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COMPARATIVE MYOLOGY OF THE PECTORAL GIRDLE OF MICROTUS PENNSYLVANICUS AND PEDOMYS OCHROGASTER

by :

Marie Hagerman

A thesis presented to the Faculty of the School of Graduate Studies in partial fulfillment of the Degree of Master of Arts

> Western Michigan University Kalamazoo, Michigan July 1964

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Marie Hagerman

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INTRODUCTION

The meadow vole <u>Microtus pennsylvanicus</u> (Ord) and the prairie vole, <u>Pedomys ochrogaster</u> (Wagner) are two species of grassland-dwelling, slightly fossorial rodents which are very similar in appearance and general body size and proportions. The objective of this study was to prepare a detailed description of the muscles of the pectoral girdle of <u>M. pennsylvanicus</u> and to compare them to <u>P. ochrogaster</u>. It was hoped that the study might indicate similarities and dissimilarities in the ways in which the two species have adapted to their mode of life and show whether or not they share common adaptations of the pectoral girdle. Although the study is primarily morphological, it was hoped that the results might give some insight into the ecological and taxonomic relationships of the two species.

METHODS AND MATERIALS

Specimens dissected were preserved by various methods. In all cases, specimens were first injected and then kept in the preservative solution. For some of the specimens a ten per cent formaldehyde solution was used; however, it was necessary to drain these specimens and rinse them in water before dissections could be made. For others, an embalming fluid made of 1 part phenol, 2 parts glycerin, 0.4 part formalin, and 0.6 part 95% alcohol was used. With this embalming fluid, rinsing was unnecessary and preservation was satisfactory for the larger and the more superficial muscles but not for the very deep smaller muscles. Some specimens were tied in an extended position, when fresh, to copper screening in order to prevent contraction of the pectoral and ventral limb muscles while hardening. Radiographs were used in several instances where exact determination of the muscle attachment would have been otherwise impossible. All dissections were done under a binocular dissecting microscope using magnifications of 14X to 60X.

After several specimens of \underline{M} . $\underline{pennsylvanicus}$ had been dissected and a detailed description of that species had been written, similar dissections were made on \underline{P} . $\underline{ochrogaster}$. The individual muscles of \underline{M} . $\underline{pennsylvanicus}$ were then compared directly with the corresponding muscles of \underline{P} . $\underline{ochrogaster}$. In the following sections the muscles of \underline{M} . $\underline{pennsylvanicus}$ are the ones described, because specimens of this

species were available in greater quantity, and remarks are made upon the corresponding muscles of \underline{P} . $\underline{ochrogaster}$ when there is a qualitative difference.

The musculature of no two specimens, even within a species, was identical. Ontogenetic differences cause much variation in apparent size and strength of the muscles, as do the type of preservative used and the position in which the animal was fixed. Inasmuch as it is impossible to eliminate intraspecific quantitative differences, an interspecific comparison made on such a basis would be invalid. Differences and similarities of origin, insertion, and topographical relationships are usually dependable and are the basis of the present study.

In the following descriptions and comparisons of muscles, all observed variation is discussed.

Several published works on the anatomy of rodents were of particular use in conducting this study. Greene's (1935) The Anatomy of the Rat and Rinker's (1954) Comparative Myology of the Mammalian Genera <u>Sigmodon</u>, <u>Oryzomys</u>, <u>Neotoma</u>, and <u>Peromyscus</u> were the most important of these. Valuable information was obtained also from Parsons (1896), Howell (1926), Hill (1937) and Orcutt (1940).

In the following sections, muscles have been arranged as in most treatments of human myology. The arrangement follows closely that used by Greene. However, she did not consider certain muscles which attach to the scapula or clavicle as belonging to the pectoral girdle; these muscles are included in this study. The muscle groups are not

arranged according to homologous innervation because no attempt was made to determine innervation, nor on developmental data since little are available for these species.

The terminology used by Hill (1937) is followed here. He states:

The terminology used 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.

Specimens consisted of 12 Microtus pennsylvanicus pennsylvanicus, from Parchment, Kalamazoo County, Michigan; 4 Pedomys ochrogaster ochrogaster from near Lawrence, Douglas County, Kansas, and 3 from near Watervliet, Berrien County, Michigan. Not every specimen was completely dissected, some being used only for checking questionable relationships.

DISCUSSION OF SPECIES

Microtus pennsylvanicus and Pedomys ochrogaster are members of the order Rodentia, the suborder Myomorpha, the superfamily Muroidea, the family Cricetidae, the subfamily Microtinae and the tribe Microtini (Miller and Kellogg 1955).

Although very similar in general appearance, the two species show the following differences: M. pennsylvanicus has a longer tail (more than 38 mm. according to Burt 1954), 6 tubercles on the sole of the hind foot (5 in P. ochrogaster), silvery-tipped rather than yellow-tipped belly hairs, 8 mammae (6 in P. ochrogaster), and 5 or 6 enamel loops on the last upper molar against 4 for P. ochrogaster.

Additionally, M. pennsylvanicus has 46 chromosomes, and P. ochrogaster 54 (Anderson 1959). According to Burt (1954), in Michigan the weight of M. pennsylvanicus varies between 20-68.6 gm., while that of P. ochrogaster varies between 22-35.2 gm..

Voles of the genera <u>Microtus</u> and <u>Pedomys</u> are Holarctic in distribution; morphologically similar forms occur in Europe, Asia, Africa and North America. Voles are commonly found in the temperate and boreal zones, with many ranging north beyond the Arctic circle. Comparatively few species live in the tropical zones (Bailey 1924; Hooper 1949). <u>M. pennsylvanicus</u> is distributed throughout the northern part of North America. <u>P. ochrogaster</u> is limited to the midwestern states and the southern portion of midwestern Canada.

Voles are normally found in grassy regions and they are anatomically and habitually suited for such vegetation, inasmuch as they have prismatic teeth which are adapted to a bulky diet and make nests of grass and maintain open runways by bending and arching the grass. The kinds of grasses, weeds and debris present seems to be an important factor in the distribution of voles (Dice 1922; Blair 1940; Eadie 1953; Martin 1956).

M. pennsylvanicus is primarily a meadow dweller, seemingly preferring the lower damp areas with rank growths of grass (Hamilton 1937c; Burt 1954). P. ochrogaster, on the other hand, occurs in higher, drier, less dense prairie grasslands (Findley 1954; Martin 1956). When either species occurs by itself it is capable of occupying most available habitats including both wet and dry grasslands (Findley 1954; Martin 1956). When both species occur in an area, both remain in their optimum habitat (Schmidt 1931; Findley 1951; 1954).

Hamilton (1937c) concluded that the home range (as defined by Burt, 1943) of M. pennsylvanicus was about one-fifteenth of an acre. Blair (1940) found that the average size of home range for an adult female was from about one-fifth to one-fourth of an acre with no significant difference between the damper and drier grasslands. However, he did find that the average home range of the male was slightly less than one-third of an acre in wet grassland and slightly less than one-half of an acre in dry grassland. Martin (1956) studying populations of P. ochrogaster found the average male range to be

0.14 acre and the average female range to be 0.12 acre. There is, thus, some evidence that \underline{M} . pennsylvanicus tends to occupy a larger area than \underline{P} . ochrogaster, and that within each species males tend to have larger home ranges than females.

An area occupied by voles is readily recognized by its system of runways, underground tunnels and burrows. Runway systems enable the voles to cover their range without exposure to enemies, and Martin (1956) reports that "runways seemed to provide a sense of security and the voles were familiar with their range only through runway travel". The depth to which <u>P</u>. <u>ochrogaster</u> will burrow runways and place its nest apparently depends upon the condition of the soil (Martin 1956). Most underground tunnels are dug when the soil is moist (Jameson 1947).

Voles build nests of dry grasses, sedges and weeds (Bailey 1924; Hatt 1930). The nests are globular and the centrally located cavity is lined with soft fine grass (Hatt 1930). New nests are usually prepared a few days before a new litter arrives with the result that nesting places are changed about every twenty-one days (Bailey 1924).

M. pennsylvanicus tends to build its nest above the ground and P. ochrogaster below the ground in a burrow, but often the reverse is true.

Other ecological differences between the two voles that should be noted are these: (1) Females of M. pennsylvanicus are territorial in behavior (Getz 1961) whereas P. ochrogaster shows considerable overlapping of home ranges and does not exhibit territoriality (Martin 1956). (2) Although populations of both species have marked yearly

fluctuations only M. pennsylvanicus belongs to the so-called cyclic species (Hamilton 1937b; Christian 1950; Martin 1956). (3) Individuals of M. pennsylvanicus are for the most part antisocial while those of P. ochrogaster are compatible (Martin 1956). Getz (1962) in comparing the interspecific and intraspecific aggressive behavior between the two voles found that there was less interspecific aggressive behavior between P. ochrogaster and M. pennsylvanicus than intraspecific aggressive behavior in M. pennsylvanicus, and that P. ochrogaster is dominant to M. pennsylvanicus in regions where their ranges overlap. In view of the type of intraspecific aggressive behavior displayed by both species and the fact that P. ochrogaster is somewhat smaller than M. pennsylvanicus, the results of this study are unexpected. Getz did not feel that this dominance was developed well enough to entirely exclude M. pennsylvanicus from the drier areas. He suggested, citing the results from a separate unpublished study, that differences in water balance may be of more importance in separating the two species into diverse ecological niches with interspecific aggressive behavior adding weight to a predetermined physiological factor.

Males and females of both species are highly polygamous (Bailey 1924; Martin 1956). Females of both species mate with older males when twenty-five days old (Bailey 1924; Hamilton 1937a, 1949; Martin 1956). Males of M. pennsylvanicus become fecund at about forty-five days (Bailey 1924; Hamilton 1937a), those of P. ochrogaster from thirty-six to forty-five days (Jameson 1947; Martin 1956; Fitch 1957). The gestation period is twenty-one days. Postpartum

mating is usual in both species, and females will often produce several immediately consecutive litters (Bailey 1924; Hamilton 1940, 1949; Martin 1956). Litter size seems to vary geographically and seasonally, with four being the normal low and eight being the normal maximum for M. pennsylvanicus (Bailey 1924; Hamilton 1941; Goin 1943; Poiley 1949). Litter size for P. ochrogaster is less well known because this species seemingly will not breed in captivity (Fisher 1945; Martin 1956); however, the litter size apparently is significantly smaller than M. pennsylvanicus (Jameson 1947; Martin 1956). There is no known definite estrous cycle for voles, and reproductive activity is continuous throughout the year, the size of the litter varying from season to season (Blair 1940; Martin 1956; Fitch 1957).

Voles grow rapidly, most of the growth being made during the first two months after which the rate is slower and more variable (Selle 1928; Martin 1956; Fitch 1957).

RESULTS

Muscles Connecting the Pectoral Appendage to the Cranium

M. cleido-occipitalis: (M. clavotrapezius, Hyman 1942) (Fig. 1, 3, 4)

Form: rectangular, flat, twisted.

Position: on lateral surface of head and anterolateral surface

of neck. Anterior to M. acromiotrapezius; covering

origin of M. occipitoscapularis. Fibers originate

posterior to ear, immediately behind post-tympanic hook

of squamosal bone, they extend anteroventrad twisting

around lateral portion of head and neck bordering lateral

edge of M. sternomastoideus and partially covering

M. cleidomastoideus.

Origin: from posterior portion of ventral lambdoidal crest.

Insertion: onto middle third of medial border of clavicle.

M. sternomastoideus: (Fig. 3)

Form: flat, rectangular, twisted.

Position: on dorsolateral surface of cranium and lateral surface

of neck. Anteroventral to M. cleidonastoideus and

M. cleido-occipitalis. Fibers extend lateroventrad

bordering external auditory meatus to midventral sternum.

Origin: from ventral border of periotic capsule of cranium.

Insertion: onto cranial half of ventral surface of manubrium of

sternum and ventral surface of medial tip of clavicle.

M. cleidomastoideus: (Fig. 3)

Form: flat, rectangular, curved.

Position: on dorsolateral surface of cranium and lateral surface of

neck. Origin is immediately lateral to M. occipitoscapularis.

Deep to M. cleido-occipitalis, posterior to M. sterno-

mastoideus. Fibers extend lateroventrad curving around

neck to clavicle.

Origin: from anterior border of periotic capsule of cranium.

Insertion: onto medial surface of medial second fifth of clavicle.

M. occipitoscapularis: (Fig. 1, 2, 4)

Form: long, flat, rectangular, ribbon-like.

Position: on dorsal surface of head, neck and cephalic portion of

back; deep to M. acromiotrapezius; lateral to M. rhom-

boideus major and M. rhomboideus minor; fibers originate

deep to M. clavotrapezius, they extend posteromediad over

anterior border of scapula inserting above origin of

anterior portion of M. supraspinatus.

Origin: from lambdoidal ridge of cranium.

Insertion: onto vertebral border of scapula anterior to spine and

ento anterior surface of dorsal tip of spine of scapula.

Muscles Connecting the Pectoral Appendage to the Hyoid

M. omohyoideus: (Fig. 3, 4)

Form: long, ribbon-like, curved.

Position: on lateral portion of shoulder, and lateral and ventral

portion of neck. Deep to M. acromiotrapezius. Fibers extend from scapula between M. supraspinatus and M. subscapularis curving around neck beneath M. cleidocccipitalis, M. cleidomastoideus and M. sternomastoideus, respectively; passing under anterior portion of M. digastricus (posterior belly) and inserting beneath M. sternohyoideus.

Origin: from suprascapular notch of vertebral border of scapula.

Insertion: onto middle portion of body of hyoid.

Muscles Connecting the Pectoral Appendage to the Vertebral Column

M. acromiotrapezius: (Fig. 1, 4)

Form: flat, broad, triangular; thick on caudal edge, becoming progressively thinner craniad.

Position: covers posterior part of head, and dorsal surface of neck and shoulders; deep to M. platysma; anterior to M. spinotrapezius and M. spinodeltoideus. Fibers converge lateroventrad, passing beneath M. omocervicalis to form a broad flat tendon that extends over anterior portion of shoulder joint.

Origin: along dorsal midline, immediately posterior to linea nuchae; from processus spinosus of all cervical and first four thoracic vertebrae, and from supraspinous fascia.

Insertion: onto distal two-thirds of spine of scapula and lateral one-fourth of inner border of clavicle.

M. spinotrapezius: (Fig. 1, 2)

Form: in two discrete portions, flat; cephalic head, fusiform;

caudal head, long, narrow and straplike.

Position: immediately lateral to dorsal midline; deep to M. platysma;

cephalic portion is posterior to ${\tt M.}$ acromiotrapezius and

dorsal to M. spinodeltoideus; caudal portion is superior

to posterior portion of M. latissimus dorsi. Fibers of

cephalic portion converging lateroventrad and caudal fibers

converging anterolaterad, both joining common tendon.

Origin: cephalic portion, from processus spinosus of fourth to

eighth thoracic vertebrae; caudal portion, by an aponeurosis

from spines of last thoracic and first four lumbar

vertebrae and from lumbodorsal fascia covering M.

latissimus dorsi.

Insertion: by a tendon onto scapular spine and a weak slip onto

M. infraspinatus.

M. latissimus dorsi: (Fig. 1, 2, 3, 5)

Form: flat, curved, oblong.

Position: origin lateral to dorsal midline; deep to caudal portion

of M. spinotrapezius. Fibers extend anteriad and then

pass lateroventrad crossing the axillary region bordering

posterior margin of M. teres major to tendon that passes

immediately distal to that of M. teres major deep to

M. biceps brachii.

Origin: from spines of eighth to twelfth thoracic vertebrae and lumbodorsal fascia to approximately level of fourth lumbar vertebra.

Insertion: onto second fifth of medial surface of shaft of humerus.

Remarks: The point of insertion on the humerus was almost as variable as the number of specimens examined. In this case the cause of much intraspecific variation is probably caused by the movement of the origin of M. dorsoepitrochlearis from the humerus to the tendon of M. latissimus dorsi (Rinker 1954).

M. rhomboideus major: (Fig. 2, 4)

Form: flat, trapezoid-shaped.

Position: on anteromedial portion of neck and back, immediately lateral to dorsal midline. Deep to posterior border of M. acromiotrapezius; anterior to cephalic portion of M. spinotrapezius; posterior to M. rhomboideus minor.

Anterior fibers are superior and continuous with those of M. rhomboideus minor. Parallel fibers pass curving laterodorsoposteriad beneath cephalic portion of M. spinotrapezius.

Origin: from processus spinosus of fourth to seventh cervical and first to fourth thoracic vertebrae and posterior portion of ligamentum nuchae.

Insertion: onto posterior two-thirds of vertebral border of scapula.

M. rhomboideus minor: (Fig. 2, 4)

Form: flat, curved, trapezoid-shaped.

Position: on anteromedial portion of back and neck; deep to

M. acromiotrapezius; medial to M. occipitoscapularis;

anterior to M. rhomboideus major. Parallel fibers extend
curving dorsolateroposteriad; posterior fibers pass deep

anterior fibers superior to and continuous with those of

to and continuous with those of M. rhomboideus major;

M. levator scapulae.

Origin: from processus spinosus of first four cervical vertebrae and anterior portion of ligamentum nuchae.

Insertion: onto middle fifth of vertebral border of scapula.

M. levator scapulae: (Fig. 5)

Form: flat, rectangular.

Position: deep on lateral surface of neck, shoulder and dorsal thorax. Anterior to M. serratus anterior. Origin is deep to M. scalenus anterior; fibers extend, curving dorsoposteriad, beneath scapula and M. subscapularis to an insertion immediately anterior to and continuous with M. serratus anterior.

Origin: from processus spinosus of all cervical vertebrae.

Insertion: onto cephalic third of medial surface of vertebral border of scapula.

M. omocervicalis: (M. levator claviculae, Greene 1935; M. atlantoscapularis, Howell 1926) (Fig. 1, 3)

Form: long, flat, curved, ribbon-like.

Position: superficial, on anterolateral portion of shoulder.

Distal portion, above M. acromiotrapezius. Fibers extend anteromediad over anterior border of scapula curving around cervical vertebrae and passing deep to antero-

ventral surface of neck.

Origin: from metacromion process of scapula.

Insertion: onto ventral arch of atlas.

Muscles Connecting the Pectoral Appendage to the Thoracic Wall

M. pectoralis major: (divisible into two portions) (Fig. 3)

Cephalic (superficial) portion: (M. pectoantibrachialis, Hyman 1942)

Form: flat, narrow, straplike.

Position: on ventral surface of the second Fibers extend from median plane lateroventrad across chest and axillary region bordering medial margin of M. clavodeltoideus and the anterior margin of caudal portion of M. pectoral s major joining tendon that passes underneath posterior portion of this muscle and M. clavodeltoideus.

Origin: from ventral and lateral surfaces of anterior third of sternal manubrium.

Insertion: onto medial surface of deltoid tuberosity of humerus.

Caudal portion:

Form: flat, broad, triangular.

Position: on ventral surface of thorax; posterior to cephalic

portion of this muscle; slightly anterior to and above

caudal portion of M. pectoralis minor. Fibers extend

from midline lateroventrad across chest and axillary

region to tendon that borders that of M. clavodeltoideus.

Origin: from dorsal two-third's of sternal manubrium, from all

sternebrae (Greene 1935; Rinker 1954) and anterior tip

of xiphisternum.

Insertion: onto distal tip of deltoid tuberosity of humerus.

M. pectoralis minor: (divisible into two portions) (Fig. 3)
Cephalic portion (anterior):

Form: flat, long, rectangular.

Position: on ventral surface of thorax; immediately underneath

M. pectoralis major; anterior to caudal portion of M.

pectoralis minor; fibers pass lateroanteriad beneath

M. clavodeltoideus and clavicle to humerus and medial

surface of scapula.

Origin: from lateral and ventral surfaces of all sternebrae.

Insertion: by two slips, lateral slip onto anterior surface of
lesser tuberosity of humerus, medial and somewhat
stronger slip onto coracoid process of scapula, medial
margin of glenoid cavity and medial surface of scapula

immediately adjacent to glenoid cavity.

Caudal portion:

Form: flat, narrow, oblong.

Position: on ventral surface of thorax; posterior to cephalic portion of this muscle; anterior to M. pectoralis abdominalis; fibers pass lateroanteriad beneath M. pectoralis major and M. clavodeltoideus to join broad tendon which covers tendon of origin of M. biceps brachii.

Origin: from xiphisternum and anterolateral surface of xiphisternal cartilage.

Insertion: onto proximal portion of lateral line of humerus, immediately below medial border of greater tuberosity of humerus.

M. pectoralis abdominalis: (third portion of M. pectoralis minor, Greene 1935; M. xiphihumeralis, Hyman 1942) (Fig. 3)

Form: long, curved, ribbon-like.

Position: on surface of thorax, posterior to caudal portion of M. pectoralis minor; fibers pass lateroanteriad beneath caudal portion of M. pectoralis minor, M. pectoralis major and M. clavodeltoideus to insert deep to lateral slip of cephalic portion of M. pectoralis minor.

Origin: by aponeurosis from linea alba and fascia of M. obliquus abdominis.

Insertion: onto lesser tuberosity of humerus.

M. subclavius: (Fig. 3)

Form: short, cylindrical.

Position: on ventral thorax; deep to M. pectoralis major. Fibers originate close to junction of manubrium and first rib, passing lateroanterodorsad beneath clavicle and between articualtion of clavicle and humerus.

Origin: from ventral and anterior surfaces of first rib and cartilage connecting rib and manubrium.

Insertion: onto medial surface of distal half of clavicle by fleshy attachment and by tendon onto ligamentum coracohumerale.

Remarks: The origin in \underline{P} . ochrogaster is from the dorsal surface of cartilage of the first rib. Insertion is on the anterior surface of the lesser tuberosity of the humerus and the medial surface of the distal tip of the clavicle.

M. serratus anterior: (Fig. 4, 5)

Form: flat, broad, digitate.

Position: on ventral and lateral wall of thorax. Digitations from first to seventh ribs are beneath M. pectoralis major and minor and M. rectus abdominis, respectively; digitations from first to eighth or ninth ribs are under M. pectoralis abdominalis. Origin of digitations from first to fourth ribs are deep to M. scalenus; slips from M. scalenus pass between fourth and fifth and fifth and sixth digitations; slips from seventh to eighth or ninth ribs interdigitate with M. obliquus abdominis externus. Fibers extend laterodorsoanteriad passing beneath scapula and M. subscapularis to insertion that is immediately posterior to and continuous with that of M. levator scapulae.

Origin: by digitations from ventral surface of first to eighth and in some specimens ninth ribs.

Insertion: onto caudal two-thirds of medial surface of vertebral border of scapula.

Remarks: The origin in \underline{P} . $\underline{\text{ochrogaster}}$ is from the first to sixth and in some specimens seventh ribs.

M. rectus abdominis: (Fig. 5)

Form: broad on abdomen, narrowing at xiphisternum to long rectangle.

Position: on ventral surface of abdomen. Fibers originate by aponeurosis from beneath M. obliquus abdominis externus and pass craniolaterad beneath M. pectoralis abdominalis, M. pectoralis minor and M. pectoralis major, respectively, and above ventral digitations of M. serratus anterior to anteroventral portion of pectoral girdle.

Origin: from symphysis pubis and linea alba.

Insertion: onto lateral edge of manubrium sterni and medial third of posterior border of clavicle.

Muscles of the Shoulder

M. acromiobrachialis: (M. clavo-acromiodeltoideus, Rinker 1954; M. acromiodeltoideus, Greene 1935) (Fig. 1, 4)

Form: triangular.

Position: superficial; covers lateral portion of shoulder; dorsal to M. clavodeltoideus; ventral to M. acromiotrapezius and M. omocervicalis; anterior to M. spinodeltoideus.

Fibers converge laterodistad to tri-tendinous insertion.

Origin: from scapular spine, between metacromion and acromion processes.

Insertion: by three slips; anterior slip onto tendon of M.

pectoralis major; middle, and strongest slip onto humerus
just beyond distal border of deltoid tuberosity; the
posterior slip onto superficial fibers of M. triceps
brachii, caput lateralis.

Remarks: The form, position and origin are similar in P.

ochrogaster. The insertional relationships differ,
however, in that the middle slip in P. ochrogaster
inserts onto the lateral surface of the deltoid
tuberosity by a strong tendon which covers the insertion of M. spinodeltoideus. All insertions are
relatively weak in M. pennsylvanicus. Ten of the
specimens of M. pennsylvanicus had a separate deep
portion, a small definitive slip, that originated on the
lateral margin of the greater tuberosity of the humerus
just distal to the insertion of M. infraspinatus and
inserted on the proximal border of the deltoid
tuberosity.

M. clavodeltoideus: (clavo-acromiodeltoideus, Rinker 1954; acromiodeltoideus, Greene 1935) (Fig. 1, 3)

Form: thick, triangular.

Position: superficial; covers ventral portion of shoulder; ventral to M. acromiobrachialis; anterior to M. pectoralis

major. Fibers pass laterodistad and converge to tendinous insertion that covers tendon of M. pectoralis major (cephalic portion) and passes beneath the caudal portion of that muscle.

Origin: from lateral two thirds of anterior border of clavicle.

Insertion: onto medial surface of deltoid tuberosity of humerus.

M. spinodeltoideus: (Fig. 1)

Form: flat, long, triangular.

Position: superficial, occupying infraspinous fossa; arises immediately lateral to insertion of M. spinotrapezius; posterior to M. acromiotrapezius and superior to M. triceps brachii. Anterior fibers converge lateroventro-anteriad along spine of scapula converging distad to join posterior fibers in tendon which passes beneath M. acromiobrachialis.

Origin: from fascia of M. infraspinatus; directly from ventral portion of caudal surface of scapular spine between point of insertion of M. spinotrapezius and metacromion process.

Insertion: by two slips; proximal and stronger slip onto dorsolateral surface of deltoid tuberosity; distal slip onto surface of M. triceps brachii, caput lateralis.

Remarks: P. ochrogaster has in addition an aponeurotic origin from the posterior third of the vertebral border of the scapula that passes beneath M. spinotrapezius (cephalic portion).

M. subscapularis: (Fig. 5)

Form: thick, triangular.

Position: in subscapular fossa. Bordered anteriorly by M. supraspinatus, posteriorly by M. teres major and dorsally on vertebral border of scapula by tendons of M. levator scapulae and M. serratus anterior. M. subscapularis is divided into fairly equal halves, fibers of each half are separated into an inconstant number of unequal fascicles; fibers of each fascicle extend lateroventrad, some inserting onto adjacent fascicles; majority of fibers converging across shoulder joint to join strong tendon.

Origin: from anterior and axillary scapular borders and by fleshy attachment from subscapular fossa.

Insertion: onto posterior border of lesser tuberosity.

M. supraspinatus: (Fig. 2, 4, 5)

Form: long, triangular, thick, in two discrete portions.

Position: fills supraspinous fossa of scapula, deep to M.

acromiotrapezius and M. occipitoscapularis. Cranial

portion passes over articulation of scapula with humerus

and beneath clavicle; major part of caudal portion joins

cephalic portion at junction of tendon and muscle fibers;

tendon converges anterolateroventrad passing beneath

M. clavodeltoideus.

Origin: cephalic portion from vertebral border of scapula anterior to spine, dorsal fourth of anterior margin of

spine, anterior border of scapula, and surface of supraspinous fossa. Caudal portion from ventral three-fourths of anterior margin of scapular spine.

Insertion: cephalic portion onto anterior margin of greater tuberosity of humerus. Caudal portion onto cephalic portion at junction of tendon and muscle fibers and fascia between two portions.

M. infraspinatus: (Fig. 1, 2, 4)

Form: triangular, thick, in two discrete portions.

Position: in infraspinous fossa of scapula; deep to M. spino-trapezius and M. spinodeltoideus. Fibers of both portions converge lateroventrad joining common tendon that passes beneath M. acromiobrachialis and over M. triceps brachii, caput longum and caput lateralis; insertion immediately proximal to M. teres minor.

Origin: cephalic portion from posterior surface of scapular spine by fleshy attachment, from anterior third of vertebral border of scapula posterior to spine and from infraspinous fossa, some fibers also derived from medial surface of M. spinodeltoideus. Caudal portion from middle third of vertebral border of scapula posterior to spine, from infraspinous fossa and from dorsal two-thirds of axillary border of scapula.

Insertion: onto lateral margin of greater tuberosity of humerus.

M. teres major: (Fig. 1, 2, 4, 5)

Form: long, cylindrical.

Position: at axillary border of scapula; posterior to M. spinodeltoideus, M. infraspinatus and M. teres minor; anterior
to M. latissimus dorsi; covered in part by M. spinotrapezius. Fibers converge lateroanteroventrad passing
beneath M. biceps brachii to tendinous insertion in
common with that of M. latissimus dorsi.

Origin: from posterior tip of vertebral border of scapula and proximal two-thirds of axillary border of scapula and from fascia of M. subscapularis.

Insertion: onto second fifth of medial surface of shaft of humerus.

M. teres minor: (Fig. 4)

Form: triangular.

Position: in infraspinous fossa of scapula; deep to M. infraspinatus; anterior to M. teres major; fibers converge lateroventrad passing beneath M. acromiobrachialis and above M. triceps brachii, caput longum and caput lateralis. Insertion is immediately distal to that of M. infraspinatus.

Origin: from distal third of axillary border of scapula and from aponeurosis arising from sheath of connective tissue which envelops M. infraspinatus and M. teres minor.

Insertion: onto lateral margin of greater tuberosity of humerus.

Remarks:

M. teres minor appears to be somewhat stronger in \underline{P} . $\underline{\text{ochrogaster}}$ since its origin is more extensive, coming from the distal two-thirds of the axillary border of the scapula. However, there is a good deal of intraspecific variation in the topography of this muscle.

Muscles of the Brachium

M. coracobrachialis: (Fig. 3)

Form: rectangular.

Position: deep, on medial surface of humerus; anterior to medial

border of M. triceps brachii, caput medialis; posterior

to M. biceps brachii, caput longum. Fibers originate

from tendon in common with that of M. biceps brachii,

caput breve, and after passing along proximal fourth of

shaft of humerus, they separate from M. biceps brachii

and continue deep to M. biceps brachii, caput breve.

Origin: from coracoid process of scapula by tendon in common

with M. biceps brachii, caput breve.

Insertion: onto distal half of medial surface of humerus.

M. biceps brachii: (Fig. 1, 2, 3)

Form: spindle shaped, thick, consists of two heads.

Position: on anteromedial surface of humerus and anterior surface

of elbow joint; medial to M. triceps brachii, caput

lateralis; anterior to M. dorsoepitrochlearis. Fibers

arise deep to M. pectoralis major and M. pectoralis

minor. Caput longum of M. biceps brachii is anterior

to caput breve. Fibers of caput breve originate and pass in common with those of M. coracobrachialis along proximal fourth of shaft of humerus, where they separate and continue superior to M. coracobrachialis to distal fourth of humerus where they join fibers of caput longum and extend along with M. brachialis between M. extensor carpi radialis longus and M. pronator teres to antibrachium where insertional tendon splits.

Origin: caput breve, from coracoid process of scapula by a tendon common to M. coracobrachialis; caput longum from dorsoanterior lip of glenoid cavity.

Insertion: by two slips; onto brachial ridge of ulna and onto tuberositas radii of radius.

M. brachialis: (Fig. 2, 4)

Form: elongate, curving, spindle-shaped.

Position: on lateral surface of brachium and anterior surface of elbow joint; deep to M. triceps brachii, caput lateralis.

From origin beneath M. spinodeltoideus and M. acromiobrachialis on posterolateral surface of proximal portion of humerus, fibers twist as they extend distad, attaching to lateral surface of deltoid tuberosity; fibers converge at elbow joint joining tendon which passes lateral to and along with that of M. biceps brachii across elbow joint and then between bifurcating tendon of M. biceps brachii.

Origin: from lateral and posterior portion of anatomical neck of humerus; in addition, some fibers are derived from deltoid ridge of humerus.

Insertion: onto anteromedial surface of ulna just distal to coronoid process.

M. triceps brachii: (Fig. 1, 2, 3)

Form: thick, quadrangular, in three discrete heads.

Position: caput longum, on lateral, posterior and medial surfaces of brachium; bordered by caput lateralis on lateral surface and M. dorso-epitrochlearis on medial surface.

Proximal lateral portion of caput longum is beneath M. spinodeltoideus, M. infraspinatus and M. teres minor.

Medial fibers originate immediately lateral to posterior border of M. subscapularis, pass distad over M. teres major and M. latissimus dorsi and then deep to M. dorsoepitrochlearis to tendinous insertion on antibrachium.

Caput lateralis on lateral surface of shaft of humerus; anterior to caput longum; lateral to biceps brachii and M. brachialis; fibers originate immediately distal to insertion of M. infraspinatus and M. teres minor passing distad beneath M. spinodeltoideus and M. acromiobrachialis, attaching to lateral surface of deltoid tuberosity from which some fibers are derived and then continue to join common tendon.

Caput medialis, on posterior, lateral and medial surfaces of shaft of humerus; deep to caput longum of M. triceps brachii, posterior to M. brachialis on lateral surface and M. coracobrachialis on medial surface. Fibers extend over posterior surface of elbow joint to common tendon.

Origin: caput longum, from ventral third of axillary border of scapula with some fibers being derived from aponeurosis of M. teres minor. Caput lateralis, from proximal third of deltoid crest and lateral surface of deltoid tuberosity of humerus. Caput medialis, from distal two-thirds of posterior surface and from distal third of lateral and medial surfaces of shaft of humerus.

Insertion: onto olecranon process of ulna by a strong tendon which extends into fascia of antibrachium.

M. dorsoepitrochlearis: (Rinker 1954; M. epitrochleoanconeus, Greene 1935; M. epitrochlearis, Howell 1926) (Fig. 3)

Form: flat, thin, rectangular.

Position: superficial, on dorsomedial surface of brachium; covers ventromedial aspect of M. triceps brachii, caput longum; posterior to M. biceps brachii, caput breve. Fibers pass distad, crossing elbow joint.

Origin: from ventral border of M. latissimus dorsi at junction of muscle and tendon.

Insertion: onto medioposterior surface of olecranon process of

ulna; in some cases there is a slip which extends onto forearm and inserts onto M. extensor digiti quinti.

<u>M</u>. <u>anconeus:</u> (Greene 1935; Rinker 1954; not same as Howell 1926) (Fig. 2)

Form: triangular.

Position: on lateral surface of elbow joint; deep to M. triceps brachii, caput lateralis; anterior to M. triceps brachii, caput medialis. Fibers pass posteroventrad, crossing elbow joint.

Origin: from lateral epicondyle of humerus.

Insertion: onto lateral surface of olecranon process of ulna.

M. epitrochleoanconeus: (Rinker 1954; M. anconeus, Howell 1926; not same as M. epitrochleoanconeus, Greene 1935) (Fig. 3)

Form: spindle-shaped.

Position: on ventromedial surface of elbow joint; deep to M.

dorsoepitrochlearis; anterior to medial border of tendon

of insertion of M. triceps brachii; dorsal to insertional

tendon of M. coracobrachialis. Fibers pass posteroventrad

and insert just distal to insertion of M. triceps

brachii.

Origin: from medial epicondyle of humerus.

Insertion: onto medial surface of olecranon process of ulna.

DISCUSSION AND CONCLUSIONS

Voles are habitually only slightly fossorial and this fact is reflected in the anatomy of their pectoral girdle, in that the muscles have only slightly thicker and more extensive attachments than the rat, a morphologically generalized muroid. The most obvious difference is the separation of the deltoid into three and in some cases four muscles in contrast to two in the rat.

Individual variation existed and seemed similar in the two species. M. latissimus dorsi, M. serratus anterior and the shoulder muscles showed the greatest amount of individual variation. Variation between right and left sides of the same animal seemed negligible. M. pennsylvanicus and P. ochrogaster approach one another quite closely in the myology of their pectoral girdles. Similar myological relationships in the two species were found in twenty-eight of the thirty-three muscles examined. Differences were as follows:

- (1) M. subclavius: origin and insertion are more extensive in M. pennsylvanicus.
- (2) M. serratus anterior: origin is more extensive in \underline{M} . pennsylvanicus.
- (3) M. acromiobrachialis: insertion of this muscle is relatively weak in M. pennsylvanicus but strong in P. ochrogaster. Most of the specimens of M. pennsylvanicus had a separate, definitive deep portion, lacking in P. ochrogaster.

- (4) M. spinodeltoideus: in addition to originating from the fascia of the infraspinatus and the scapular spine, this muscle in P. ochrogaster has an aponeurotic origin from the posterior third of the vertebral border of the scapula.
- (5) M. teres minor: P. ochrogaster has a more extensive and stronger origin.

With the exception of M. subclavius, all of these points of difference between the two species are in the shoulder musculature. The total effect of the differences appears to be a slight tendency toward greater power and less speed in P. ochrogaster compared with M. pennsylvanicus; this tendency is in harmony with the somewhat more fossorial habits of the former species. Even so, fossorial adaptation is so slight that this study supports the view of Campbell (1938) that digging is due to "behavior pattern alone."

Taxonomically, characters of the teeth have long been used as the main clues to relationships among the Microtinae (Hooper and Hart 1962), but a variety of workers have added evidence giving weight to Howell's (1926) view that the teeth are not necessarily the major criterion to be used in judging the Microtinae taxonomically (Hooper and Hart 1962). For example, Hamilton (1946) and Dearden (1958) concluded that classification of the subfamily Microtinae would be very different from what it is currently if based on the affinities of the baculum. They found that M.

pennsylvanicus exhibited a marked difference from P. ochrogaster which showed a structural affinity to Pitymys pinetorum (Bailey).

Hooper and Hart (1962) combining the results of their work on the morphology of the glans penis of North American microtines with previous studies consider Pitymys and Pedomys to be so closely related that they "should be arranged as subgenera of the one genus, Pitymys" or that they, combined with M. mexicanus and M. fulviventer should be listed within the subgenus Pitymys of the genus Microtus.

The authors also state that evidence from their studies indicates that pennsylvanicus along with its allies montanus, townsendi, longicaudus, californicus, oeconomus and oregoni should fit into the one subgenus Microtus, oeconomus and oregoni should fit into the one subgenus Microtus. On the other hand, Simpson (1945) following Hinton (1926) maintained the genus Pitymys as a separate taxon but combined Pedomys with Microtus. The generic and specific nomenclature used in this study has been that of Miller and Kellogg (1955). They place Microtus pennsylvanicus, Pedomys ochrogaster and Pitymys pinetorum in separate genera.

The results of this study appear to support the view of a close relationship between M. pennsylvanicus and P. ochrogaster.

It is clear, however, that until more information is available on the total range of inter-specific variation in the pectoral myology of the Microtinae, no firm conclusion is possible. Further dissections, especially of such critical species as Pitymys pinetorum, are necessary before pectoral myology can become a useful systematic trait for the group.

SUMMARY

A detailed study of the pectoral myology of the meadow vole $\underline{\mathbf{M}}$. $\underline{\mathbf{pennsylvanicus}}$ (Ord) was prepared and the results compared to the corresponding muscles of $\underline{\mathbf{P}}$. $\underline{\mathbf{ochrogaster}}$ (Wagner). Differences and similarities of origin, insertion, and topographical relationships were the characteristics studied.

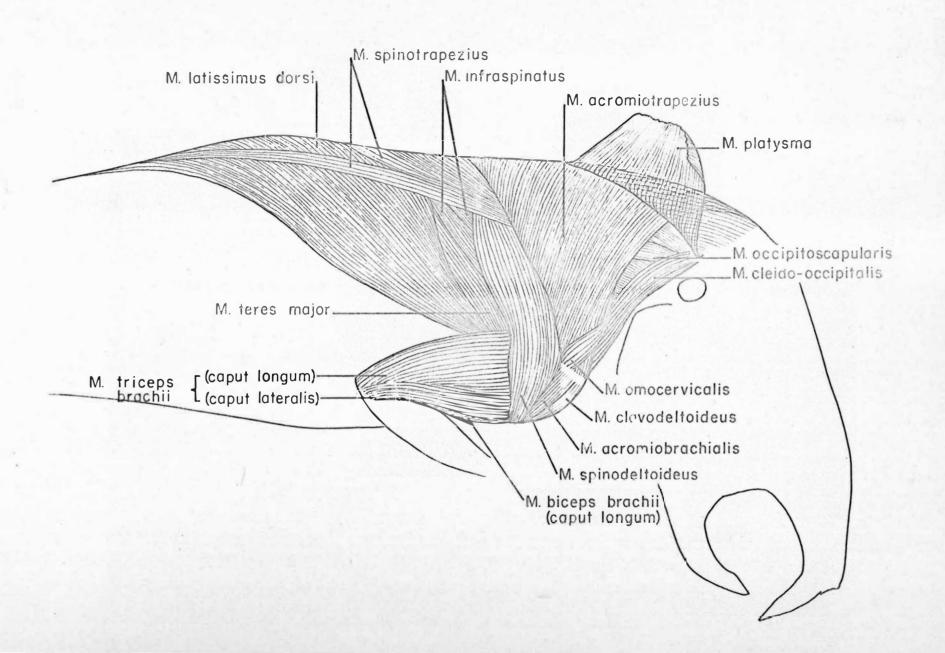
The myological relationships of the pectoral girdle of \underline{M} .

<u>pennsylvanicus</u> and \underline{P} . <u>ochrogaster</u> are very similar. Twenty-eight of the thirty-three muscles studied have common relationships; only five have significant differences.

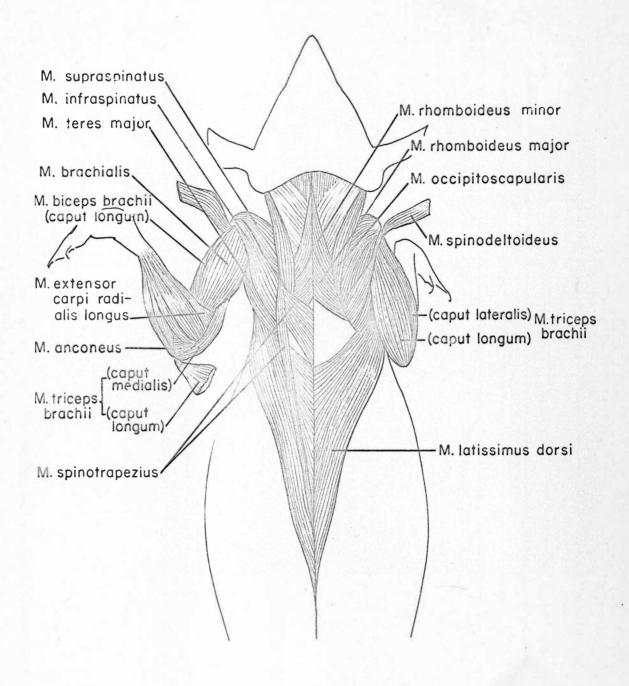
The two species show only slight adaptations towards fossoriality. Knowledge of the myology of the pectoral girdle of the other allied forms is necessary for definite conclusions regarding the relative taxonomic positions of the two species.

APPENDIX

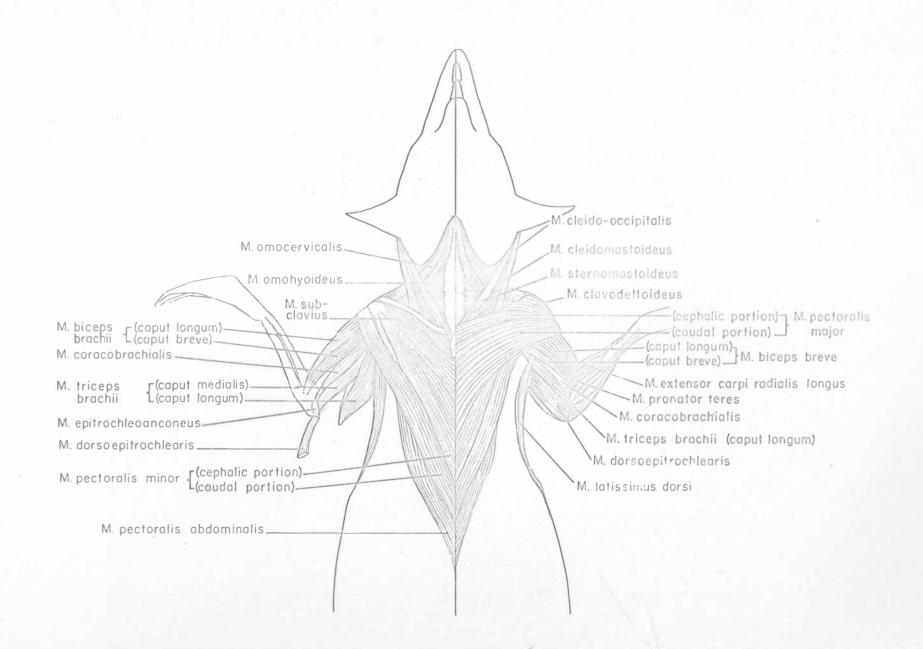
Lateral view of the superficial muscles in \underline{M} . pennsylvanicus.



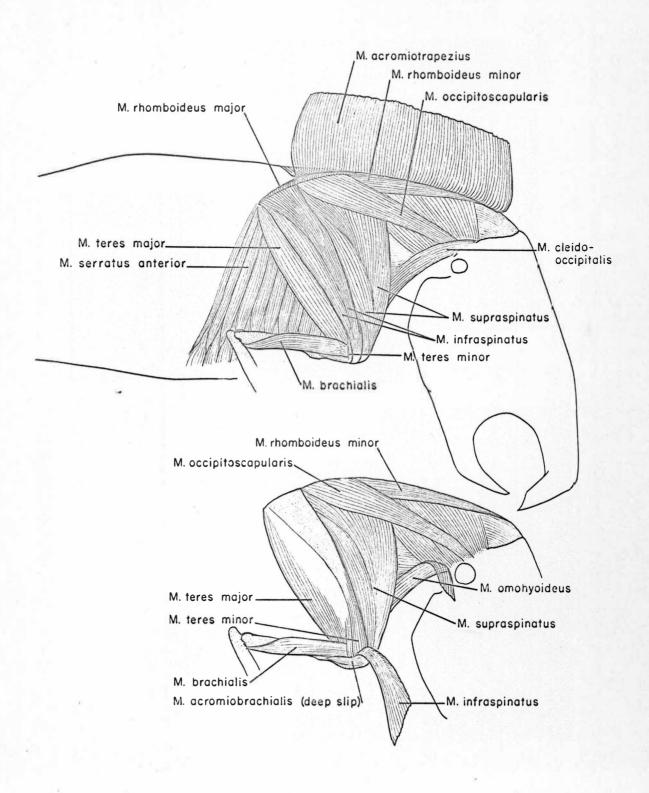
Dorsal view of the anterior part of the body of \underline{M} . pennsylvanicus.



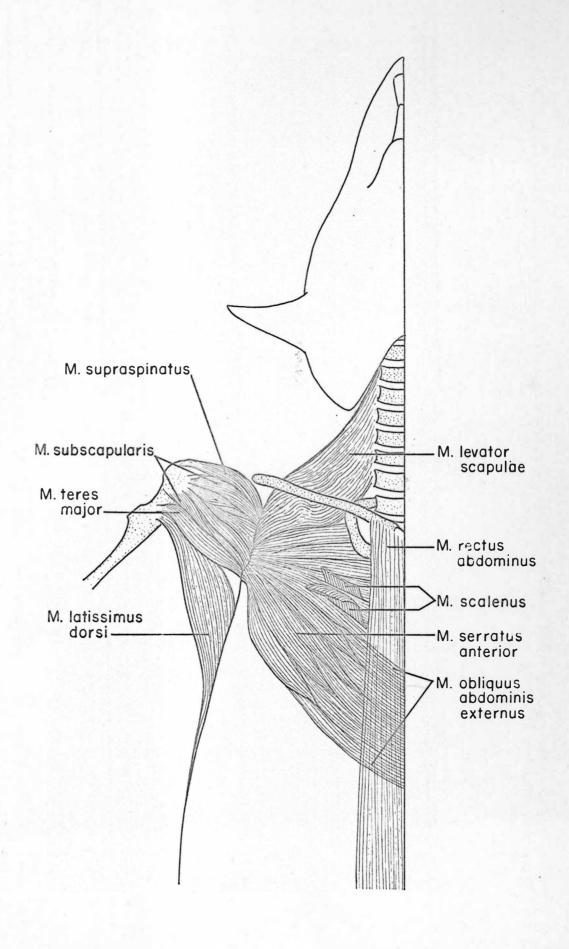
Ventral view of anterior half of \underline{M} . pennsylvanicus.



Lateral view of \underline{M} . pennsylvanicus, showing deep muscles of the shoulder.



Ventral view of $\underline{\mathbb{M}}$. pennsylvanicus, showing the deep muscles of the pectoral girdle.



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