadratus femoris
M. adductor mag.
M. gracilis post.
M. gracilis ant.
M. vastus intermed.
M. adductor brev.
M. soleus
M. plantaris
M. peron. long.
M. tibialis ant.
M. ext. dig. long.
D
N. to hamstrings
M. gluteus med.
N. pudend. int.
M. quadratus fem.
M. add. mag.
N. peroneus
A. popliteus
M. vastus lat.
M. caudofem.(?)
M. presemimemb.
M. semimemb.

Fig. 15

FIGURE 16

A. Sketches showing the origin of M. rectus femoris in (1) *Sigmodon,* (2) *Neotoma*, (3) *Oryzomys,* and (4) *Peromyscus.*

B. Diagrammatic representation of cross sections through the posterior pelvic region of (1) *Mustela frenata*, (2) *Sciurus vulgaris*, (3) *Tamias striatus*, and (4) *Sigmodon hispidus.* Bones shown are the ischium, pubis, the first caudal vertebra, and the distal end of the femur. The nerve to the hamstring muscles is shown as a dot just lateral to the ischium. The circle on the femur represents the popliteal artery. For a discussion of the significance of these sketches, see page 104.

C. Medial aspect of the thigh of *Oryzomys.* Note in particular the relative development of M. gracilis posterior.

D. Medial aspect of the thigh and ventral lumbar region in *Sigmodon.*

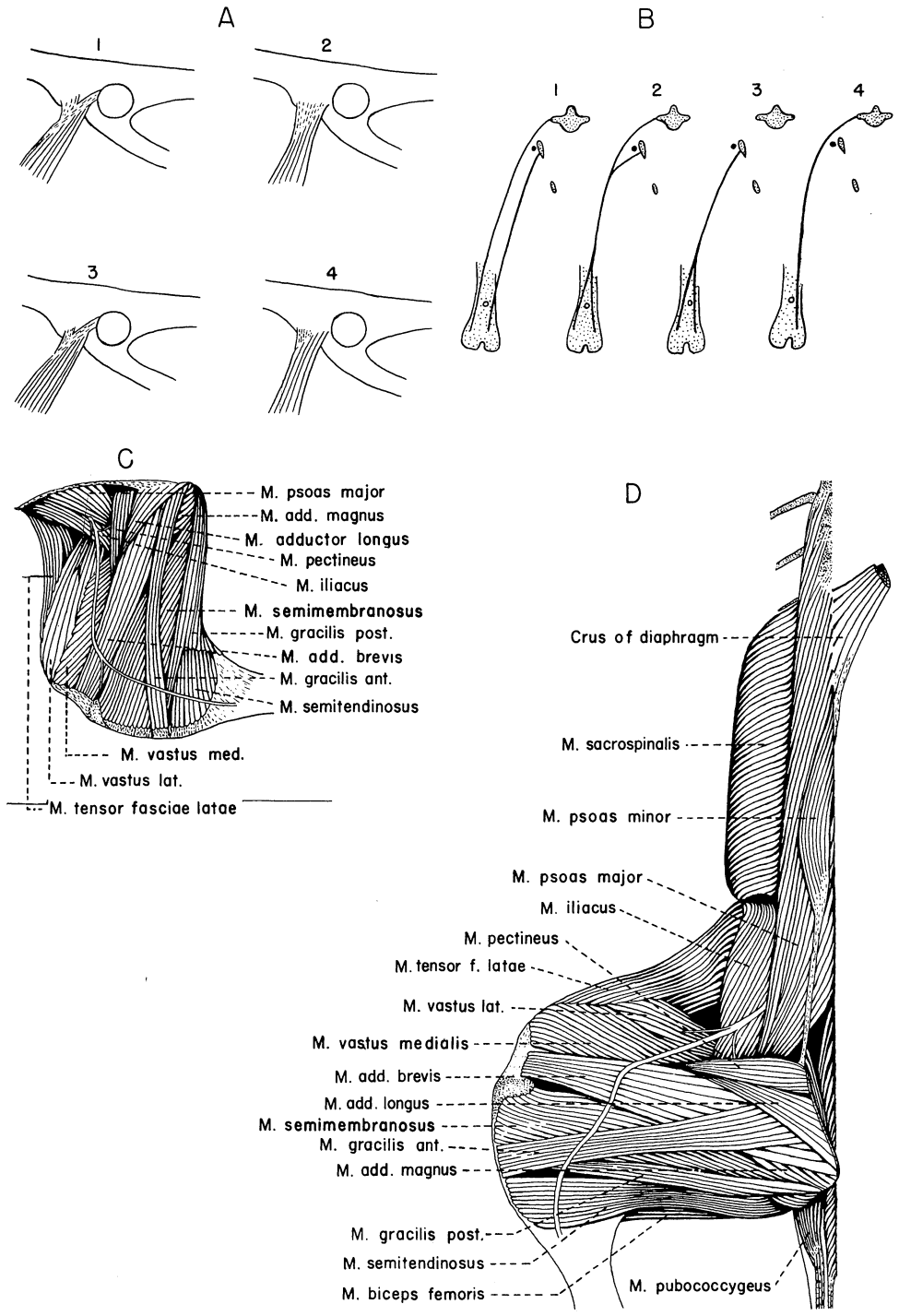

A
1
2
3
4
B
1
2
3
4
C
M. psoas major
M. add. magnus
M. adductor longus
M. pectineus
M. iliacus
M. semimembranosus
M. gracilis post.
M. add. brevis
M. gracilis ant.
M. semitendinosus
M. vastus med.
M. vastus lat.
M. tensor fasciae latae
D
Crus of diaphragm
M. sacrospinalis
M. psoas minor
M. psoas major
M. iliacus
M. pectineus
M. tensor f. latae
M. vastus lat.
M. vastus medialis
M. add. brevis
M. add. longus
M. semimembranosus
M. gracilis ant.
M. add. magnus
M. gracilis post.
M. semitendinosus
M. biceps femoris
M. pubococcygeus

Fig. 16

FIGURE 17

A. Medial view of the leg and foot of *Sigmodon*, with the superficial muscles of the flexor group of the leg removed.

B. Lateral view of leg and foot in *Sigmodon*.

C. The dorsum of the foot of *Sigmodon*, showing the relationships of the various tendons.

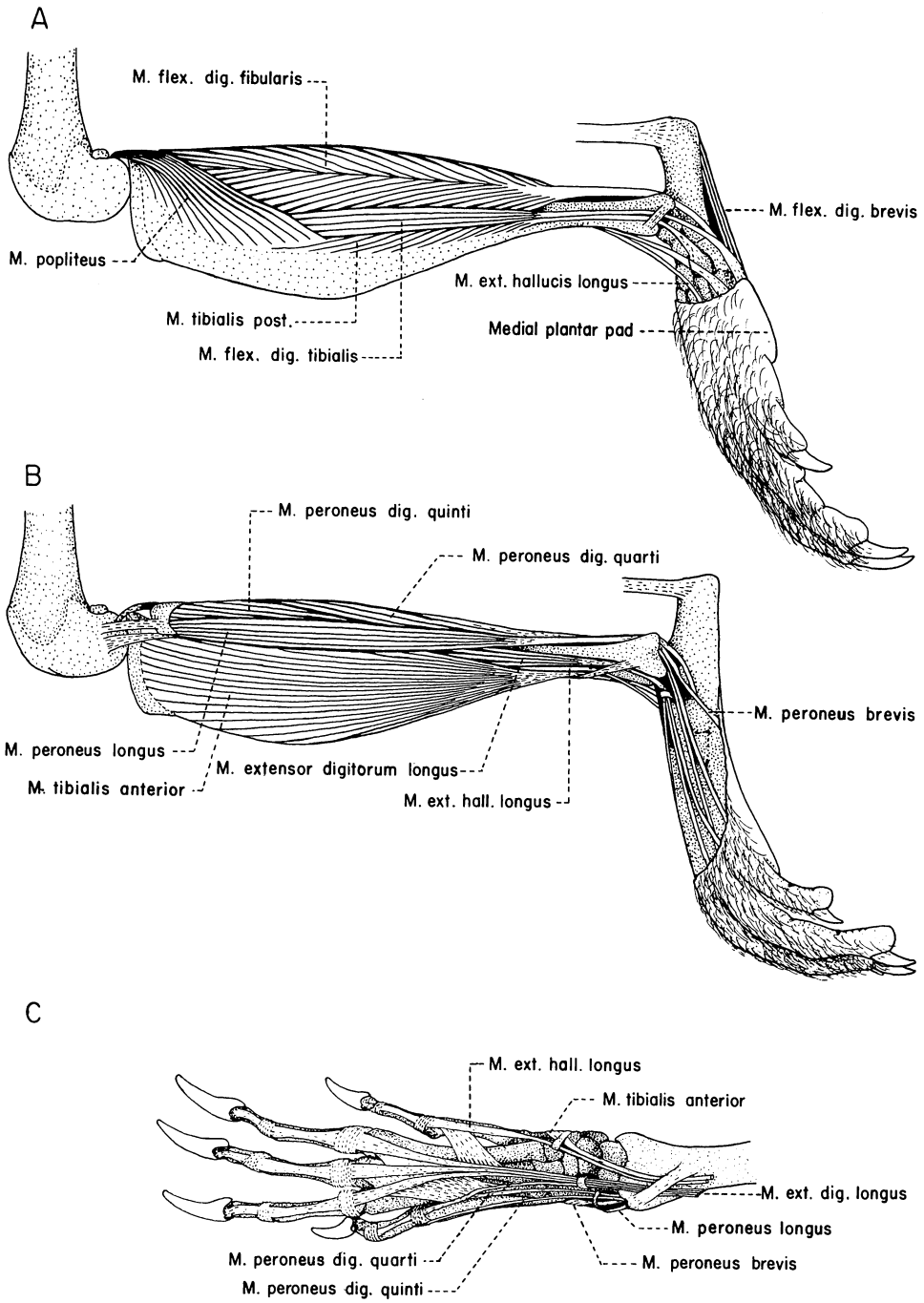

A
M. flex. dig. fibularis
M. flex. dig. brevis
M. popliteus
M. ext. hallucis longus
M. tibialis post.
Medial plantar pad
M. flex. dig. tibialis
B
M. peroneus dig. quinti
M. peroneus dig. quarti
M. peroneus brevis
M. peroneus longus
M. extensor digitorum longus
M. tibialis anterior
M. ext. hall. longus
C
M. ext. hall. longus
M. tibialis anterior
M. ext. dig. longus
M. peroneus longus
M. peroneus dig. quarti
M. peroneus brevis
M. peroneus dig. quinti

Fig. 17

FIGURE 18

A, B, C, and D. Views of the plantar aspect of the feet of *Peromyscus*, *Neotoma*, *Sigmodon*, and *Oryzomys*, respectively, showing the relationships of the tendons of M. flexor digitorum tibialis and M. plantaris. The tendon of M. flexor digitorum tibialis is the one which enters the plantar region from the side of the foot, on the right.

E. (1) Plantar, (2) dorsal, and (3) side views of the tendinous rings which surround the tendons of M. flexor digitorum fibularis and M. flexor digitorum profundus in the foot and hand in *Sigmodon* and receive the insertions of the tendons of M. flexor digitorum brevis (pes) and M. flexor digitorum sublimus (manus). (See page 110.)

F. Plantar aspect of the foot of *Sigmodon*.

G. Deeper view of the plantar aspect of the foot of *Sigmodon*.

H. The deep plantar muscles in *Sigmodon*.

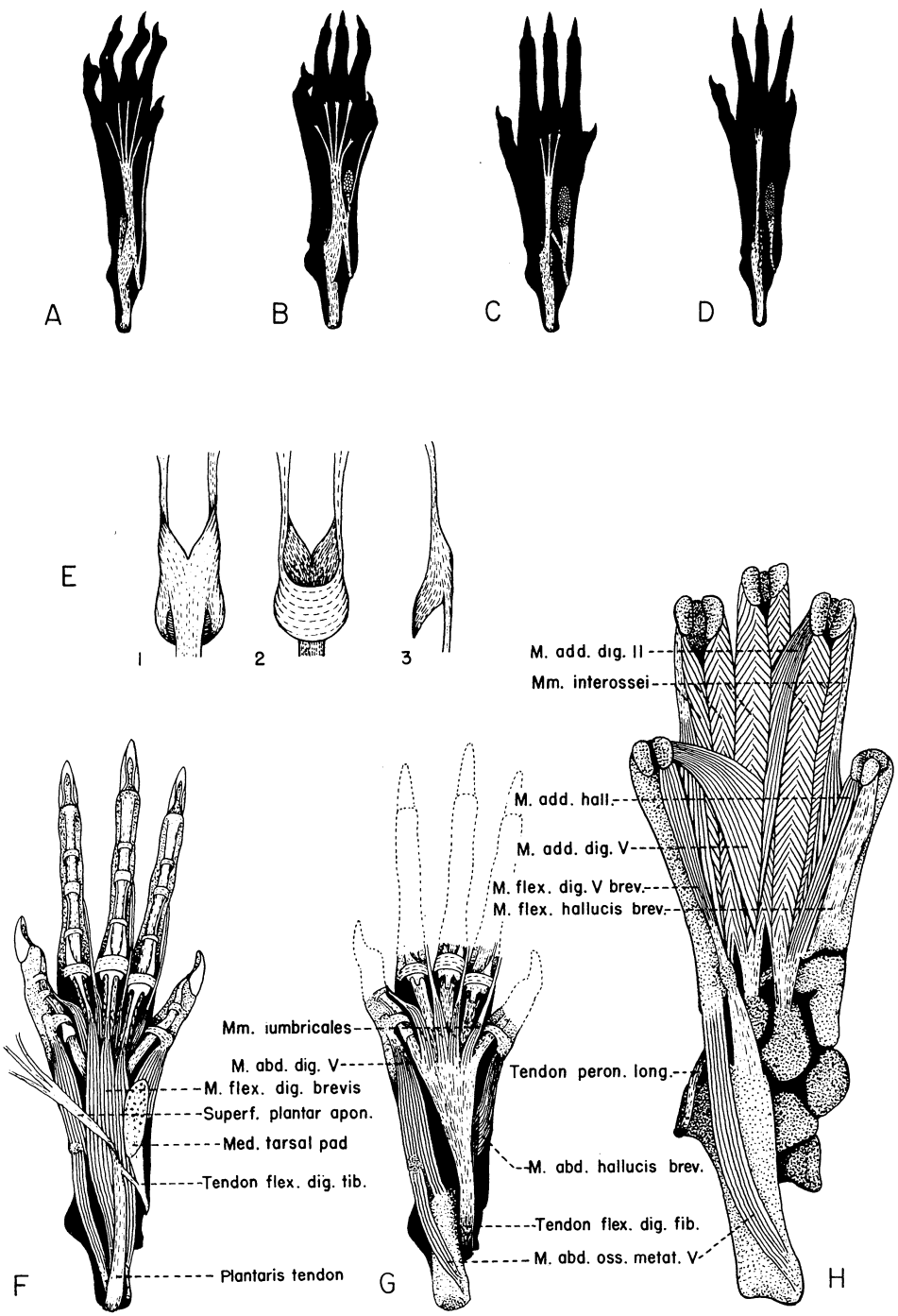

A
B
C
D
E
1
2
3
M. add. dig. II
Mm. interossei
M. add. hall.
M. add. dig. V
M. flex. dig. V brev.
M. flex. hallucis brev.
Mm. lumbricales
M. abd. dig. V
M. flex. dig. brevis
Superf. plantar apon.
Med. tarsal pad
Tendon flex. dig. tib.
Plantaris tendon
Tendon peron. long.
M. abd. hallucis brev.
Tendon flex. dig. fib.
M. abd. oss. metat. V
F
G
H

Fig. 18

(CONTINUED FROM INSIDE FRONT COVER)

No. 30. The Darters of the Genera Hololepis and Villora. By Carl L. Hubbs and Mott Dwight Cannon. (1935) Pp. 93, 3 plates, 1 figure $0.50
No. 31. Goniobasis of the Coosa River, Alabama. By Calvin Goodrich. (1936) Pp. 60, 1 plate, 1 figure $0.35
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