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Skeletal and Muscular Adaptations to a Subterranean Environment of *Microtus oregoni serpens*

(Mammalia - Rodentia)

by

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Abstract.

This study was undertaken primarily to ~~discover~~ examine the skeletal and muscular anatomy of a small species of field mouse, *Microtus oregoni serpens* Merriam, which inhabits the Puget Sound area of British Columbia and Washington. This species is largely subterranean in its habits and in an attempt to discern the degree of specialization for its habitat comparison was made between *serpens* and *Microtus townsendi townsendi*, (Bachman) and *Microtus longicauda vellerosa*, (Allen) species which burrow to a limited degree only. A detailed comparison of the external features, skeletal and muscular anatomy of the three species was made and a juvenile specimen of *Microtus richardsoni richardsoni*, (De Kay) was used for some comparisons. Certain parts of *Microtus oregoni serpens* were found to be strongly modified in a direction which seems to better adapt the animal to its subterranean mode of life. The external features which are of adaptive significance are the soft plush-like pelage, the short tail and the arrangement of the vibrissae the longest ones being furthest from the snout rather than scattered. The eyes are only about one-half the size of those of the larger species and associated with them is an interesting modification of the orbicularis oculi muscle whereby it is strongly ~~modified~~ developed doubtless as an aid in preventing dirt from entering the eyes.

Microtus oregoni serpens does not have conspicuously enlarged or elongated fore-feet but among the modifications for digging which do occur are the shortening of the limbs and the inclusion of a larger part of them within the body skin. Almost the entire musculature of the anterior segment of the body is more stongly developed in *serpens* including the muscles of the shoulder, chest, and fore-limbs and to some extent the masticatory musculature and the musculature of the spinal column. The

muscles attached to the pectoral girdle show the most marked modifications, they are almost universally better-developed in serpens than in townsendi or longicauda. Correlated with a greater development of the pectoralis muscles is the development of a keel on the manubrium sterni and the sternebrae in serpens, providing a larger area for muscle attachments.

Microtus oregoni serpens seems to represent one of the earliest stages of adaptive specialization of a mammal for subterranean life externally approaching the condition found in specialized burrowers such as the mole but having no radical skeletal modifications.

Introduction.

Microtus oregoni serpens Merriam, is a small species of field mouse inhabiting the Puget Sound region of British Columbia and Washington. It is largely subterranean in its habits, excavating a maze of small burrows fairly close to the surface. This study has been concerned primarily with the skeletal and muscular anatomy of this mouse. In an attempt to discern the degree of specialization for its subterranean habitat, comparison has been made between serpens and Microtus townsendi townsendi (Bachman), a species living a less fossorial existence, and Microtus longicaudus vellerosus (Allen), a species which burrows to a very limited degree only.

A juvenile specimen of Microtus richardsoni richardsoni (De Kay) was used for certain comparisons and a description of the external features of one specimen Microtus pennsylvanicus drummondi (Audubon and Bachman) is included.

The muscles are grouped according to a plan described by Howell (1936) and modified by Hill (1937). In general the innervation of the muscles was not investigated in the present study. For comparison of the muscles the terms used are largely those of Howell (1926). The bones were described according to the plan used by Hill (1937) and comparisons are given where variations occur.

The muscle and bone dissections of serpens were done three times and many of the muscles were checked in a fourth specimen; the muscles and bones of townsendi and longicauda were dissected in one specimen only of each species but as very few variations occur between the two latter species other than those of size and tail structure the two dissections served, in some measure, to check each other. The specimen of richardsoni was a juvenile and, in consequence, was of but limited use for comparative purposes.

An attempt has been made to correlate the muscle and skeletal variations and to relate them to functions of the muscles and, ~~if~~ where possible, also, to the habits of the species.

External Features

Microtus oregoni serpens is a small-sized rodent with an elongate, slightly fusiform body. The head is relatively small but its general shape is also elongate. A slight cervical constriction is present. The skin is tight all over the body and the pelage is fine, soft, and thick with a velvety texture not found in townsendi or longicaudus. Scattered guard hairs occur over the surface of the body.

The tactile vibrissae vary in length from very long on the outer margins to short in the region of the rhinarium but the majority of the bristles are intermediate between these two extremes. There are no distinct interramal and carpal vibrissae but there are a few bristles present on the radial side of the first digits, though never enough to be termed a tuft. Similar scattered bristles occur on the hind feet. Eyelashes are absent.

There are four pairs of mammae, two pectoral and two inguinal.

The two halves of the upper lip meet below the rhinarium to form a very short philtrum. The lobes of the lower lip fuse but the lip is free for some distance. The nearly-naked rhinarium is triangular in shape with the apex directed ventrally. The external nares open laterally and have their margins wrinkled and scroll-like. An internarial groove is present.

The small, weak-looking eyes bear vestigial nictitating membranes and are provided with small lachrymal glands.

The ears average 12 mm. in the long axis and are oval in shape. The anterior portion of the helix is folded and the antihelix forms a ridge margining the conchal cavity. The external ear is almost completely naked with a few scattered hairs on its surface. (~~Average of 5 specimens.~~)

The tail is very much shorter than the body having an average (of 5) measurement of 18 mm. for specimens with an average body length of 131 mm.

The fore and hind limbs are slender, the proximal parts of both limbs are included in the body skin down to the level of the distal ends of the humerus and femur. The front feet are small and delicate and possess spade-shaped claws which are approximately 2 mm. in length.

The pollex is separated from the other digits, is not opposable, and lacks a nail ending, instead, with a horny tip. All the digits are short and the metacarpal elements are about equal in length to the digits, thus the manus as a whole is fairly long and slender. The volar surface is covered with a horny rugose skin bearing five plantar tubercles. The two carpal pads are large, the thenar pad covers most of the falciform bone. There is no distinct "heel" on the fore-foot.

The hind feet are less specialized. The second, third and fourth digits are longer than the other two, the fifth digit being the smallest. The claws are not very long and are concave resembling an overgrown human finger nail. Microtines are plantigrade and the feet are not greatly elongated. The plantar surface bears a series of five warty tubercles consisting of plantar, apical and interdigital pads and a metatarsal pad which is represented by the thenar pad at the base of the hallux.

Comparison of the External Features.

The relative proportions of certain external features of serpens, townsendii, longicauda, and drummondi are shown in the following table.

Name	N	Total Length	Length of Tail	Length of Head	Length of Hind Limb	Length of Fore-limb
serpens	18	131 mm.	32 mm.	32 mm.	18 mm.	14.5 mm.
townsendii	16	176 mm.	55 mm.	35 mm.	26 mm.	18 mm.
longicauda	20	185 mm.	62 mm.	35.mm.	23 mm.	20 mm.
drummondi	14	155 mm.	40 mm.	44 mm.	21 mm.	15 mm.

The measurements of total length, length of tail, and of hind limb are the average of measurements taken from a large number of specimens.

Microtus serpens and drummondi are alike in that they possess rather slender feet as compared to the relatively stout feet of townsendii, longicauda and richardsoni. The pollex is without a nail in all cases, in serpens and townsendii it ends in a hard tip and the other species lack a true pollex the latter being represented by a slight elevation. None of the species possesses an opposable pollex. As regards claw structure, none of the species examined is provided with conspicuously long or heavy claws of the type found on the fore-feet of many burrowing animals. However, those of serpens and drummondi are relatively much more slender than are those of townsendi and longicauda. The volar surfaces of the feet are harder and rougher in serpens and townsendi than in the other species in which it appears to be relatively smooth.

Apical pads are present in all species as also are interdigital pads between digits three and four and carpal pads.

The hind feet are less specialized in all five species. The second, third, and fourth digits are always the longest. The claws are short on all species except *longicauda* in which they are long, sharp and decidedly curved. The foot is definitely lengthened in all of the species. The plantar surfaces are always bare but those of *serpens* and *longicauda* are less scutellate being hard and roughened. The plantar pads are small in *serpens* and *drummondi* and longer in the other species. The hind feet of *serpens* and *townsendi* are most alike, *longicauda* has an extra plantar pad.

Considerable variation of length, general shape, scutellation and hairiness is found in the tails of the four species. The tails of *serpens* *drummondi* are similar in length but not in texture the latter being covered with~~out~~ distinct scales similar to those found on the tail of *townsendi*. *Longicauda* has the longest and most bushy tail in contrast to *serpens* which has the shortest. The latter feature may be advantageous to an animal which lives underground.

Considerable variation is exhibited with regard to looseness of skin and amount of pelage. *Serpens* and *richardsoni* have tight skins, *longicauda* has a slightly looser and *townsendi* a still looser skin which is still, however, much tighter than that of *drummondi*. The skins seem to be looser on the terrestial forms.

The pelage of *serpens* is fine, soft, and velvety, in the terrestial forms it is heavier, thicker, and longer although that of *drummondi* is fairly thin. *Richardsoni* has the most dense hair, it is very heavy on the dorsal side and finer on the underside.

The tactile vibrissae are distinct in *serpens*, the majority of the hairs being of medium length with the longest ones laterally placed. *Drummondi* has fewer and shorter bristles and *townsendi* has a much larger percentage of long hairs which are scattered. In *richardsoni* and *longicauda* the majority of the vibrissae are long and the longest ones seem to be more medially placed. Scattered guard hairs occur in all of the species. Eye-lashes are absent in serpens and townsendi but there are a few present in richardsoni, drummondi, and longicauda along the dorsal margin of the eye.

The structure of the nares and rhinarium in serpens seems to present some adaptive specialization. In this species the nostrils have crenulated margins while those of townsendi and longicauda bear three or four deep grooves on the lateral surfaces, and those of drummondi and richardsoni are smooth. There is a deep internarial groove in serpens while this is indifferently developed in the other species.

Serpens has the smallest eyes while those of the other species are larger and in townsendi and longicauda are twice the size of those of serpens.

The ears of serpens appear to be of intermediate size, measuring the same length as those of the much larger longicauda. Those of drummondi and richardsoni are similar in size but larger. Considered in percent of total length the ears are seen to be of similar size in all of the species. The pinnae are oval in serpens and longicauda and more rounded in the other species. The anterior part of the helix is folded in each case but this is most noticeable in serpens where it may have an adaptive value for subterranean life.

Skeletal System

Vertebral Column-

The vertebral column consists of seven cervical, thirteen thoracic, seven lumbar, and five sacral vertebrae. The number of caudal vertebrae varies from seventeen to nineteen. The angle between the cervical and thoracic segments in *serpens* is approximately 100° and the thoracic segment is strongly arched; the latter character being much more marked in *serpens* than it is in *townsendi*, *longicauda*, or *richardsoni*. This angle was measured in *townsendi* as approximately 80°.

Cervical Vertebrae-

The cervical vertebrae represent approximately 12½% of the presacral length and approximately 14% of the thoracolumbar length. In prepared specimens they appear to be dove-tailed together and almost co-ossified.

Atlas-

The atlas is oval in shape with the transverse axis the longer, the ventral arch being shorter. The wings are large in proportion to the size of the body of the atlas and are roughened as tubercular. The cranial articulating surfaces are large and shallow. No dorsal spine is present in any of the species. There is a difference in size between the atlas of *serpens* and *townsendi* or *longicauda* the latter being slightly larger than would be expected on the basis of relative size.

There is a general tendency to flattening in the cervical vertebrae of all the species but this is least evident in *longicauda*.

Axis- (Epistropheus)

The dens of the axis is fairly long and ovoid. The cranial articulating facets are triangular and convex. The spine is at a 30^{o} angle with the vertical and is relatively large, i.e., compared to the size of the axis. The vertebral foramen is large and almost circular and the centrum slightly concave dorsally. The transverse process is well-developed and not merely represented by a v-shaped arch such as Hill describes for *Thomomys* (1937). In *longicauda* and *townsendi* the transverse processes are less well-developed and are better described as elevations than as true processes.

Vertebrae 3 - 7-

The other cervical vertebrae are much alike but become progressively more slender posteriorly. The bodies of the vertebrae are elongate in the transverse axis and shorter in the other two axes but the foramen is always more circular than ovoid so the degree of elongation cannot be very great. The cranial articulating surfaces are concave and the caudal surfaces are convex. The spinous processes should probably be considered to be absent. The transverse processes are directed laterally throughout. The dorsal and ventral tubercles on the transverse processes are poorly differentiated.

There are no true differences between the cervical vertebrae of *serpens* and *townsendi*. No spines are found on the dorsal arches in either species. The transverse processes are never branched. In *longicauda* the vertebrae are more flattened in the vertebral axis making the transverse foramen more ovoid than it is in *serpens* or *townsendi*. The articular processes are more definitely distinguishable in *longicauda*, i.e., they project craniad to a greater degree. There is also a slight spine present on the dorsal arch of the fifth, sixth, and seventh vertebrae and the bodies of vertebrae are more ovoid in this species.

Thoracic Vertebrae-

The thoracolumbar region contains twenty vertebrae, thirteen thoracics and seven lumbars. The first two are very similar to the cervicals and the others become progressively larger, the most caudal ones being almost twice as long as the cervicals. The vertebral foramina become smaller caudally while the spinous processes increase in height in the same direction progressively. The spines all incline slightly caudad with the angle of inclination becoming greater in the more caudal vertebrae.

Both dorsal and ventral elements of the transverse processes are developed, the former serve for muscle attachment and the latter articulate with the ribs. The dorsal elements may be indistinctly divided into metapophyses and diapophyses in the eleventh thoracic segment. The articulating surfaces are similar to those found in the cervical vertebrae.

In all three species the thoracic vertebrae show the same general tendencies of the foramina to decrease in size in the more caudal vertebrae and of the spines to become more elongated and caudally directed. Dorsal and ventral elements of the transverse processes are found in all of the species. The same tendency toward flattening, found in the cervical vertebrae of longicauda, is found here. The variations found are less specific in the thoracic vertebrae than in the cervicals but the differences are not great in either case.

Lumbar Vertebrae-

The lumbar vertebrae in serpens are stouter and nearly twice as long as the thoracics. An inconspicuous medial ridge is present on each vertebra. The vertebral foramina become decreasingly smaller toward the end of the lumbar series and the spinous processes become very slightly increased in height posteriorly. The articulating surfaces are like those of the thoracics. Diapophyses are present on all of the lumbars although they are poorly developed in the first few.

This series is similar in each of the species. The mammillary processes are more distinct in townsendi and longicauda. As few muscle variations occur in this area few variations in the vertebrae are likely to have occurred.

Sacral Vertebrae-

Five sacral vertebrae were found in all specimens of serpens dissected and according to Hill (1937) five is the usual number in Microtones. The vertebrae, but not the spinous processes, appear to be fused. The first sacral vertebra is similar in size to the last lumbar, the other four become progressively smaller. The vertebral canal is small and the spines are higher than those in the lumbar region. The cranial articular surfaces are like those of the lumbars, cranial and caudal articular processes are vestigial. The ilium is joined to the first sacral vertebra.

No variations other than ones of size were found.

Caudal Vertebrae-

Seventeen to nineteen caudal vertebrae may occur. They become progressively smaller posteriorly. The vertebral canal is incomplete but there are wide vestigial spines present. Cranial articulating processes are absent or minute and caudal articulating processes are absent. Chevron bones are present between the vertebrae but they do not form arches.

There are many more caudal vertebrae present in townsendi and longicauda than in serpens but as some of the vertebrae were undoubtedly lost in the cleaning of the bones counts are useless. Serpens has short caudal vertebrae which become progressively shorter and less well-developed posteriorly. Townsendi has more robust vertebrae which are still relatively short and show the same tendency to decrease in size. The metapophyses, spinous processes and zygopophyses are better-developed in townsendi than in serpens but the development of these features is decidedly greatest in longicauda; the spine being much more obvious and enlarged. There is less tendency for the vertebrae to become shorter posteriorly in the latter species, instead they become more delicate while remaining approximately the same length.

Sternum-

The sternum of serpens consists of a manubrium, four similar sternebrae, and a xiphisternum. There is no evidence of intercalary bones. A slight keel is present and serves to increase the area of attachment of the pectoral muscles which are particularly heavy in this species.

In longicauda and townsendi the manubrium and the sternebrae have flat dorsal surfaces, i.e., the keel is missing suggesting a correlation with the development of the pectoral muscles.

Manubrium-

The manubrium sterni is almost heart-shaped; with a well-developed jugular notch, a wide anterior surface, a caudally-directed apex, and smooth, sloping sides. Clavicular facets are present on the anterior surface at the angle of the jugular notch and there is a roughened pit for the first costal cartilage on the lateral margin just below the enlarged anterior portion. The second costal cartilage is attached at the junction of the manubrium and the first sternebra.

The manubrium is elongate in townsendi and longicauda but it does not possess the heart-shaped anterior end found in serpens. The facets which show the position of the clavicular and costal cartilages are located in approximately the same position in all of the species.

Sternebrae-

In serpens the four sternebrae are alike in shape but they become progressively smaller posteriorly. They are all definitely keeled.

In townsendi and longicauda there is the same tendency to decrease in size but there is no sign of a keel.

Xiphisternum-

The xiphisternum is elongate, slender, and continuous caudally with a large heart-shaped cartilage. It forms a very slight angle with the last sternebra and is directed caudally.

In longicauda and townsendi the xiphisternum is more attenuate and delicate.

Ribs-

There are thirteen ribs in serpens all of them double-headed but the last. The capitulum articulates with the centrum and the tuberculum with the transverse process. The heads tend to become united on the more posterior ribs. The first rib is much shorter and somewhat stouter than the others. All of the ribs bear costal cartilages, those of the first seven reaching the sternum and that of the eighth being united to the seventh. No interspecific variations in the ribs were noted.

Skulls-

The skulls of serpens, townsendi and longicauda are very similar, any differences which do occur being very slight.

The skull of serpens is broader in proportion to its total length, the width being 49% of the length as compared to 44% in townsendi and longicauda, and the greater width occurs in the parietal bones rather than in greater curvature of the zygomatic arch.

Dorsal View-

The nasal bone is relatively shorter in serpens, being 27% of total length of the skull as compared to 31% in townsendi and 29% in longicauda. The surfacesof the nasal bones are ridged slightly in serpens but smooth in the other species. The frontal bones become very narrow in the central part of their length in each case, this is less evident in longicauda than it is in the other species. The parietals are almost square and are large in all species. The interparietal is rectangular with the vertical axis shorter. The lines of suture of the zygomatic arch are indistinct. The lambdoidal crest is more distinct in townsendi and longicauda than it is in serpens.

As a positive indication of muscle attachment there are slight processes just ventral to the cranio-ventral border of the infraorbital foramen from which the masseter superficialis originates, this process is decidedly better-developed in serpens than it is in the other species. This fact is in accordance with the greater development of fibres in this portion of the muscle in that species.

The zygomatic arch is relatively the same width in all of the species which means that there is no bone formation to correspond to the greater development of the other parts of the masseter in serpens.

In profile the three skulls are very similar but the anterior portion of the skull is more curved in serpens. There are no visible variations in the infraorbital ridging which agrees with Howell's statement (1926) that the "infraorbital ridging is not the direct result of muscular stimulus". No evidence of the amount of development of the temporalis muscle is visible on the skulls. However, the posterior divergence of the zygomatic arch appears to be slightly greater in townsendi than in serpens which may result from the exclusion of the temporalis muscle over a larger area in the former species.

Ventral Aspect-

The tympanic bullae may be described as ovoid in all of the species but their length compared to total length of the skull varies, measuring 29% in serpens, 32% in townsendi and 31% in longicauda. The incisive foramina are all decidedly elongate and similar to that illustrated by Howell (1926) in which he attributes the length to the size of the Jacobsen's organs of the nasal passages since the nasal arteries and the naso-palatine arteries, which also pass through the foramen, are small. The pterygoid plates are similar in size and shape in all of the species but the mesopterygoid appears to be slightly longer in serpens. The occipital surface in each case exhibits an anterior inclination which is considered to be characteristic of rodents with fossorial habits but as it is equally well-developed in the forms which are not regarded as being subterranean this structure possibly is not related to habitat. The occipital is known to vary in other forms with regard to angularity and definition of the processes and it seems quite likely that the slight differences which do occur should be attributed to age. The mastoid process is heavier in serpens which, according to Howell, (1926) is an indication of better development of the sternomastoid, cleidomastoid, and complexus muscles in this species.

Mandibles-

The mandibles are very similar in the three species. The coronoid process varies slightly being a trifle more hooked in serpens and longer in townsendi. The angular process is least thickened at the posterior border in serpens but is the same general shape in each specimen. Both the dorsal and the ventral masseteric ridges are always heavy. The symphysis menti is movable and the two halves of the lower jaw are evidently connected by an elastic material most of which dissolves when the bones are boiled. The point of attachment of the M. transversus mandibularis is marked on either side by a slight fossa.

Teeth-

The incisors are broader and shorter in M. serpens. The length of tooth row of the cheek teeth in percent of total skull length measures 21.6% in serpens, 24.8% in townsendi and 22% in longicauda. The maxillary tooth row is nearly parallel in each case. There are no noticeable differences in breadth of the molars in any of the species.

The skull of richardsoni is much larger with heavier ridging, this is especially true of the lambdoidal ridge and the occipital condyles. The nasal bones are a different shape in this species being much broader in the anterior end in proportion to the width at the posterior end. The zygomatic arch is broader giving the entire skull the appearance of breadth. The parietals are longer and narrower and the interparietal bone is much shorter in the horizontal axis. The tendency for the frontals to become narrow in the central region is most evident in richardsoni.

This ventral surface is more similar to the other skulls but the diastema is longer in percent of total length being 40.5% as compared to 29% in serpens and 34 and 31% in townsendi and longicauda respectively. The incisive foramen is small measuring only 2 mms. in length as compared to 5 mms. in townsendi and 3.5 mms. in serpens.

The coronoid process is shorter in richardsoni. Both the upper and lower incisors are longer, and the former project noticeably beyond the plane of the extremity of the rostrum.

Pectoral Girdle and Limb

Scapula-

The scapula is shaped roughly like a 30-60-90° triangle with the vertebral border convex and forming an angle greater than 90° with the anterior border. The cranial border is straight and forms a sharp angle with the anterior border.

The scapula tends to be elongated rather than broadened. The large and very distinct coracoid process is fused with the scapula but does not show any tendency to divide into two centres, a large supraglenoid tuberosity projects laterally at its base. The glenoid fossa is ovoid (much longer than wide), the coracoid forming slightly less than one-third of the fossa. The infraglenoid tuberosity is less well-developed. The insertion of M. teres major is marked by a minute third fossa on the lateral surface, which is separated from the infraspinous fossa by the axillary ridge.

The vertebral border of the scapula is thickened probably in response to the insertion of the stout serratus anterior, levator scapulae and rhomboideus muscles. The costal surface is almost flat, but with a shallow groove opposite the spine. There is no evidence of secondary ridging lateral to it.

The lateral surface is divided by the spine into supraspinous and infraspinous fossae. The supraspinous fossa is the larger and is roughly triangular in shape, with the portion near the coracoid much reduced. The spine is very prominent being approximately one-half the width of the scapula in height; possibly this development is in response to the subscapular group of muscles which are enlarged in serpens. The acromion process is represented by a thickening on the end of the spine equal to approximately one-third of the length of the latter. A fairly prominent metacromion process is present.

Length of the scapula varies with age (Howell 1924) but in the specimens measured the following percentages of functional arm length were obtained: 50.8% in serpens; 48% in townsendi; 49.9% in longicauda; and 42% in richardsoni. On this basis serpens has decidedly the longest scapula, a modification that may be correlated with the large muscle attachments found on it. Howell (1924), mentions that young animals have a shorter scapula and this probably explains the divergence found in my specimen of richardsoni.

The scapulae tend to be the same general shape in all of the species but in townsendi and longicauda the width at the vertebral border is considerably greater in proportion to length that it is in serpens. The vertebral border is more thickened in serpens than in the other species. The coracoid is always fused with the scapula.

Clavicula

The slender clavicle measures 6 - 6.25 mm. in serpens. The sternal end is club-shaped and articulates with the anterior (cranial) surface of the manubrium sterni at its centre.

Only clavicles of serpens and townsendi were available for comparison and no significant differences appeared.

Functional length of the fore-limb-

The scapula can be thrust forward and backward through muscle action, i.e., it is movable and should be considered as forming part of the functional length of the fore-limb. This movement compensates for the greater length of the hind limb which is attached to an immovable pelvis. However, functional limb length is measured by Howell (1926) as the length from the scapular-humeral joint to the sole of the foot since this is a plantigrade animal. He feels that a definite point on the scapula could not be designated from which to take measurements and hence it is better to measure from the joint. Actually the length taken is only the sum of the length of the humerus and radius.

This length measured 22 mm. in serpens; 25.3 mm. in townsendi and 25.8 mm. in longicauda.

Humerus-

In serpens the humerus is long and slender with well-developed muscular processes. The head is large and ovoid forming an angle of about 150^{o} with the shaft. The neck is poorly-developed. The greater tubercle is large and has a groove in the centre into which M. supraspinatus and M. infraspinatus insert, a depression markeing the point of insertion of M. teres major is also present.

The intertubercular sulcus, in which the tendon of the long head of M. biceps lies, is fairly deep. The lesser tubercle is about one-half the size of the greater tubercle. A poorly-defined depression marks the area of insertion of the tendon of M. subscapularis.

The shaft is slender. The lateral ridge extends more than one-third (less than one-half) of the distance from the head to the condyles and has faintly-marked areas of muscle attachment. The median ridge is indistinct, poorly defined scars marking the points of insertion of the tendons of M. teres major and M. latissimus dorsi. The lateral epicondylar ridge is distinct and the lateral epicondyl well-developed although small. The medial epicondyl is larger and a distinct roughness marks the point of attachment of the coracobrachial muscle. The condyles are separable into a large medial trochlea which articulates with the semilunar notch of the ulna and a capitulum of similar size that articulates with the head of the radius.

In percentage of functional limb length the humerus measures 54% in *serpens*; 47% in *townsendi*; 44% in *longicauda*; and 50% in *richardsoni*. In *serpens* the humerus is longer and more slender than it is in *townsendi* and *longicauda* although it is still a slender bone in the latter species. In *richardsoni* it is more massive and is an entirely different shape.

The head of the humerus is approximately the same relative size in *serpens*, *longicauda*, and *townsendi* but is much larger in *richardsoni*. This relationship also applies to the development of the greater and lesser tubercles. ~~trochanters~~. The neck shows a greater degree of development in *townsendi* and *longicauda* than it does in *serpens*. The medial ridge appears to be better-developed in *townsendi* and *longicauda* than in *serpens* but this may have been only a relative difference. The lateral ridge is large and well-developed in all species, that of *longicauda* being the longest. The condyles are always separable into a trochlea and capitulum and the medial epicondyl is always large and distinct. In percentage of functional arm length the widths of the condylar borders measured 25% in *serpens*; 30% in *townsendi*; 28% in *longicauda*; and 32.6% in *richardsoni*.

Ulna-

The ulna is long and slender with a long olecranon process that measures one-sixth of its total length and provides a large area for insertion of M. triceps. The caudal end of the process is curved mediad. The semi-lunar notch is deep, semi-circular, and collar-like, with a radial facet on the craniolateral border which receives the head of the radius. The coronoid process located on the craniodistal margin of the notch projects medially. The ulna is excavated on the lateral surface forming a small, short lateral fossa which is very incomplete.

The distal end of the ulna has a groove through which passes tendons of most of the extensor muscles and another which permits the passage of the tendon of M. extensor ulnaris. The styloid process is V-shaped and fits into a depression between the triquetum and pisiform bones.

In percent of functional limb length the ulna measured 63.6% in _serpens_; 64.8% in _townsendi_; 65% in _longicauda_; and 58% in _richardsoni_. The percent of the ulnar length which is represented by the olecranon process measured 17.8% in _serpens_; 13% in _townsendi_; 12% in _longicauda_; and 14.4% in _richardsoni_.

The variations between species are very slight, but the same relationships that were found in the humerus re-occur here. The only difference worthy of note is in the trioccipital process which is deeper and therefore better-developed in _serpens_.

Radius-

The head of the radius is ovoid with a groove on the lateral surface which articulates with a small ridge on the ulna and thus reduces movability of the radio-ulnar joint. The neck of the radius is probably attached to the ulna by ligaments but these were not seen. However, practically no independent movement can be possible since the bones remained together even when cleaned by boiling.

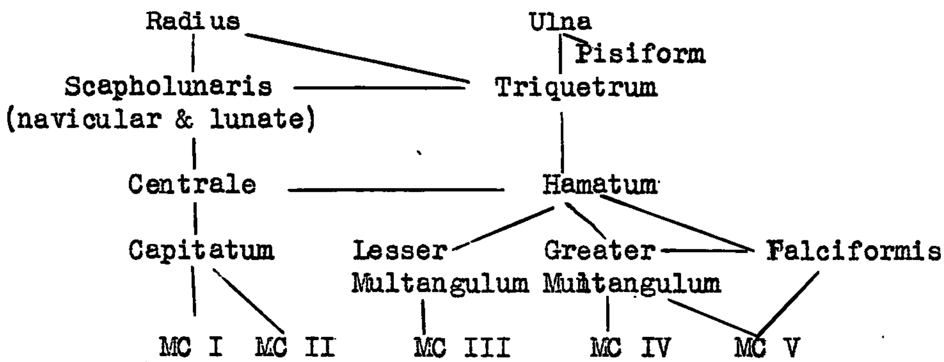
The cranial border is oblique and extends caudally from the proximal end for about one-half of the length of the radius. The tendon of M. adductor pollicis inserts into a slight groove on the lateral surface about 1 mm. distal to the oblique line.

The body of the radius is very slender but the tuberosity is well marked and is situated on the medial border near the head. The "pseudostyloid" process described by Hill (1937) is poorly differentiated. The volar surface is nearly flat (not concave). The articular grooves are similar in each of the species.

In per cent of ulnar length the radius measured 78% in serpens; 79% in townsendi; 79.9% in longicauda; and 78% in richardsoni.

Carpus -

The following diagram illustrates the relationships of the nine bones of the carpus:



In each specimen examined the bones were similarly arranged. The bones are larger in longicauda and townsendi which have much larger feet.

Metacarpus -

The first metacarpal is about the same length as the fifth and about two-thirds of the length of the third and fourth. The second is slightly longer than the first. Proximally the metacarpals articulate with the distal carpal bones. Small sesamoid bones occur at the carpophalangial joints.

Phalanges -

The first two phalanges of each digit are elongate, the second being approximately two-thirds of the length of the first. The fourth digit is the longest and bears the largest claw. The latter relationship is not as pronounced in longicauda or townsendi as it is in serpens.

Pelvic Girdle and Limb

Os Coxae-

The os coxae are long and slender with well developed muscular processes. The sacrum and ilium are fused, the latter being attached to the first sacral vertebra. The ischium measures approximately one-half the length of the ilium. The coxal bones are united by a short symphysis which is approximately one-fifth the length of the pubis. The large and deep acetabulum is situated caudal to the middle of the innominate bone and is formed by the junction of the ilium, ischium and pubis. The lips of the cup are incomplete on the caudoventral side at the point of attachment of the ligamentum teres. The cavity at the "bottom" of the acetabulum is irregular in shape. The triangular obturator foramen is situated ventral and caudal to the acetabulum with its main axis horizontal.

The ilium extends from the cranial end of the acetabulum in a cranial direction. The cranial end is thickened and flattened. The crest is produced laterally forming a recurved spine from which originates part of M. gluteus medius. The iliac ridge is poorly defined. The gluteal fossa is not very deep but it is fairly wide with a definite ridge separating the areas of attachment of M. gluteus medius and M. gluteus minimus. The dorsal and ventral borders of the ilium are nearly parallel. The dorsal border is indented near the caudal end by the sciatic notch. On the ventral border opposite the sciatic notch there is a slight indentation where M. psoas major inserts; and a slight iliopectineal eminence caudal to the latter.

The ischium forms the remaining part of the dorsal and caudal parts of the hip bone. The ischial tuberosity does not seem to be divided into dorsal and ventral tubercles but the dorsocaudal margin is thickened to form a distinct ridge. The dorsal tuberosity is large and prominent. The ischial spine is poorly developed.

The pubis extends in a caudal direction with a slender body which is apparently completely separated from the acetabulum. The cranial limit is marked by an iliopectineal eminence and the ventral border is oblique forming an angle of about 15° with the body. This angle straightens out in the area of the symphysis.

In percent of functional limb length the os coxae measure 48.2% in serpens; 40.6% in townsendi; 48.8% in longicauda; and 47.6% in richardsoni. In percent of the length of the innominate bone the ilium measures 54.8% in serpens; 60.0% in townsendi; 56.1% in longicauda; and 54.8% in richardsoni. Any specific variations which are found in the pelvic girdle are not as marked as those found in the pectoral girdle and limb.

The pubic symphysis is closed in all of the species. The caudal border of the ischium is not straight in longicauda but rather forms an angle of about 135° at the central point. This variation is not as marked in townsendi.

Functional length of the hind limb-

Functional length of the hind limb was computed according to Howell's plan (1926). This is a purely arbitrary system whereby the lengths of the femur and tibio-fibula are summed and added to one-half of the length from the heel to the distal end of the longest metatarsal. Measured in this way the limb length measure 33.7 mm. in serpens; 41.8 mm. in townsendi; and 42 mm. in longicauda.

Femur-

The femur which is long and relatively slender has large processes for muscle attachments The neck forms an obtuse angle with the shaft and is greatly constricted. Ligamentum teres is attached to a deep and circular pit on the head. The greater trochanter is large; the lesser trochanter smaller and with its main axis at an angle of about 60° to the surface of the femur. The trochanteric fossa is large, deep and irregular. The trochanteric crest is complete, i.e., it connects the trochanters. There is no intertrochanteric line on the cranial surface of the crest. A third trochantic (or lateral ridge, Hill (1937)) is present and extends about three-eighths of the total length from the proximal border caudad. There are several sunken lines on the medial surface distal to the lesser trochanter which mark the areas of insertion of tendons of M. iliacus, M. pectineus, and M. adductor longus. The proximal end is bent slightly craniad but the remainder of the shaft is nearly straight. The distal end is enlarged to form two condyles which are about equal in size. The poplitealgroove is deep and U-shaped and the patellar groove shallow and rather narrow. Neither the lateral nor the medial epicondyl has become markedly roughened by the attachment of ligaments.

The femurs of the three species show no extensive differences in structure; the head is slightly more overhanging in serpens than in townsendi or longicauda. In percent of functional limb length the femur measures 37% in serpens; 40.1% in townsendi; 39.7% in longicauda; and 36% in richardsoni.

Tibio-fibula-

The tibia and fibula are ankylosed for nearly one-half of their lengths the proximal 55% of the length of each bone being free. The articular surfaces for the femur are large and the medial and lateral condyles are of approximately the same size. The articular surface is concave in transverse section. The tuberosity is part of the common proximal epiphysis. The position of the insertion of the large patellar tendon is indicated by a scar between the condyles.

The body of the tibia between the proximal epiphysis and the union with the fibula is long and crescent-shaped. The crest (or lateral border) begins caudal to the tuberosity and runs almost parallel to the lateral surface. The area of insertion of M. semimembranosus is located near the medial border distal to the epiphyseal line and distal to the latter are the insertions of M. gracilis and M. semitendinosus. The medial crest begins distal and caudal to the condyles and curves first mediad and then laterad, becoming indistinct.

Relative to the tibia, the fibula is more caudal than lateral in position and the head forms part of the proximal epiphysis. Near the epiphyseal line there is a roughened area which marks the point of attachment of the fibular collateral ligament. The body of the fibula is very slender and the interosseous crest is poorly defined.

The conjoined tibia and fibula is long and slender. There are ridges on the laterocranial surface near the malleoli which represent the margins of the two bones. The distal end of the tibiofibula consists of both grooves and malleoli. The tendon of M. peroneus longus passes through an oblique groove on the lateral surface. The medial malleolus bears two faint grooves through which pass tendons of M. flexor tibialis and M. tibialis posterior. The distal end of the tibiofibula articulates with the talus and calcanium.

The tibiofibula is longest in serpens. Measured in percent of functional limb length the results are 52.7% in serpens; 50.2% in townsendi; 50% in longicauda; and 52% in richardsoni. It is decidedly longer than the femur in all cases. The percent of the bone which is separate is 42.8% in all species.

Foot-

The rigid fusion of the tibia and fibula probably has an appreciable effect on lessening the amount of rotation of which the foot is capable. Flexion of the toes makes measurement of the foot very difficult, however, the following measurements which have been converted to percent of functional limb length were obtained: 41.1% in serpens; 44.2% in townsendi; and 45% in longicauda.

Tarsus-

The following diagram illustrates the positions of the eight bones of the tarsus:

$$\begin{tikzcd}[column sep=small]
 & & & \text{Tibio-fibula} \arrow[d, dash] & & & \\
 & & & \text{Talus} \arrow[dll, dash] \arrow[dd, dash] \arrow[drr, dash] & & & \\
 & \text{Calcaneum} \arrow[d, dash] & & & & \text{Tarsale medialis (Tibialis)} \arrow[dll, dash] \arrow[d, dash] & \\
 & \text{Cuboideum} \arrow[d, dash] & & \text{Navicular} \arrow[d, dash] \arrow[drr, dash] & & {} & \\
 & \text{Cuneiform III} \arrow[dl, dash] \arrow[dr, dash] & & \text{Cuneiform II} \arrow[d, dash] & & \text{Cuneiform I} \arrow[d, dash] \arrow[dr, dash] & \\
\text{Met. V} \arrow[rr, dash] & & \text{Met. IV} & \text{Met. III} & & \text{Met. II} & \text{Met. I}
\end{tikzcd}$$

Metatarsus-

The fifth metatarsal is the smallest being shorter than the first which articulates with the cuneiform and with the second metatarsal as described by Hill (1937).

Phalanges-

The phalanges of the hind foot are short bones. They are much shorter and more slender than the corresponding bones of the manus.

Branchiomeric Musculature

Masticatory group (fig. 15) supplied by the masticatory nerve (branch of trigeminal).

M. masseter:

a) M. masseter superficialis- is a sheet of muscle arising ventral to the infraorbital foramen and inserting on the ventral margin of the mandible and on the masseteric ridge.

b) M. masseter lateralis profundus, pars anterior- arises from the rostrum and adjacent part of the zygomatic arch and passes to the lateral surface of the mandible (over a large area).

c) M. masseter lateralis profundus, pars posterior- arises from the lateral and medial surfaces of the zygomatic arch and inserts on the angular process of the mandible.

d) M. masseter medialis, pars anterior- arises from the medial surface of the zygomatic arch and inserts onto the coronoid process of the mandible.

e) M. masseter medialis, pars posterior- arises from the angle of the zygoma (medial surface) and inserts on the ramus of the mandible (over a large area).

The entire muscle is enclosed in a heavier fascia in townsendi and longicauda than it is in serpens but in the latter species there are more muscle fibres present in the superficial part. In richardsoni the fascia is very much heavier as is also the platysma and the panniculus carnosus. The origin and insertion of each part is the same in all of the species; a rule which holds for the majority of the muscles.

M. temporalis- is a large and easily discerned muscle, especially in the region of insertion. It arises by an aponeurosis from the temporal ridge lateral to the interparietal with no sign of division into deep and superficial fibres. However two distinct areas of insertion occur, the superficial fibres insert on the tip of the coronoid process and the deep fibres on the medial surface of the same process.

M. temporalis occupies a relatively larger area in townsendi and longicauda but it contains fewer fibres. In richardsoni it is decidedly smaller.

M. pterygoideus externus- takes origin from the parapterygoid plate and fibres run laterall and caudad to insert on the medial surface of the mandibular condyle.

M. pterygoideus internus- is supplied by the medial branch of the mandibular nerve. It arises from the pterygoid fossa, i.e., the area between the lateral and medial pterygoid plates and inserts onto the medial surface of the angular process of the mandible. This muscle is decidedly heavier in serpens than in any of the other species. In townsendi it arises from the lateral surface of the internal pterygoid plate. Considering the degree of development found in the other masticatory muscles it is a well-developed muscle in richardsoni.

Mylohyoid group (fig. 16) supplied by the mylohyoid branch of the mandibular nerve

M. mylohyoideus- arises from the mylohyoid ridge (i.e., the ridge ventral to the cheek teeth) of the mandible and inserts on the hyoid arch.

M. transversus mandibularis- is a poorly-defined muscle consisting of a few fibres which run transversely between the halves of the mandible. It is visible when the digastricus is cut away.

In townsendi and longicauda it gives the appearance of being slightly heavier although there are still very few fibres present. The origin and insertion is more clearly defined in the latter species.

M. digastricus- is divisible into two parts. The anterior belly arises from the body of the hyoid and from the arch ventral to this and inserts on the oblique ridge of the mandible and on the fossa caudal to the symphysis of the mandible. The right and left parts are separated.

The posterior belly arises from the paraoccipital process (jugular process) and inserts on the hyoid arch by a tendon. Both parts are well-developed and they are separated by a constriction in all of the species although most noticeably largest in serpens. In richardsoni the muscle is more strap-like.

Constrictor colli group- supplied by the superficial branches of the facial nerve.

M. platysma (fig. 15) shows no tendency to divide into sphincter colli primitivus as described by Howell (1926). Two well-developed heads to the sheet of muscle are found, one in the head and the other in the neck region. The cranial part arises from the mid-dorsal line (under levator auris longus), the base of the ear, and the parietal region (under funtalis), and inserts onto the skin in the lip region.

The superficial layer lies in the ventral neck region where it arises along the mid-ventral line from the pectoral region to the symphysis mandibuli, and inserts on the fascia of the masseter and of the shoulder.

The muscle sheet adheres more closely to the skin in townsendi and longicauda than it does in serpens making it more difficult to define its limits. There is a much greater development of muscle fibres in the platysma of richardsoni than in any other species.

M. postauricularis- (levator auris longus) is divided into cranial and caudal portions. The cranial part arises from the spines of the first three or four cervical vertebrae and inserts onto the base of the ear (anterior to the insertion of the caudal portion). The caudal part arises from the fourth and fifth vertebrae and inserts onto the base of the ear and onto the interparietal bone lateral to the ear.

In *townsendi* this muscle is not as well-developed, it inserts onto the skin of the ear and the area immediately cranio-dorsal to the ear. It is well-developed in *richardsoni* and is directed more laterally than in the other forms.

M. auriculolabialis- not found.

M. sternoauricularis- not found.

M. nasolabialis- (zygomasticus) is a very indistinct muscle in *serpens*, consisting of a sheet of muscle which arises on the surface of the zygomatic arch and inserts at the upper corner of the mouth, i.e., becomes attached to the mystacial pad of connective tissue. It is similar in *townsendi* and *longicauda* but is less developed in *richardsoni*.

M. maxillolabialis- (levator labii) is well-developed and easily distinguishable. It originates on the premaxilla in the region of M. orbicularis oculi and inserts on the mystical pad of the upper lip. It is a slightly heavier muscle in *serpens* than it is in *townsendi*.

M. maxillonasalis- (dilator ~~nous~~ naris) passes under M. maxillolabialis after it has arisen from the surface of the nasal bone directly in front of the eye and close to M. orbicularis oculi. It is a thin muscle which becomes tendinous and inserts on the lateral side of the anterior nasal opening. This muscle also shows the best development in *serpens* although the variations are slight.

M. orbicularis oculi- (fig. 15) is well-developed in serpens. Fibres run around the eye and adhere to the skin in some cases. The fibres arise from the hamulus of the lachrymal bone and from the fascia around the eye. In townsendi and longicauda the muscle is very poorly developed with the fibres less numerous and more difficult to follow.

M. orbicularis oris- is well-developed in serpens and divided into at least five slips which arise from the mandible, near the incisive alveoli, and from the medial line ventral to the nostrils. In townsendi and longicauda the slips are not as readily separable.

M. buccinatorius- runs under levator labii (maxillolabialis) and in a direction at right angles to it. It originates from the rostrum along a ridge formed by the upper incisor and from the area anterior to the lateralis profundus pars anterior portion of M. masseter. It inserts onto M. orbicularis oris.

In townsendi and longicauda this muscle inserts upon M. orbicularis oris by five distinct slips that originate from a single head upon the rostrum.

A thin muscle was found in serpens passing from under the edge of M. buccinatorius and fusing with M. orbicularis oris or passing under it. This may correspond to the sphinter muscle of the pouch which is described by Hill (1937). The muscle measured approximately 3.1 mm. in width and 6 mm. in length. It was found in each specimen of serpens dissected.

Hyoid constrictor group- supplied by the facial nerve and derived from the ventral constrictor of the hyoid arch.

M. digastricus- is described with the mylohyoid group.

M. stylohyoideus- was discovered only after some searching as there is very little muscle fibre present, the larger portion of the mass consisting of connective tissue. It arises from the same area as the posterior belly of M. digastricus and passes under the latter muscle to insert on the hyoid.

In townsendi and longicauda the muscle is poorly defined and in these species it inserts on the greater corner of the hyoid in a position which is much more lateral than the area of insertion in serpens.

M. jugulohyoideus- was not found. According to Hill (1937) this muscle disappears with the loss of the stylohyal cartilage.

M. stapedius- not found.

Trapezius group- (fig. 18) These may be branchiomeric muscles with a secondary cervical innervation. Ontogenetically the group arises from the mesenchyme of the branchial arches. (Edgeworth, 1911; Lewis, 1910)

M. sternomastoideus- is well-developed in serpens but shows no evidence of a double insertion as described by Greene (1935) in Rattus. It arises from the lateral surface of the manubrium sterni and inserts on the mastoid surface of the squamosal.

In townsendi it is a fairly well-developed muscle which arises from the clavicle at its point of junction with the manubrium sterni.

M. cleidomastoideus- runs under M. sternomastoideus but is a thinner muscle. It arises from the lateral half of the clavicle and inserts with

M. sternomastoideus onto the tip of the mastoid process.

M. cleido-occipitalis- (clavatrapezius) is a well-defined muscle which is readily discovered running obliquely between the trapezius and sterno-mastoid muscles. It originates from the lateral third of the posterior border of the clavicle and inserts on the superior nuchal line.

M. trapezius- (fig. 18) is divisible into M. acromiotrapezius and M. spino-trapezius.

M. acromiotrapezius- is a well-developed, heavy muscle which arises from the superior nuchal line and from the mid-dorsal line over the first four thoracic vertebrae and inserts onto the spine of the scapula and the acromion process.

In townsendi and longicauda the origin is from the same area as it is in serpens but in the latter the muscle development is sufficiently great to give the effect of a ridge on either side of the mid-dorsal line. By comparison, the muscle is flat in townsendi and longicauda.

M. spinotrapezius- is divisible in serpens into a small posterior and a large anterior portion. The smaller part arises from the sixth and seventh thoracic vertebrae and inserts on the spine of the scapula. The larger part, arises from the adjoining fascia and the mid-dorsal line and inserts on the spine and crest of the scapula.

In townsendi and longicauda the posterior portion is long and strap-like and the anterior portion is limited, arising from the fascia above the fifth thoracic vertebra and inserting with M. acromiotrapezius onto the spine of the scapula. In richardsoni only the posterior portion is present.

Myotomic Musculature

Lingual muscles- supplied by the hypoglossal nerve. The muscles of this group were not dissected out.

Muscles of the Body

A. Dorsal Division

The epaxial muscles are supplied by branches of the dorsal rami of the spinal nerves.

Superficial spino-occipital group-

M. splenius- arises from the nuchal ligament and inserts on the superior nuchal line for almost its entire length. In the other species the origin is also from the nuchal ligament but it is a heavier and more obvious muscle in *longicauda* than in either *serpens* or *townsendi*. The difference may have been due, in part, to the preservative used.

Sacrospinalis group- (fig. 17)

M. sacrospinalis- is found in a position lateral to M. longissimus dorsi and consists of a number of slips which pass over three ribs to insert on the fourth or onto the transverse processes of the lumbar vertebrae. The slips arise from the ilium, sacral and lumbar vertebrae, and the ribs.

In *townsendi* there are not as many fibres to each slip of the muscle as there are in *serpens* and the anterior slips pass over only two ribs to insert on the third craniad. In *richardsoni* as in *serpens* the slips pass over three ribs.

M. iliocostalis- appears to be continuous with M. sacrospinalis. It is divisible into three parts, the lumbar part inserts on the last five or six ribs, the dorsal part on the middle ribs, and the cervical part on the first rib and the last two or three cervical vertebrae. Each slip passes over three ribs to insert on the fourth craniad.

M. longissimus- consists of bundles of muscle fibres which arise from the mammillary processes and pass over two vertebrae to insert on the third craniad. Insertions occur on the caudal ten ribs and on the accessory processes of the thoracic and lumbar vertebrae. The several sub-divisions usually described for this muscle are not well-differentiated in the Microtine species studied.

M. extensor caudae lateralis- arises from the transverse processes of the last two sacral and the first few caudal vertebrae and inserts on the articular processes of the caudal vertebrae. The tail of serpens is reduced and the muscles that move it show a corresponding reduction. In townsendi the better developed muscle originates on the last three sacral vertebrae.

M. spinalis dorsi- is united with the fibres of M. semispinalis in both serpens and townsendi.

Semispinalis group- (fig. 17) includes muscles which have fibres arising from transverse processes and inserting on the spines or lamellae of vertebrae.

M. semispinalis capitis- is a large single muscle in serpens which arises from the transverse processes of the second to seventh cervical vertebrae and from the first to ninth or tenth thoracic vertebrae and inserts onto the middle part of the superior nuchal line.

In townsendi and longicauda the muscle is roughly divisible into regions which probably correspond to the ones given by Howell (1926). The anterior part or biventer cervicis arises from the cervical vertebrae including the axis and the posterior part from the first six or seven thoracic vertebrae. Both portions insert on the superior nuchal line.

M. semispinalis- consists of fibres which interconnect the spinous processes. They arise from the mammillary processes of the lumbar and last few thoracic vertebrae and from the transverse processes of the other thoracic vertebrae. Generally the fibres pass over two vertebrae to insert on the spine of the vertebra threecraniad but considerable variation occurs and in some parts only one segment is passed over.

M. extensor caudae medialis- is continuous with M. semispinalis. The fibres arise from the spines of the last sacral and first few caudal vertebrae and pass over two vertebrae for insertion. The entire muscle shows greater development in townsendi and longicauda than it does in serpens.

B. Ventral Division

Includes all the remaining skeletal muscles of both the body and the appendages. Branches of the ventral rami of spinal nerves supply these muscles.

Cervical prevertebral group- supplied by branches which arise from the ventral rami as they emerge from the intervertebral foramina.

M. rectus capitis anterior- arises from the margin of the transverse process and ventral arch of the atlas and inserts on the basal part of the occipital (anterior portion) and to the medial half of the jugular process (posterior portion). This muscle is less clearly-defined in townsendi and longicauda than it is in serpens.

M. longus capitis- (longus atlantis) originates from the carotid tubercle of the sixth cervical vertebra and the ventral parts of the fourth and fifth cervical vertebrae and inserts on the tuberosity near the occipito-sphenoidal suture.

In townsendi this muscle covers a larger area but it does not contain as many fibres as are found in serpens.

M. longus colli- is divisible into caudal and cephalic portions. The cephalic part arises from the ventral surface of the sixth cervical vertebra and from the ventral part of the transverse processes of the third to sixth cervical vertebrae and inserts on the ventral part of the axis.

The caudal part arises from the heads of the first two ribs and from the lateroventral surface of the first three thoracic vertebrae and the last cervical vertebrae and inserts on the ventral tubercle of the sixth cervical vertebra.

Lumbar prevertebral group-

M. quadratus lumborum- arises from the last lumbar and the first sacral vertebrae by tendons and inserts on the bodies of the last two or three thoracic vertebrae and on the lateral surfaces of the first three lumbar vertebrae (no costal insertions were found). This muscle shows the least development in serpens. In townsendi and longicauda it is a decidedly heavier muscle and this is also true to some extent of richardsoni.

M. psoas minor- may have been derived from M. quadratus lumborum according to Gregory and Camp (1918). It arises from the iliopectineal eminence and inserts on the bodies of the first four or five lumbar vertebrae.

Caudal flexor group-

M. flexor caudae lateralis- arises from the pelvic surface of the ilium (origin is restricted to the sacrum) and inserts on the chevron bones of the tail and on the ventral surfaces of the caudal vertebrae.

M. flexor caudae medialis- is divisible into three parts. The cranial part originates from the radius and the transverse processes of the second and third sacral vertebrae. The intermediate part arises from the bodies of the second to fifth sacral vertebrae and the caudal part, which is small, arises from the first two caudal vertebrae. All of the parts insert with M. flexor caudae lateralis on the chevron bones of the tail. This muscle is developed most in longicauda and least in serpens.

Medial ventral cervical group-

The muscles of this group develop ontogenetically from a single rudiment (Edgeworth, 1916). The geniohyoid is supplied by the hypoglossal nerve and the infrahyoid muscles are innervated by a special nerve which arises from the loop between the first and second cervical nerves independent of the hypoglossal.

M. geniohyoideus- iswell-developed in serpens but it is not a large muscle. It arises from the hyoid arch and inserts on the symphysis of the mandible

In townsendi and longicauda the origin is from the posterior corner of the hyoid.

M. sternohyoideus- is the chief muscle lying ventral to the trachea. It arises from the posterior end of the manubrium sterni and from the costal cartilage of the second rib and inserts onto the lower border of the body of the hyoid.

As is the case with many of the cervical muscles M. sternohyoideus is much more clearly defined in townsendi and longicauda than it is in serpens. The muscle is largest in richardsoni.

M. sternothyreoideus- is a well-developed muscle which arises from the lateral part of the thyroid cartilage and inserts on the hyoid.

M. omohyoideus- is well-defined and fairly large in serpens. It arises from the cephalic border of the scapula and inserts onto the hyoid (deep and lateral to M. sternothyreoideus).

Medial thoraco-abdominal group-

M. rectus abdominus- is attached to the crest of the ilium, the first rib, and the manubrium sterni. The two halves of the muscle are divided in the abdominal region by the linea alba. The muscle on each side arises by several slips some of which cross the mid-ventral line.

The external oblique, internal oblique and transversalis abdominalis muscles are all very thin and practically impossible to separate in any of the species. The external oblique is continuous with M. serratus anterior, i.e., its fibres interdigitate with those of the latter muscle and it inserts onto the crest of the ilium and the body of the pubis. It spreads out like a thin fan over the ventral and lateral surface of the body.

Lateral cervical group- supplied by dorsal branches of the ventral rami of the cervical nerves. M. scalenus is also innervated by the first two or three intercostal nerves.

M. rectus capitis lateralis- arises from the transverse process of the atlas and inserts on the medial ridge of the jugular process.

M. scalenus- is divisible into two parts. The dorsal portion arises by a tendon from the transverse process of the atlas and inserts on the third, fourth and fifth ribs. The ventral portion arises by a tendon from the dorsal muscle and from the transverse processes of the last six cervical vertebrae and inserts on the dorsal part of the last six cervical vertebrae and on the cranial surface of the first rib.

No appreciable variations were discovered in any of the muscles of the lateral cervical or the lateral thoracoabdominal groups.

Lateral thoracoabdominal group- (fig. 16) supplied by the intercostal and first lumbar nerves and by the inguinal nerve.

M. serratus posterior superior- arises at the mid-dorsal line between and beneath the scapulae and over the first thoracic vertebrae and inserts on the cranial side of the fourth to ninth ribs.

M. serratus posterior inferior- arises from the last thoracic and the first two lumbar vertebrae and inserts onto the caudal surfaces of the last four ribs.

M. sternocostalis- not found.

Mm. subcostalis- (intercostalis interni) arises from the pleural surfaces of all but the first rib and from the transverse processes of the first two lumbar vertebrae and inserts on the second rib craniad.

Mm. levatores costarum- (intercostalis externi) arise by tendons from the accessory processes of the thoracic vertebrae and run caudoventrad to insert on the ribs.

M. transversalis thoracis- arises from the xiphisternum and the last three sternebrae and inserts on the costal cartilages of the second to tenth ribs.

Appendicular Musculature

The limb muscles are divided into extensor and flexor systems which are supplied by dorsal and ventral branches, respectively, of the brachial and lumbodorsal plexus. Most of the muscles attached to the pectoral girdle show a marked increase in size in serpens.

Muscles of the Pectoral Girdle and Limb

A. Extensor System

Costo-spino-scapular group- (fig. 19)

M. levator scapulae- is quite distinct from M. serratus anterior but continuous with it in serpens. It arises from the transverse processes of the first four or five cervical vertebrae and inserts onto the vertebral border of the scapula.

M. serratus anterior- arises by fleshy digitations from the first to sixth or seventh ribs and inserts onto the vertebral border of the scapula posterior to levator scapulae.

M. levator scapulae and M. serratus anterior are two not distinctly separable muscles in townsendi and longicauda. They are not, however, a combined single muscle such as that described by Hill (1937).

M. rhomboideus- is a single, large muscle in serpens which arises from the spines of all the cervical and the first four thoracic vertebrae and inserts on the lateral margin of the vertebral border of the scapula.

In townsendi and longicauda it is a smaller and thinner muscle. In serpens the muscle is actually larger than it is in townsendi although the latter species is one and one-third times as large as the former by volume.

M. occipitoscapularis- (rhomboideus capitis) arises from the lambdoidal ridge and inserts on the vertebral border of the scapula. This muscle is relatively heavy in all of the species.

M. omocervicalis- (levator claviculae) arises from the transverse process of the atlas and inserts on the metacromion process of the scapula.

Latissimus-subscapular group- supplied by the subscapular nerves.

M. latissimus dorsi- arises from the spines of the last two or three thoracic and the first two lumbar vertebrae and inserts through the axilla between the extensor and flexor muscles onto the shaft of the humerus. In townsendi this muscle inserts onto the axilla by three widely-separated heavy digitations rather than by a single insertion as found in serpens.

M. teres major- originates from the axillary border of the scapula and inserts onto the medial ridge of the humerus. In serpens it is slightly better-developed than in the other species.

M. subscapularis- can be divided into four bipennate parts which arise from the subscapular fossa and insert by tendons onto the lesser tubercle of the humerus.

Deltoid group- (fig. 18) supplied by the axillary nerve.

M. deltoideus- is divisible into two parts in serpens; M. acromiodeltoideus and M. spinodeltoideus.

M. acromiodeltoideus- arises from the lateral half of the clavicle and the acromion process of the scapula and inserts onto the deltoid ridge of the humerus. In serpens this muscle is very well developed and covers the entire lateral portion of the shoulder. In townsendi and longicauda it does not cover as great an area and consequently is not as prominent.

M. spinodeltoideus- is a small rather indistinct muscle which arises from the spine of the scapula and inserts onto the deltoid ridge beneath M. acromiodeltoideus. It displays no significant differences in the species examined.

M. teres minor- arises from the ventral part of the axillary border of the scapula and inserts onto the greater tubercle of the humerus. It was found to be a narrow but distinct muscle in all of the species.

Suprascapular group- supplied by the suprascapular nerve.

M. infraspinatus- is a bipennate muscle which arises from the whole of the infraspinous fossa and inserts onto the greater tubercle of the humerus. In townsendi and longicauda it is not as distinctly bipennate as it is in serpens.

M. supraspinatus- is also bipennate but it is a heavier muscle than M. infraspinatus. It arises from the whole of the supraspinous fossa and the spine of the scapula and inserts by a tendon onto the greater tubercle of the humerus.

Triceps group- supplied by the radial nerve.

M. triceps brachii- arises by three distinct heads in serpens. Caput longum is the largest part of the muscle but it is not separable into superficial and deep parts as described by Hill (1937) in Thomomys. It takes origin from the axillary border of the scapula for most of its length and from the infraglenoid tuberosity and inserts with Caput laterale and caput mediale onto the olecranon process of the ulna. In serpens the insertion is extensive. Caput laterale arises from the greater tubercle of the humerus and caput mediale from the medial surface of the humerus caudal to the insertion of M. teres major.

The same three heads are found in all of the species but variation in size of the belly of the muscle occurs, the greatest development being found in serpens.

Triceps shows the same tendency to shortening in serpens that is found in all the muscles of the brachium.

M. anconeus- is a rather small muscle, arising from the caudal surface of the lateral epicondyle and inserting onto the lateral surface of the olecranon process. In townsendi and longicauda this muscle appears to be relatively larger but there is little actual difference in size.

M. dorsoepitrochlearis- inserts with M. triceps onto the olecranon process. In townsendi and longicauda the two are indistinct, but in serpens the two muscles are completely separable. The dorsoepitrochlearis takes origin from the fascia of M. latissimus dorsi and M. teres major. In townsendi and longicauda no origin from the fascia of M. teres major was found.

Extensor group of the fore-arm- extensor carpi radialis is supplied by the radial nerve before it divides. The other two muscles are supplied by the deep ramus of the dorsal interosseous nerve.

M. brachioradialis- not found.

M. extensor carpi radialis longus- is a slender but well-defined muscle which arises from the lateral epicondylar ridge of the humerus. It is continuous with a tendon which passes over the carpus medial to its centre and inserts onto the radial surface of the second metacarpal.

In <u>townsendi</u> the muscle is larger than that found in <u>serpens</u> and insertion takes place near the base of the second metacarpal.

<u>M. extensor carpi radialis brevis</u>- arises from the lateral epicondylar ridge superficial to M. extensor carpi radialis longus with which it passes over the carpus to insert on the dorsal surface of the third metacarpal. This muscle is broader in <u>townsendi</u> than it is in <u>serpens</u>.

<u>M. supinator</u>- arises at the elbow joint by a stout tendon which is attached to the radial collateral ligament and inserts into the cranial border of the radius. This is the deepest muscle of the antibrachium and it is not particularly well-developed in any of the species.

<u>M. abductor pollicis</u>- arises from the ulnar surface of the radius and from the body of the ulna and inserts by a double tendon which passes through a groove in the wrist to the first phalanx of the pallex and the first metacarpal.

The other extensor muscles of the fore-arm are similar in all of the species but as the tendons are smallest in <u>serpens</u> they are most difficult to find in that species. In <u>richardsoni</u> the foxx feet are large and the tendons are correspondingly developed.

<u>M. extensor digitorum communis</u>- arises from the lateral epicondyle of the humerus and inserts onto digits two to five at the bases of the distal phalanges by tendons which pass under the transverse ligament.

<u>M. extensor indicis et pollicis</u>- arises from the lateral epicondyle and radial collateral ligament and inserts onto the dorsum of the pollex. A

second slip joins part of M. extensor digitorum communis which passes to the second digit. The tendon of this muscle passes over the tendon of M. extensor carpi radialis brevis on the manus.

M. extensor digiti quinti proprius- is a slender muscle which arises from the lateral epicondyl of the humerus and inserts into the second phalanx of the fifth digit, its tendon passing under the transverse ligament. A slip to the fourth digit may also exist but it was very slender and indefinite.

M. extensor carpi ulnaris- arises from the distal part of the lateral epicondyl and from the lateral ridge of the ulna and inserts by a tendon, which passes along a groove on the ulnar side of the wrist, to an area near the base of the fifth metacarpal.

Flexor System

Pectoral group- (fig. 18) supplied by the two anterior thoracic nerves with the exception of M. subclavius which is supplied by a special nerve.

These muscles are much larger in serpens than in any of the other species. When the muscles were dissected from each specimen the volume of muscle from serpens was found to be practically identical with that from the specimen of townsendi although the latter had a body volume almost one and one-third times as great as that of the former.

M. ectopectoralis (pectoralis major)- is divisible into superficial and deep parts. This is a very heavy muscle with a superficial part arising from the manubrium sterni and inserting on the deltoid ridge of the humerus and a deep part arising from the manubrium and from the first four sternebrae and inserting on the deltoid ridge and the fascia of the arm.

The divisions into superficial and deep parts are more definite in townsendi and longicauda than they are in serpens.

M. entopectoralis (pectoralis minor)- is a large muscle which arises from the second to fifth sternebrae and the xiphisternum and inserts on the deltoid ridge and the coracoid process. In townsendi and longicauda no fibres take origin from the xiphisternum.

M. pectoralis abdominalis- (xiphihumeralis) arises from the xiphisternum and runs deep to M. ectopectoralis to insert on the lateral ridge of the humerus.

M. cutaneus maximus- is part of the panniculus carnosus which arises from the humerus and the surface of M. ectopectoralis by fibres which converge in the glutial region and at the base of the tail. This muscle was largest in richardsoni.

Flexor group of the arm- supplied by the musculocutaneous nerve with the exception of some fibres of M. brachialis which are innervated by the radial nerve.

M. coracobrachialis- arises from the coracoid process of the scapula together with the short head of biceps brachii, and inserts on the distal two-fifths of the median ridge of the humerus caudal to the insertion of M. teres major. No distinct separation into two parts was found. In townsendi and longicauda the muscle covers a larger area than it does in serpens.

M. biceps brachii- is divisible into two parts. Caput longum takes origin in the glenoid fossa and inserts on the tuberosity of the ulna. Caput breve arises from the coracoid process of the scapula and inserts into the tuberosity of the radius. In townsendi the division is not as distinct as it is in serpens.

M. brachialis- takes origin from the lateral surface of the humerus and the base of the greater tubercle and inserts with caput longum of M. biceps on the ulna. In townsendi and longicauda two origins were found which were similar to those described by Hill (1937) for Thomomys. In these species a second origin lacking in serpens occurs from the cephalic border of the humerus.

Flexor group of the fore-arm- supplied by the median and ulnar nerves.

M. epitrochleo-anconeus- is supplied by the ulnar nerve. It is a short muscle which arises from the medial epicondyl of the humerus and inserts on the olecranon process of the ulna. In serpens the tendency is for this muscle to be nearly covered by the insertion of the long head of M. triceps brachii. In townsendi the muscle is much more clearly-defined.

M. flexor carpi ulnaris- is a single muscle in serpens which arises from the caudal surface of the olecranon and inserts on the pisiform bone. The epicondylar head described by Hill (1937) was not found in any of the species and may represent the primitive condition.

M. palmaris longus- arises from the medial epicondyl and inserts into the fascia of the hand. The insertion may extend to the falciform bone but it was very indistinct in serpens. In townsendi it was more readily followed and insertion on the falciform bone was observed.

M. flexor carpi radialis- arises from the medial epicondyl and inserts on the second and third metacarpals but the exact source of innervation could not be determined.

M. pronator teres- is a stout, well-defined, muscle which arises from the medial epicondyl of the humerus and inserts on the cephalic border of the radius.

M. flexor digitorum sublimis- corresponds to the condylo-ulnar flexor (described by McMurrich, 1902b). It arises from the medial epicondyl and inserts on the second phalanges of the middle three digits with the most ulnar part dividing to insert on both the fourth and fifth digits. This muscle really consists of three bipennate muscles bound together.

M. flexor digitorum profundus- is divisible into three heads. The ulnar head arises from the proximal part of the medial surface of the ulna. The central (condylar) head arises from the medial epicondyl and the radial head from the proximal third of the radius.

Tendons from the three heads unite at the wrist to form a common tendon which divides into five parts each of which inserts on the terminal phalanx of a digit. In townsendi and longicauda the insertion on the pollex was missing.

M. pronator quadratus- runs in an almost transverse direction between the radius and ulna. It arises from the distal quarter of the ulna and inserts on the corresponding part of the radius.

Muscles of the Pelvic Girdle and Limb

A. Extensor System

None of the muscles, attached to the pelvic girdle, exhibit variations in the three species which are sufficiently great to be considered adaptive.

Iliacus group- (fig. 20) is analogous to the subscapular group of the fore-limb. Some fibres of M. pectineus are supplied by the obturator nerve and are probably derived from the adductor group; the other fibres of M. pectineus and the other members of the group are supplied by branches of the femoral nerve.

M. iliacus- is a stout, well-defined muscle which arises in the iliac fossa and from the transverse processes of the last lumbar vertebra. It inserts on the lesser trochanter, deep to M. psoas major and partly on the shaft of the femur.

M. psoas major- may have been derived from M. quadratus lumbarum as described by Gregory and Camp (1918). It arises from the iliopectineal iminence and inserts onto the borders of the first three lumbar vertebrae.

M. pectineus- arises from the pubis craniad to the origin of M. adductor longus and inserts on the medial shaft of the femur.

Gluteal group- analogous to the latissimus dorsi-subscapular muscles of the fore-limb.

The muscles of this group occur in two layers. The lateral or superficial layer consists of M. fasciae latae, M. gluteus maximus, M. femorococcygeus and M. tenuissimus. M. fasciae latae is supplied by terminal branches of the superficial gluteal nerve; M. tenuissimus by a branch of the common peroneal nerve and the others by the superior gluteal nerve.

M. tensor fasciae latae- consists of a muscle sheet which, in serpens, is not as extensive as that described by Howell (1926) in Neotoma, or Greene (1935) in Rattus. It takes origin under M. gluteus maximus (and is continuous with it) at the crest of the ilium and inserts on the lateral fascia of the thigh and on the patella. Continuity with M. gluteus maximus was also found in townsendi and longicauda.

M. gluteus maximus- is a broad and relatively heavy muscle which arises from the spines of the third to fifth caudal vertebrae and inserts, by a tendon, on the greater trochanter of the femur.

M. femorococcygeus- arises from the transverse processes of the first two or three caudal vertebrae (perhaps also the last sacral) and inserts on the distal part of the femur and perhaps on the patella. The limits of this muscle were very hard to discern.

M. tenuissimus- not found.

Medial layer:

M. gluteus medius- lies beneath M. gluteus maximus. It takes origin from the spines of the first four sacral vertebrae, from the fascia and from the crest of the ilium and inserts on the greater trochanter of the femur.

M. piriformis- is not completely separable from M. gluteus minimus. It is, in serpens, a broader muscle than that described by Hill (1937) or Howell (1926) taking origin from the spines of the third and fourth sacral vertebrae and inserting on the greater trochanter caudomedial to the gluteal muscles.

M. gluteus minimus- is situated under M. gluteus medius and is similar in shape to the latter. It arises from the iliac ridge and inserts on the greater trochanter beneath M. gluteus medius.

Quadriceps femoris group- analogous to the triceps group of the brachium. The muscles of this group are supplied by the femoral nerve.

M. rectus femoris- has only one head in serpens and this arises from the area close to the acetabulum and from the end of the iliac ridge and inserts on the patella. In townsendi and longicauda two distinct heads situated very close together were found.

M. vastus lateralis- is a very heavy muscle which covers most of the lateral surface of the leg. It arises from the greater trochanter and lateral ridge of the femur and inserts on the patella.

M. vastus medialis and M. vastus intermedialis- are very closely associated but are separable. M. vastus medialis arises from the cranial and medial (distal position) borders of the thigh. M. vastus intermedialis arises from the entire extensor surface of the shaft of the femur. They insert together on the patella.

M. sartorius- was not found.

Tibial extensor group- analogous to radial and long extensors of the forearm, although represented by only three muscles which are supplied by the deep peroneal nerve.

M. extensor digitorum longus- arises from the lateral condyl of the femur (near the patellar groove) and then becomes divided into four tendons which pass under the ligamentum transversum, and inserts on the terminal phalanges of digits two to five. This muscle is sometimes called M. extensor digitorum communis.

M. extensor hallucis longus- arises from the interosseous membrane between the tibia and fibula and from the fascia of adjacent muscles and inserts onto the terminal phalanx of the hallux.

M. tibialis anterior- is a very large and heavy muscle that arises from the proximal half of the body of the tibia, the head of the tibia, and from aponeuratic fibres from region of the knee and inserts onto the first cuneiform. A secondary insertion of the first metatarsal may occur but the fibres were very indistinct.

Peroneal group- muscular branches of this group are associated with both the deep and the superficial branches of the common peroneal nerve. The peroneal muscles appear to be analogous to M. extensor carpi ulnaris, M. extensor indicis and pollicis and M. extensor digiti quinti of the fore-arm.

M. peroneus longus- originates on the latero-craniad process of head of the fibula, passes between tibialis anticus and peronei quarti and quinti and through a groove in the lateral malleolus to insert onto the first cuneiform and first metatarsal bones.

M. peroneus brevis- arises from the cranial surface of the fibula and from the interosseous membrane, a tendon passes behind and under the lateral malleolus and inserts into a tuberosity of the fifth metatarsal.

Mm. extensores brevis- is described by Hill (1935) as consisting, in Thomomys, of four muscles but only three were found in Microtus.

M. peroneus digiti quarti- arises from the head of the fibula, passes with M. peroneus longus, M. peroneus brevis, and M. peroneus digiti quinti under the lateral malleolus and becomes inserted on the metatarsal of the fourth digit.

M. peroneus digiti quinti- arises from the latero-caudad head of the fibula and inserts into the distal end of the fifth metatarsal.

M. extensor digitorum brevis- arises from the dorsal surface of the calcaneum and inserts onto the second and third digits but the place of insertion was very indistinct in the specimens used.

B. Flexor System

Adductor group- innervated by the obturator nerve. Functionally these muscles may be compared with the pectoral group of the fore-limb whether or not they are seriously homologous.

M. gracilis- is a wide, heavy muscle which is divisible into caudal and cranial portions. The caudal part arises from the pubis caudal to the obturator foramen and inserts on the anterior surface of the tibia. The cranial part arises from the border of the pubis deep to M. adductor longus and inserts with the caudal portion. The same two heads were found in all of the species.

M. adductor brevis- is the middle muscle in the adductor group. It arises from the ventral margin of the pubis ventral to the obturator foramen and cranial to the symphysis pubis and inserts on the medial (flexor) surface of the femur between M. adductor magnus and M. adductor longus.

M. adductor magnus- arises from the region of the symphysis pubis and inserts on the medial surface of the femur immediately distal to M. adductor brevis.

M. adductor minimus- was not found. Possibly it is joined to M. adductor magnus in this genus.

M. adductor magnus proprius- arises from the area between the obturator foramen and the ventral tuberosity of the ischium and inserts on the lateral ridge of the femur.

M. obturator externus- arises from the lateral border of the obturator foramen and inserts on the trochanteric fossa of the femur. This muscle was very hard to discern in all of the species.

Ischiotrochanteric group- supplied by branches of the tibial nerve.

M. obturator internus- takes origin from the medial surface of the ischium and inserts on the trochanteric crest and fossa.

M. gemellus superior- is rather poorly defined in serpens but takes origin in the area of the spine and dorsal border of the ischium and inserts in the trochanteric fossa in company with a tendon of M. obturator externus.

M. gemellus inferior- arises from the cranial surface of the ischial tuberosity and inserts onto the tendon of obturator internus. This muscle is not divided into dorsal and ventral parts in serpens.

M. quadratus femoris- originates on the lateral surface of the ischium and inserts onto the caudal surface of the femur and perhaps onto the lesser trochanter.

Hamstring group- innervated by a special branch of the tibial nerve. This group is analogous to biceps brachii and forms the largest muscle group in the body.

M. caudofemoralis- arises from the transverse processes of the first two caudal vertebrae and inserts onto the flexor (lateral) surface of the femur, proximal to the condyles and onto the patella.

M. semimenbranosus- originates from the caudal border of the ischium and inserts, by a tendon, on the mediocranial surface of the tibia. It is a very large muscle which is easily identified from either the lateral or medial surfaces.

M. semitendinous- is a fan-shaped muscle which arises from the spines of the last sacral and first two caudal vertebrae and inserts into the medial surface of the tibia with gracilus.

M. biceps femoris- has only one head in the species of Microtus studied and this arises from the dorsal ischial tuberosity and inserts onto the distal end of the femur, the lateral surface of the head of the tibia and the dense fascia of the leg and tendo calcaneum.

Flexor group of the leg- supplied by the tibial nerve, except M. quadratus plantae which is innervated by the lateral plantar nerve, a branch of the tibial.

M. gastrocnemius- is divided into lateral and medial heads. The lateral head arises from the lateral epicondyl of the femur and from a sesamoid bone in the tendon. The medial head arises from the medial epicondyl and from a sesamoid in the tendon. Both heads insert into the tuberosity of the calcaneus.

M. plantaris- with the gastrocnemius muscles belongs to the superficial layer of muscles. It arises from the lateral epicondyl by a tendon which passes over the heel beyond the tendon calcaneus, and divides into at least two tendons which are inserted, by slips, on the second phalanges of all the digits.

M. soleus- is a spindle -shaped muscle arising from the head of the fibula and inserting on the calcaneum in company with the gastrocnemius muscles.

M. popliteus- arises from the lateral epicondyl of the femur and inserts on the proximal third of the medial surface of the tibia.

M. flexor digitorum tibialis- arises from the medial ridge of the tibia and is associated with M. popliteus. It becomes tendinous and passes through a groove in the medial malleolus at which point the tendon divides into two parts. One portion inserts on the plantar surface of the first metatarsal and the other part unites with the tendon of M. flexor digitorum fibularis.

M. tibialis posterior- is closely associated morphologically with M. flexor tibialis. It arises with the latter and, becoming tendinous, passes over the medial part of the ankle to insert on a sesamoid bone of the tarsus.

M. flexor digitorum fibularis- (flexor digitorum longus) is a large muscle which occupies the space between tibia and fibula and passes between the astrogalus and ankle bones to sole of foot. It arises from the tibia, and fibula and from the interosseous membrane and inserts onto all five digits in close association with M. flexor digitorum tibialis.

M. quadratus plantae- not discovered.

Discussion

In the course of this study a detailed comparison has been made of the muscular and skeletal anatomy of three species of Microtines, *Microtus oregoni serpens*, *M. townsendi* and *M. longicauda*. In addition some comparisons have been drawn between the foregoing species and *M. richardsoni* as represented by a single juvenile specimen. Most, if not all, species of *Microtus* burrow to a greater or less degree but *M. o. serpens* differs from the other three species studied in being primarily subterranean in its habits. On the basis of this study it is possible to state that there seems to be very little variation of an interspecific nature in the muscular anatomy of species within the genus *Microtus*. *M. townsendi* and *longicauda* do have some minor divergencies such as the robust tail muscles, the relatively much longer os coxae, the presence of eyelashes, and the absence of a pollex in *longicauda*. Also in the latter species the cervical vertebrae are more flattened and the spines and zygopophyses show a greater degree of development.

The exception to this condition is to be seen in *M. o. serpens* in which certain parts of the animal are apparently strongly modified in a direction which seems to better adapt this animal to its subterranean mode of life. Superficially, *M. o. serpens* is a small Microtine at least one-third smaller in mass than adults of *M. townsendi* and *M. longicauda*. External features which are of adaptive significance are the soft, plush-like pelage, the short tail, and the arrangement of the vibrissae, the longest ones being furthest from the snout rather than scattered. Of probably adaptive significance are the ears, which are furred on the inner surface, and provided with a pronounced fold on the anterior part of the helix.

The eyes of oregoni ~~*serpens*~~ are only about one-half the size of those of the larger species, the same relationship is seen in the lachrymal glands. Associated with the smaller eyes is an interesting modification of the orbicularis oculi muscle whereby this becomes strongly developed, doubtless as an aid in preventing dirt from entering the eyes.

Unlike most genera of burrowing mammals o. *M.serpens* does not have conspicuously enlarged or elongated claws and fore-feet. However, many other modifications of the fore-limbs for digging occur. Conspicuous among these is the shortening of the limbs and the inclusion of a larger part of them within the body skin. Almost the entire musculature of the anterior segment of the body is much more strongly developed in oregoni ~~*serpens*~~ than in any of the other species and it is logical to associate this development with increased ability in excavating burrows. This specialization of the musculature involves most prominently the muscles of the ~~masticatory~~ shoulder, chest and fore-limb but to a lesser degree certain of the masticatory muscles and the musculature of the spinal column are also involved.

A detailed examination of these muscular specializations reveals that the masticatory muscles, i.e., masseter, temporalis, pterygoideus externus and pterygoideus internus, show some specific variations. The superficial part of the masseter muscle contains more muscle fibres in oregoni ~~*serpens*~~ than it does in *townsendi* or *longicauda;* the fascia which covers the muscle is also heavier in oregoni *serpens* than in the latter forms but that found in *richardsoni* is decidedly the heaviest, possibly because it is to be a larger animal. This relationship is also seen in the development of the cutaneous maximus and platysma. Other parts of the masseter are more uniform, with oregoni *serpens* having muscles which appear to be slightly the largest. The temporalis muscle is not as extensive in oregoni *serpens* as it is in *townsendi* but it is a more robust muscle in the former. There are no differences between the external pterygoid muscles but the internal pterygoid is decidedly larger in oregoni *serpens*.

Few skeletal modifications corresponding to these variations in masticatory musculature have occurred but a small process from which part of the masseter superficialis originates has developed ventral to the cranio-ventral border of the infraorbital foramen; there is no definite evidence on the skull of greater development of the temporalis muscles in any of the species although the posterior divergence of the zygomatic arch may be a trifle broader in *townsendi* to accommodate the greater breadth of the temporalis muscle in this species. The angular process of the mandible into which the enlarged pterygoideus internus is inserted is, if anything, less thickened in ~~*serpens*~~ which is hard to explain since the muscle enlargement was uniformly present in three specimens.

The neck muscles show some specific variations, the mylohyoideus is similar in the three species but the transversus mandibularis contains more fibres in *townsendi* than are found in this muscle in *serpens* or *longicauda*. The digastricus is better developed in *serpens* being decidedly stouter when comparisons of length to breadth are taken. In each of the species it is a single muscle with a constriction between the anterior and the posterior bellies; although this constriction is barely detectable in *richardsoni*. Both the elevators and the depressors of the lower jaw are thus seen to show their greatest development in the subterranean form.

The platysma is best developed in ~~*serpens*~~, the post-auricularis portion of the muscle is more distinctly separable from the platysma in *serpens* and the platysma generally has more muscle fibres in the latter.

In townsendi and longicauda it is difficult to trace because the fibres adhere very closely to the skin. This same tendency is found in such muscles as the spinotrapezius and the cutaneous maximus. All of the superficial head muscles are more definitely defined in serpens than they are in townsendi and longicauda. The occipitalis muscle is separated from the platysma with difficulty in townsendi but it is easily discovered in serpens. The interscutularis is always a thin muscle in Microtines but it is apparently missing in longicauda although this may have been peculiar to the one specimen. The preauricularis (frontalis) adheres to the skin more tightly in townsendi and longicauda and hence is more difficult to trace. Orbicularis oculi is much less distinct in townsendi and longicauda than in serpens and the orbicularis oris is devisible into distinct slips in serpens only. The general enlargement of the superficial head muscles may not be related to environment but the greater development of the muscles around the eyes and mouth are undoubtedly an advantage to an underground form. These variations have not affected the skull formation in any case.

The muscles of the hyoid constrictor group do not show any marked variations. In the trapezius group the origin of the sternomastoideus is found on the edge of the clavicle at its junction with the manubrium sterni in townsendi and longicauda rather than from the lateral surface of the manubrium as was found in three specimens of serpens. There is little variation between the cleidomastoideus and cleidooccipitalis muscles. The acromiotrapezius muscle is decidedly different in serpens having an insertion which is so heavy that it forms a thick ridge on either side of the mid-dorsal line giving the impression of a raised portion. In comparison the muscle appears to be flat in townsendi and is even less well-developed in longicauda. In *richardsoni* the fixative used had had a drying effect on the muscles which may have accounted for the heavy appearance of them. In any case *serpens* has much the largest acromiotrapezius muscle of any of the species which were dissected. The spinotrapezius muscle is unique in *serpens* in that it is divisible into two distinct parts, in *townsendi* the anterior portion is very limited and in *longicauda* and *richardsoni* it is a single muscle. The trapezius muscle draws the scapulae dorsally, upward and forward and the greater development in *serpens* of these muscles would give it greater strength and flexibility. Correlation between this muscle development and the structures of the scapulae seems to be impossible as far as shape is concerned although the vertebral border of the scapula is slightly more thickened in *serpens*.

In the dorsal division of the myotomic musculature there seem to be more fibres in each division of the sacrospinalis, iliocostalis, and longissimus muscles of *serpens*. The muscles which are attached to the axis, the semispinalis capitis, spinalis dorsi and rectus capitis posterior major are slightly better developed in *serpens* although the difference is not sufficient to account for the development of transverse processes in *serpens* instead of merely a slight elevation on their sites as is seen in *townsendi* and *longicauda*. The other body muscles do not show sufficient differences for conclusions of any kind to be drawn from them with the exception of the tail muscles which are decidedly reduced in *serpens*. They are much better developed in *longicauda* than in either of the other species.

The muscles attached to the pectoral girdle show the most marked differences of any of the muscles. They are almost universally better developed in serpens than they are in townsendi or longicauda. The levator scapulae and serratus anterior muscles are easily divisible into separate muscles in serpens but this is not as clearly the case in townsendi or longicauda where they are separable with difficulty, if at all. Possibly since these muscles are used to draw the scapulae craniad, ventrad, and against the thoracic wall and have become enlarged to perform this function they have become two separate muscles in the course of development. The rhomboideus muscle is actually smaller in townsendi than it is in serpens which means that it is a great deal smaller when considered relatively, its function is to draw the scapula toward the vertebral column. The latissimus dorsi is inserted into the axilla by widely separated digitations in townsendi, in serpens and longicauda the insertion is single. The acromio-deltoideus is very prominent in serpens being so well developed that it alters the appearance of the position of the fore-limbs giving them the appearance of being drawn craniad. The spinodeltoideus is also larger in serpens. The last two muscles raise and rotate the humerus and greater development must be a decided help in digging.

The pectoralis muscles are the most remarkable of the muscles attached to the pectoral girdle and limb. When dissected from the specimen they were found to have a volume which was almost exactly the same in serpens and townsendi although the latter had a total body volume of almost one and one-third times that of the former. This greater development is correlated with the development of a keel on the manubrium sterni and the sternebrae in serpens to give a greater area for muscle attachment. Since these muscles serve to draw the fore-limb toward the chest the enlargement found in serpens is in accordance with the enlargement of the extensor muscles found in the same animal.

The fore-limb is shortened in *serpens* in per cent of total body length and hence the muscles are also shortened. The muscles of the brachium are not as clearly defined (readily distinguishable) in *serpens* but are heavier muscles when proportion of length to width is considered. The muscles of the anti-brachium give the appearance of being even smaller than they really are owing to the differences in sizes of the species. Possibly the muscles are well-developed as a compensatory measure for the shortening.

The muscles of the back and those attached to the pelvic girdle and limb show practically no specific differences. Apparently the hind limbs do not become especially adapted to a subterranean existence since they are not required for digging.

Microtis o. serpens appears to represent one of the earliest stages of adaptive specialization of a mammal for a subterranean life. In this species the fur, eyes, ears, and tail all show approach to the condition found in such highly specialized burrowers as the moles. The musculature reveals many obvious changes in mass and some subdivision but other than a slight lengthening of the scapula and a fore-shortening of the humerus and radius no radical skeletal changes have occurred. The position of the fore-limb has not been modified and the fore feet and claws are not enlarged.

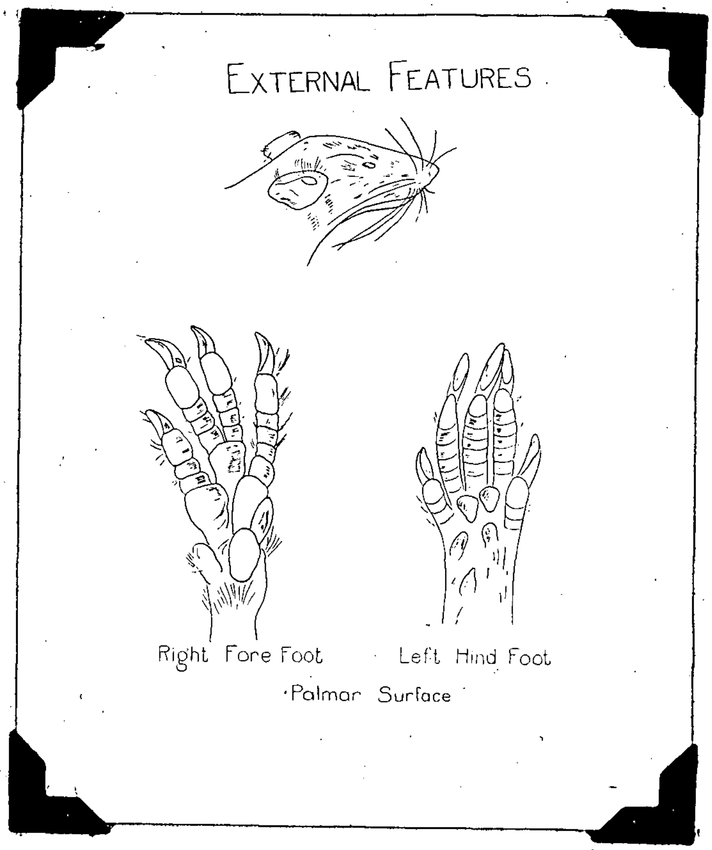

EXTERNAL FEATURES
Right Fore Foot
Left Hind Foot
Palmar Surface

Fig. 1

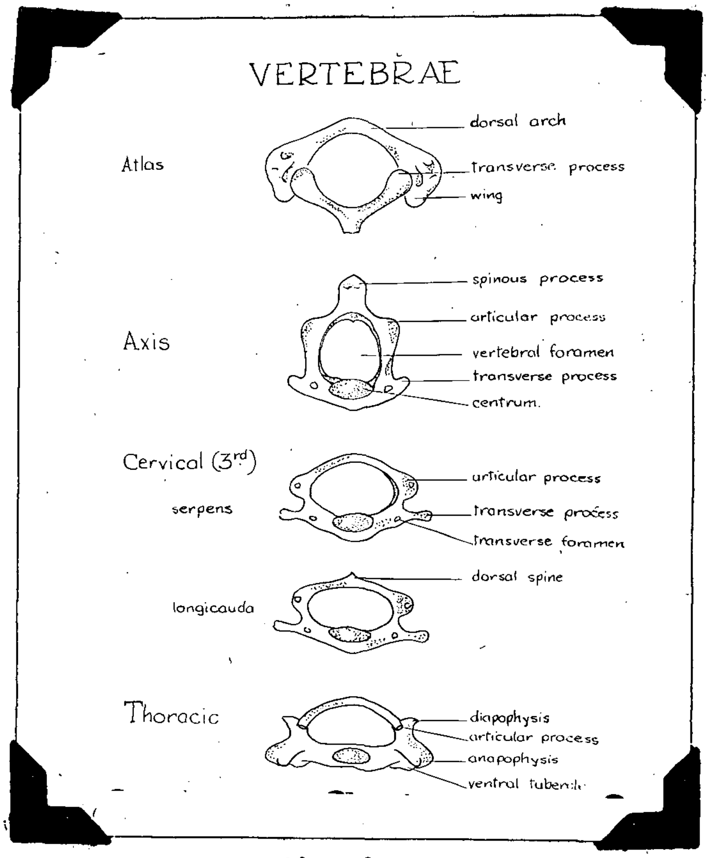

VERTEBRAE
Atlas
dorsal arch
transverse process
wing
Axis
spinous process
articular process
vertebral foramen
transverse process
centrum.
Cervical (3^{rd})
serpens
articular process
transverse process
transverse foramen
longicauda
dorsal spine
Thoracic
diapophysis
articular process
anapophysis
ventral

Fig. 2

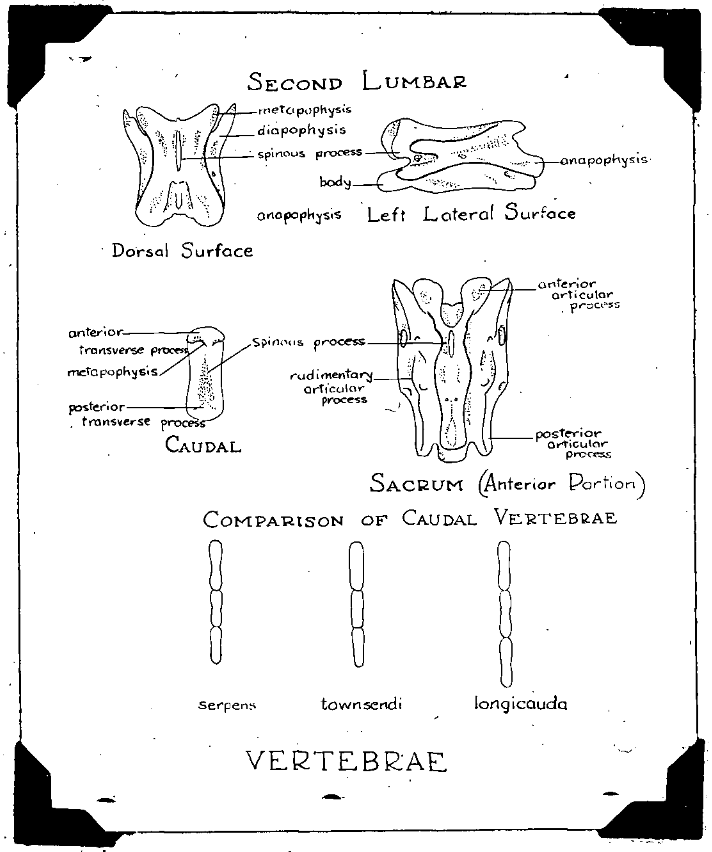

SECOND LUMBAR
metapophysis
diapophysis
spinous process
body
anapophysis
anapophysis
Left Lateral Surface
Dorsal Surface
anterior transverse process
metapophysis
posterior transverse process
Spinous process
CAUDAL
anterior articular process
rudimentary articular process
posterior articular process
SACRUM (Anterior Portion)
COMPARISON OF CAUDAL VERTEBRAE
serpens
townsendi
longicauda
VERTEBRAE

Fig. 3

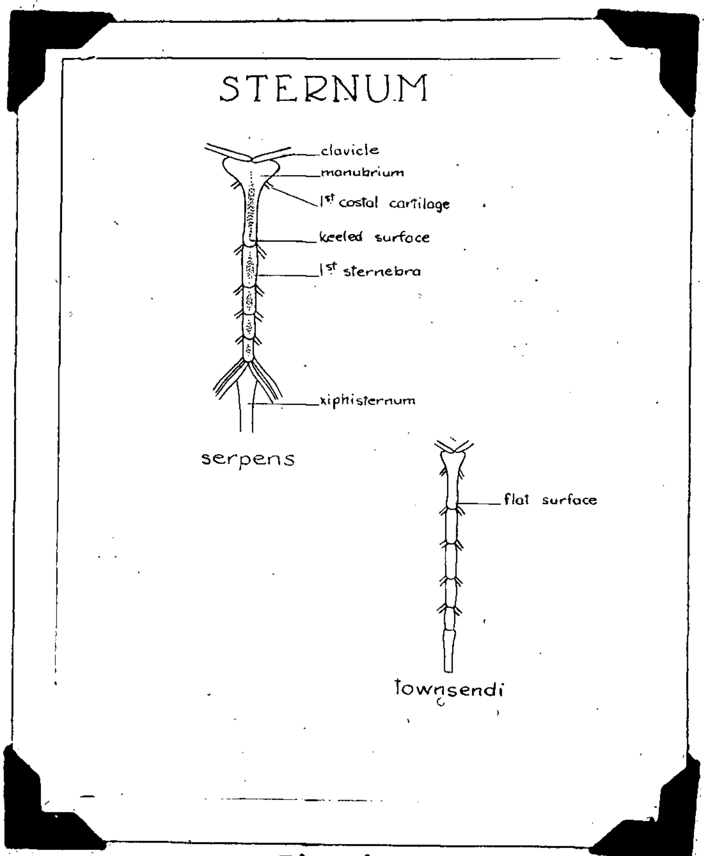

STERNUM
clavicle
manubrium
1st costal cartilage
keeled surface
1st sternebra
xiphisternum
serpens
flat surface
townsendi

Fig. 4

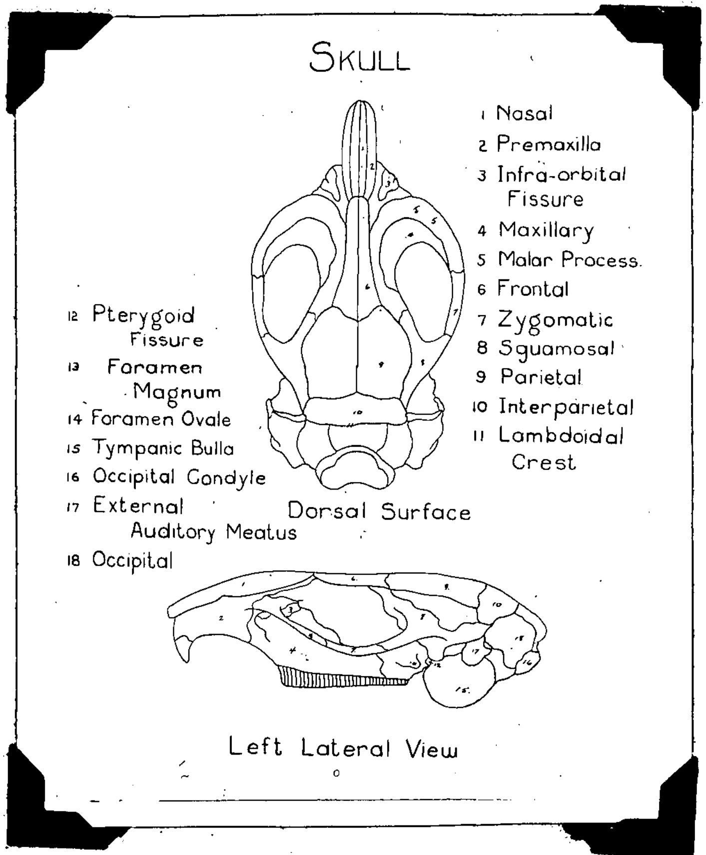

SKULL
1 Nasal
2 Premaxilla
3 Infra-orbital Fissure
4 Maxillary
5 Malar Process.
6 Frontal
7 Zygomatic
8 Squamosal
9 Parietal
10 Interparietal
11 Lambdoidal Crest
12 Pterygoid Fissure
13 Foramen Magnum
14 Foramen Ovale
15 Tympanic Bulla
16 Occipital Condyle
17 External Auditory Meatus
18 Occipital
Dorsal Surface
Left Lateral View

Fig. 5

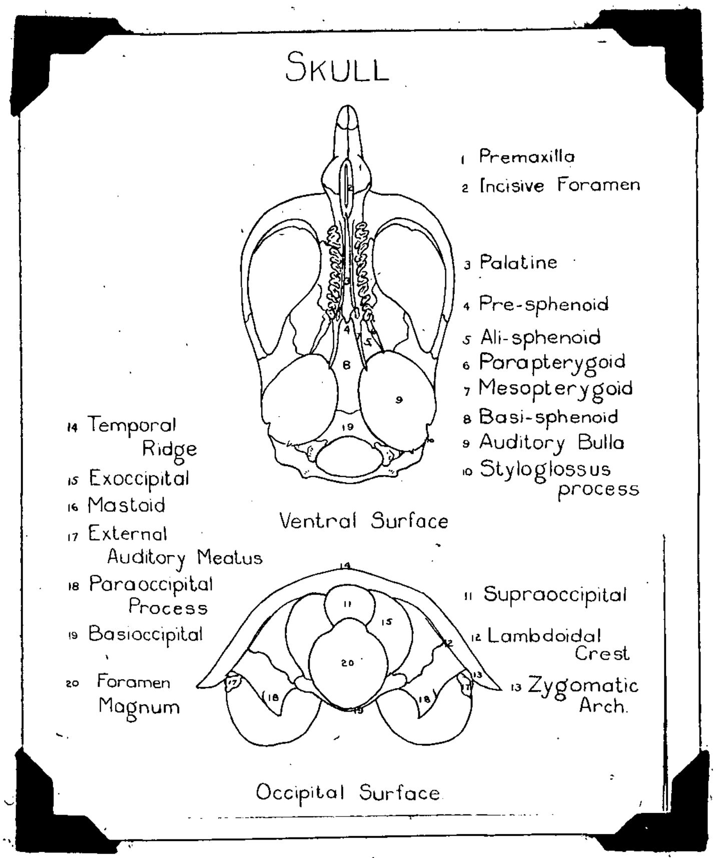

SKULL
1 Premaxilla
2 Incisive Foramen
3 Palatine
4 Pre-sphenoid
5 Ali-sphenoid
6 Parapterygoid
7 Mesopterygoid
8 Basi-sphenoid
9 Auditory Bulla
10 Styloglossus process
14 Temporal Ridge
15 Exoccipital
16 Mastoid
17 External Auditory Meatus
18 Paraoccipital Process
19 Basioccipital
20 Foramen Magnum
Ventral Surface
11 Supraoccipital
12 Lambdoidal Crest
13 Zygomatic Arch.
Occipital Surface

Fig. 6

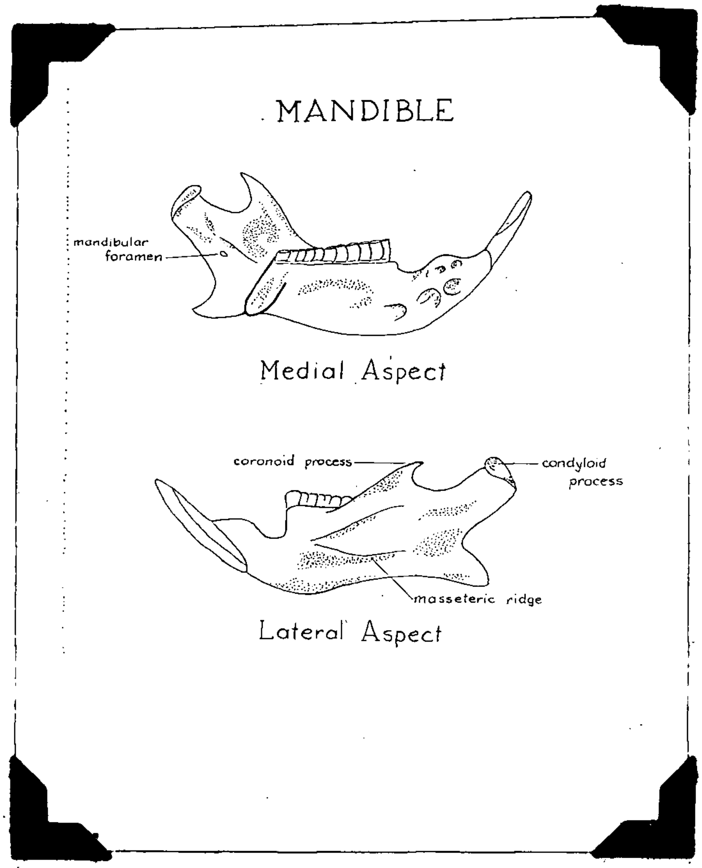

MANDIBLE
mandibular foramen
Medial Aspect
coronoid process
condyloid process
masseteric ridge
Lateral Aspect

Fig. 7

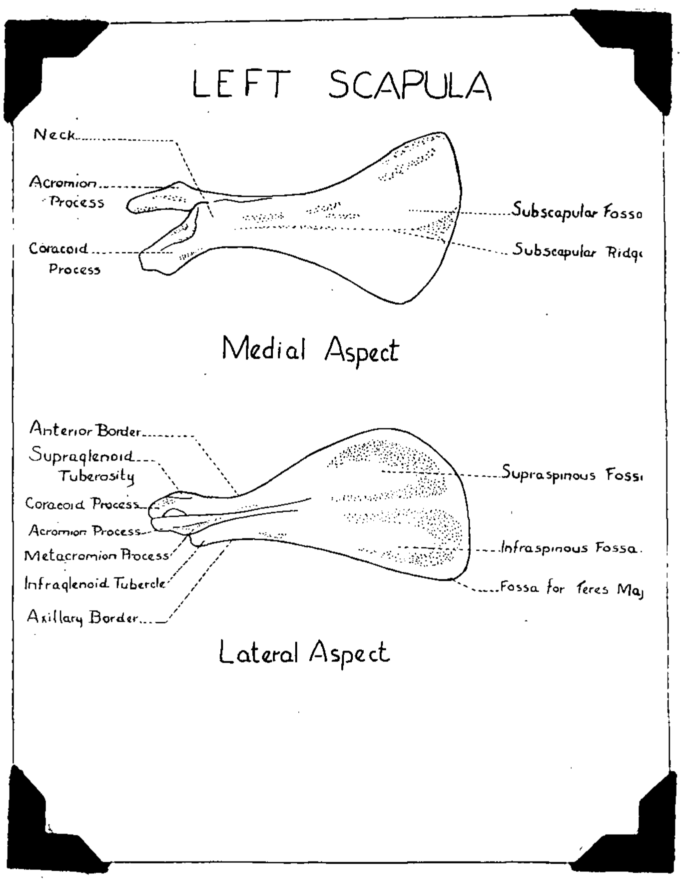

LEFT SCAPULA
Neck
Acromion Process
Coracoid Process
Subscapular Fossa
Subscapular Ridg
Medial Aspect
Anterior Border
Supraglenoid Tuberosity
Coracoid Process
Acromion Process
Metacromion Process
Infraglenoid Tubercle
Axillary Border
Supraspinous Foss
Infraspinous Fossa
Fossa for Teres Ma
Lateral Aspect

Fig. 8

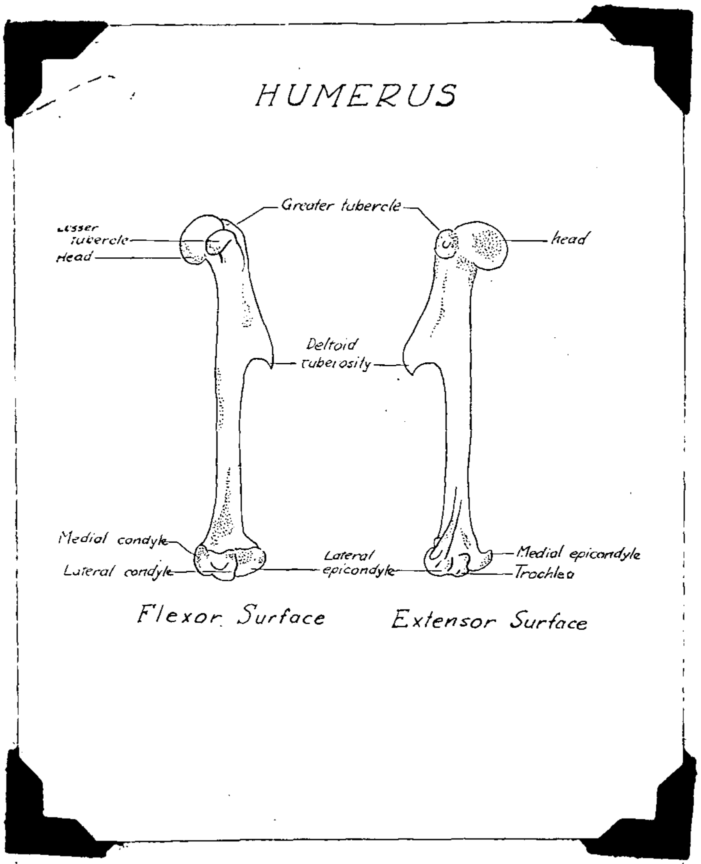

HUMERUS
Greater tubercle
Lesser tubercle
Head
head
Deltoid tuberosity
Medial condyle
Lateral condyle
Lateral epicondyle
Medial epicondyle
Trochlea
Flexor Surface
Extensor Surface

Fig. 9

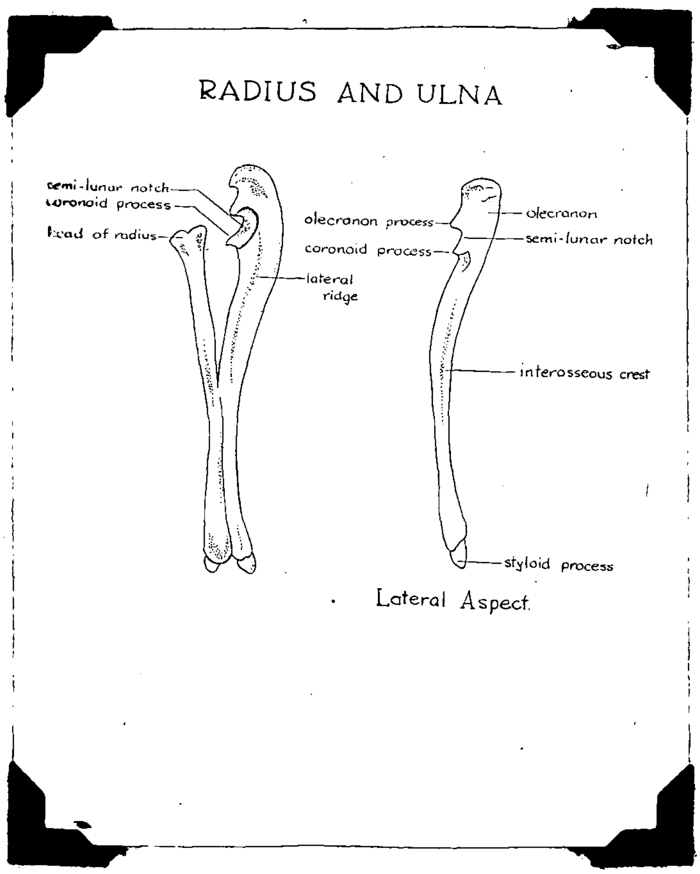

RADIUS AND ULNA
semi-lunar notch
coronoid process
head of radius
lateral ridge
olecranon process
coronoid process
olecranon
semi-lunar notch
interosseous crest
styloid process
Lateral Aspect

Fig. 10

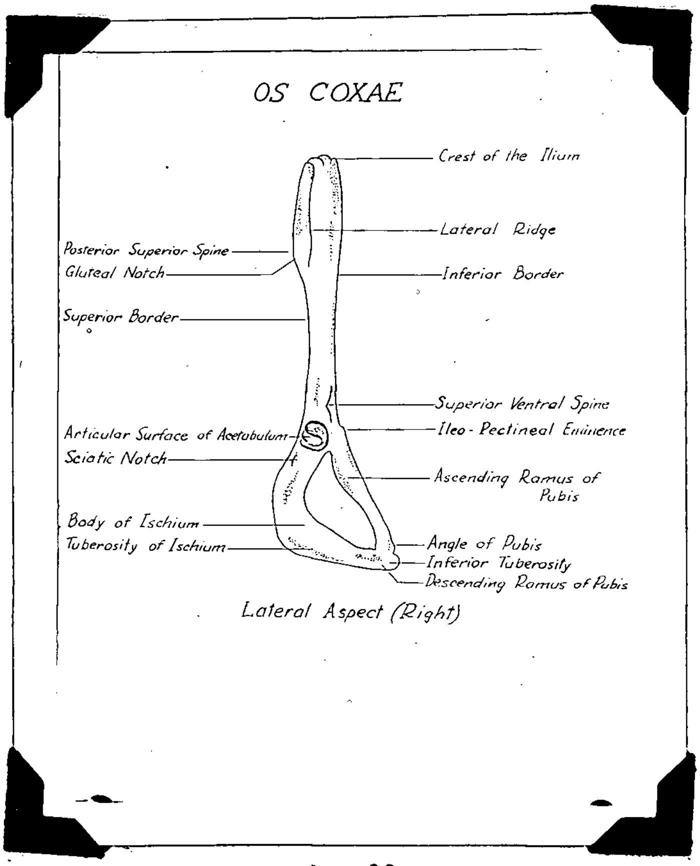

OS COXAE
Crest of the Ilium
Lateral Ridge
Posterior Superior Spine
Gluteal Notch
Inferior Border
Superior Border
Superior Ventral Spine
Ileo-Pectineal Eminence
Articular Surface of Acetabulum
Sciatic Notch
Ascending Ramus of Pubis
Body of Ischium
Tuberosity of Ischium
Angle of Pubis
Inferior Tuberosity
Descending Ramus of Pubis
Lateral Aspect (Right)

Fig. 11

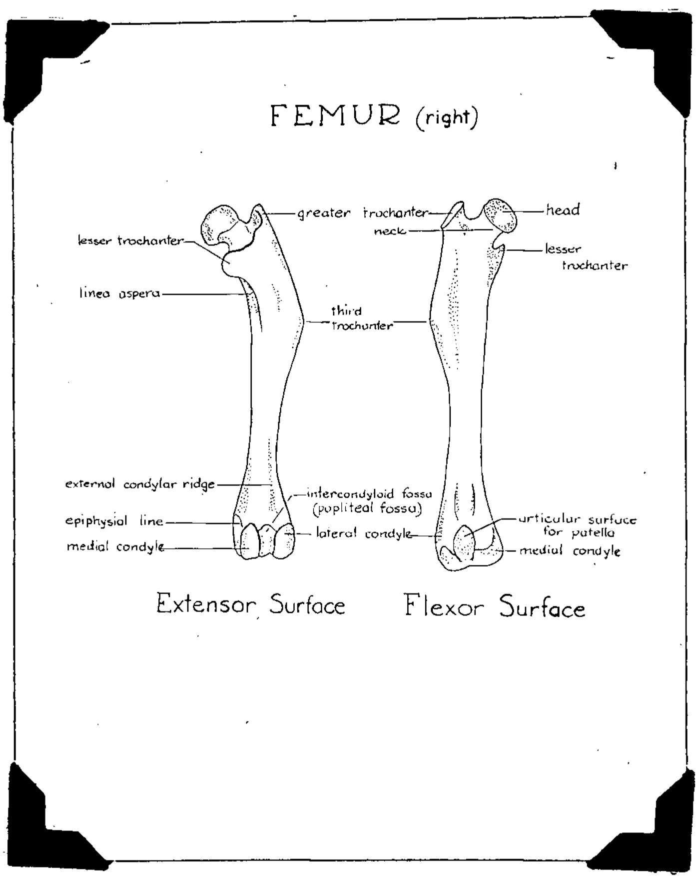

FEMUR (right)
greater trochanter
head
neck
lesser trochanter
lesser trochanter
linea aspera
third trochanter
external condylar ridge
interconduloid fossa (popliteal fossa)
epiphysial line
articular surface for patella
medial condyle
lateral condyle
medial condyle
Extensor Surface
Flexor Surface

Fig. 12

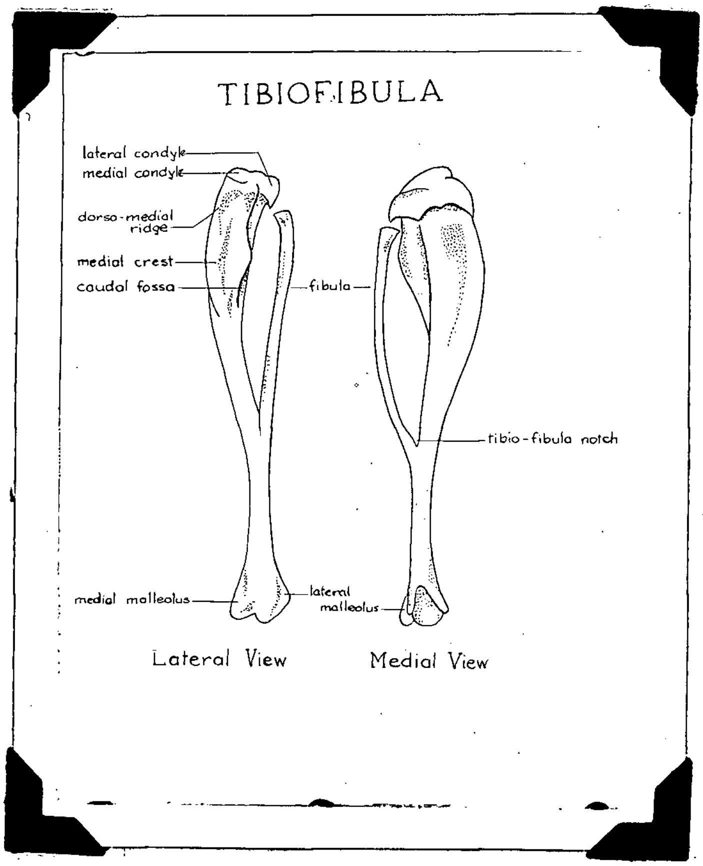

TIBIOFIBULA
lateral condyle
medial condyle
dorso-medial ridge
medial crest
caudal fossa
fibula
tibio-fibula notch
medial malleolus
lateral malleolus
Lateral View
Medial View

Fig. 13

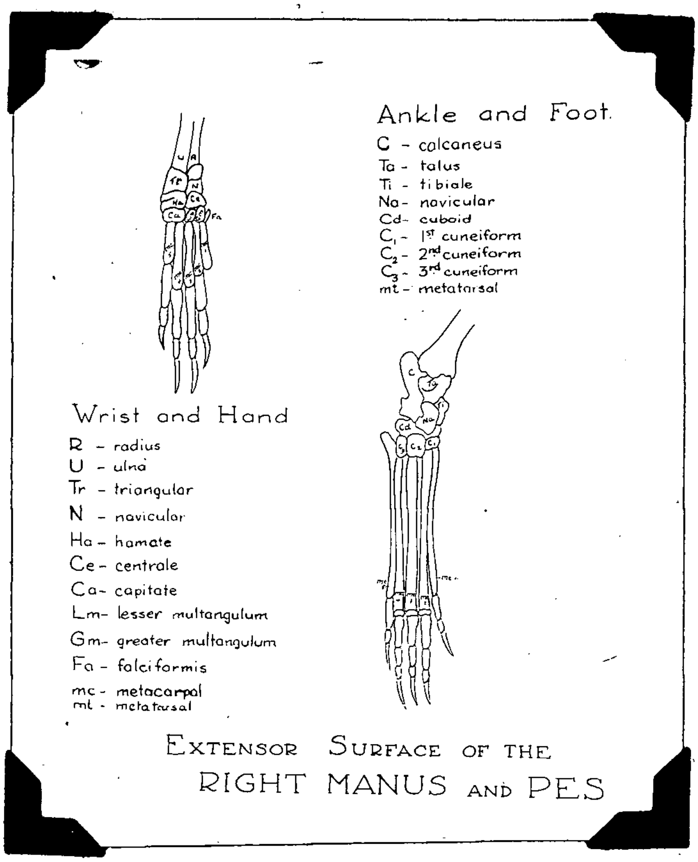

Ankle and Foot
C - calcaneus
Ta - talus
Ti - tibiale
Na - navicular
Cd - cuboid
C1 - 1st cuneiform
C2 - 2nd cuneiform
C3 - 3rd cuneiform
mt - metatarsal
Wrist and Hand
R - radius
U - ulna
Tr - triangular
N - navicular
Ha - hamate
Ce - centrale
Ca - capitate
Lm - lesser multangulum
Gm - greater multangulum
Fa - falciformis
mc - metacarpal
mt - metatarsal
Extensor Surface of the
Right Manus and Pes

Fig. 14

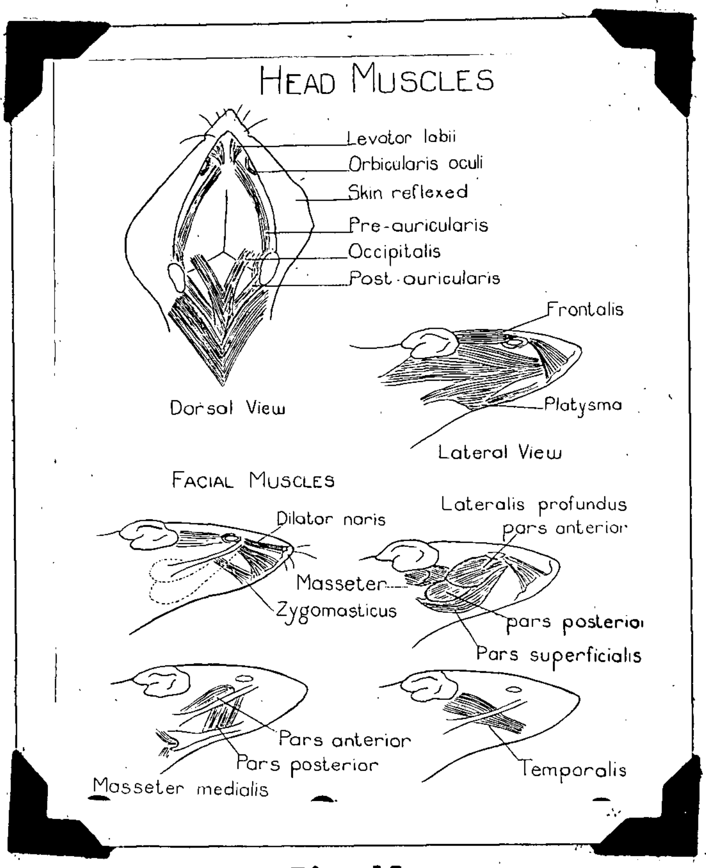

HEAD MUSCLES
Levator labii
Orbicularis oculi
Skin reflexed
Pre-auricularis
Occipitalis
Post-auricularis
Frontalis
Dorsal View
Platysma
Lateral View
FACIAL MUSCLES
Dilator naris
Lateralis profundus
pars anterior
Masseter
Zygomasticus
pars posterior
Pars superficialis
Pars anterior
Pars posterior
Masseter medialis
Temporalis

Fig. 15

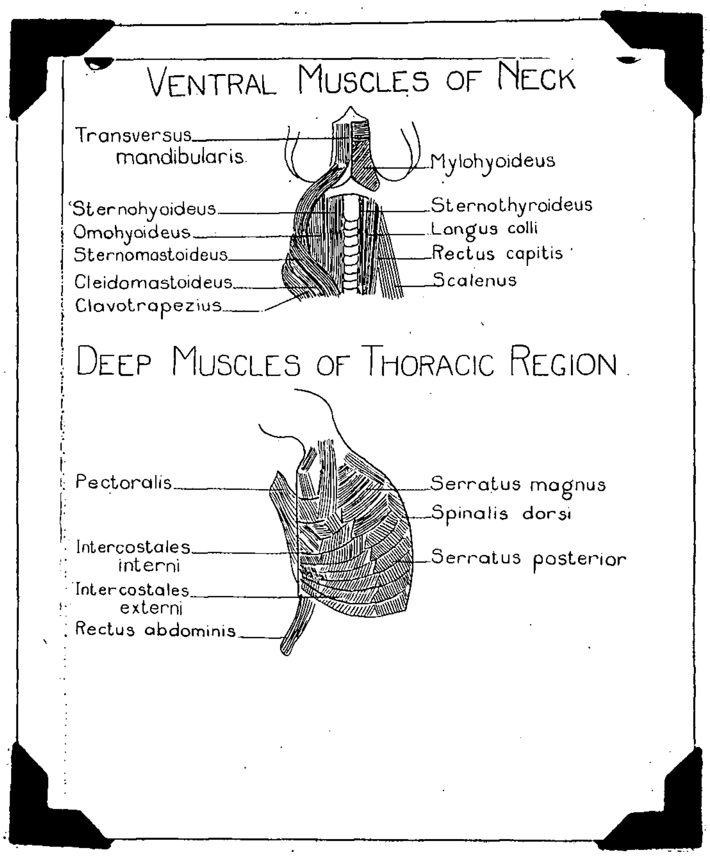

VENTRAL MUSCLES OF NECK
Transversus mandibularis
Mylohyoideus
Sternohyoideus
Omohyoideus
Sternomastoideus
Cleidomastoideus
Clavotrapezius
Sternothyroideus
Longus colli
Rectus capitis
Scalenus
DEEP MUSCLES OF THORACIC REGION
Pectoralis
Intercostales interni
Intercostales externi
Rectus abdominis
Serratus magnus
Spinalis dorsi
Serratus posterior

Fig. 16

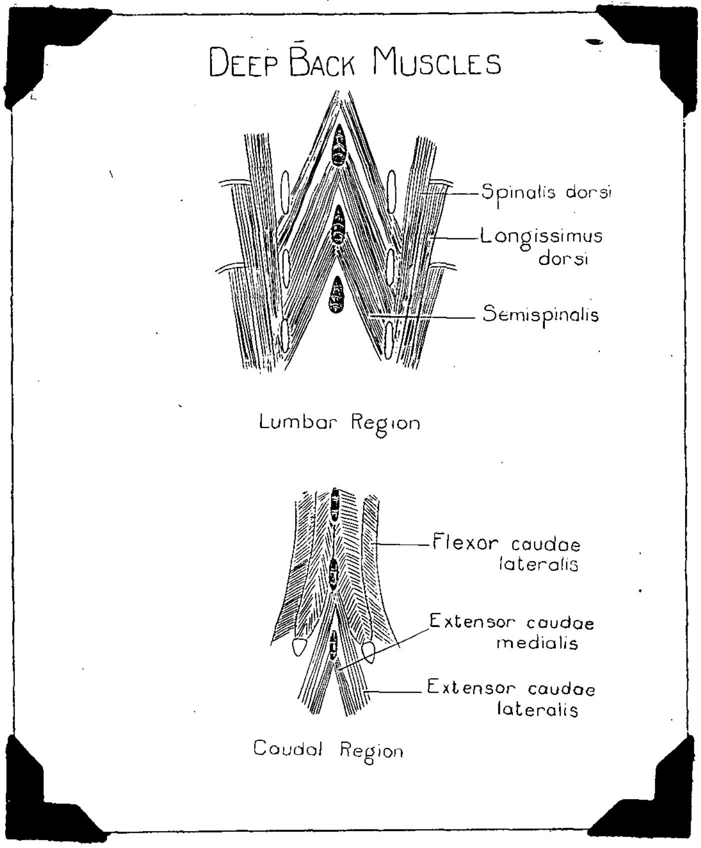

DEEP BACK MUSCLES
Spinalis dorsi
Longissimus dorsi
Semispinalis
Lumbar Region
Flexor caudae lateralis
Extensor caudae medialis
Extensor caudae lateralis
Caudal Region

Fig. 17

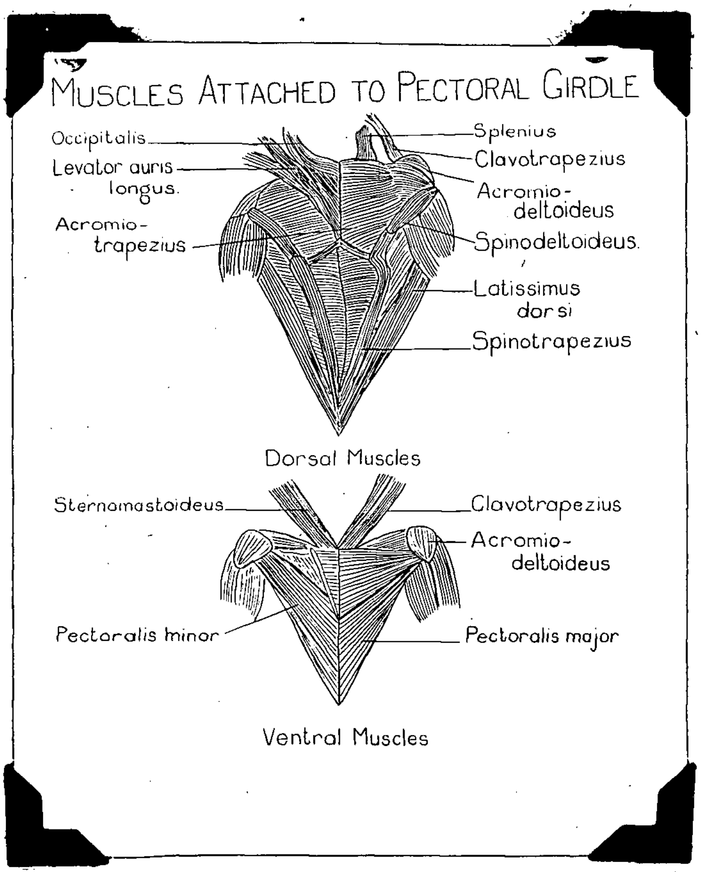

MUSCLES ATTACHED TO PECTORAL GIRDLE
Occipitalis
Levator auris longus.
Acromio-trapezius
Splenius
Clavotrapezius
Acromio-deltoideus
Spinodeltoideus.
Latissimus dorsi
Spinotrapezius
Dorsal Muscles
Sternomastoideus
Clavotrapezius
Acromio-deltoideus
Pectoralis minor
Pectoralis major
Ventral Muscles

Fig. 18

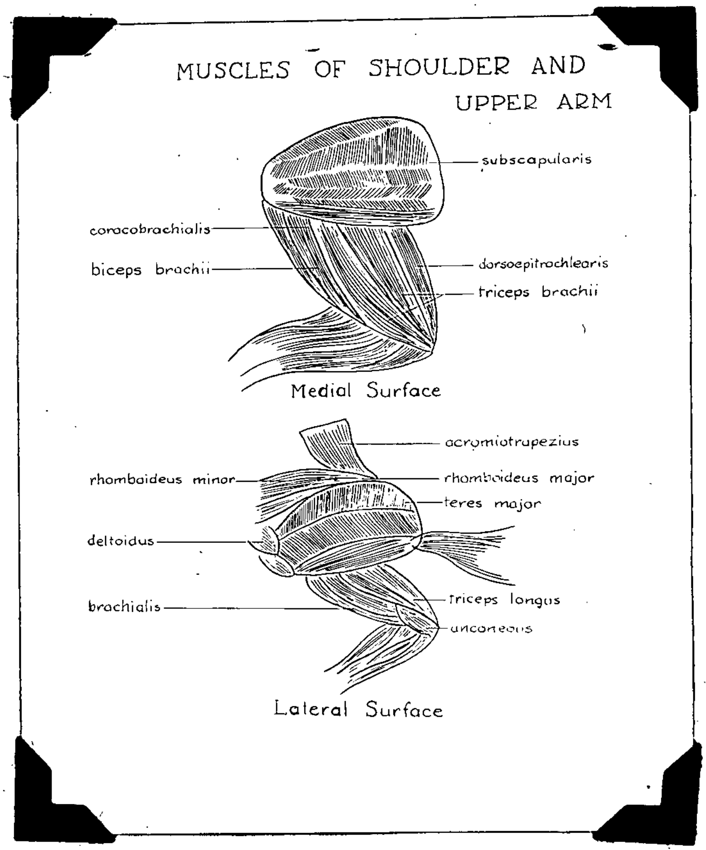

MUSCLES OF SHOULDER AND
UPPER ARM
subscapularis
coracobrachialis
biceps brachii
dorsoepitrochlearis
triceps brachii
Medial Surface
acromiotrapezius
rhomboideus minor
rhomboideus major
teres major
deltoidus
brachialis
triceps longus
anconeous
Lateral Surface

Fig. 19

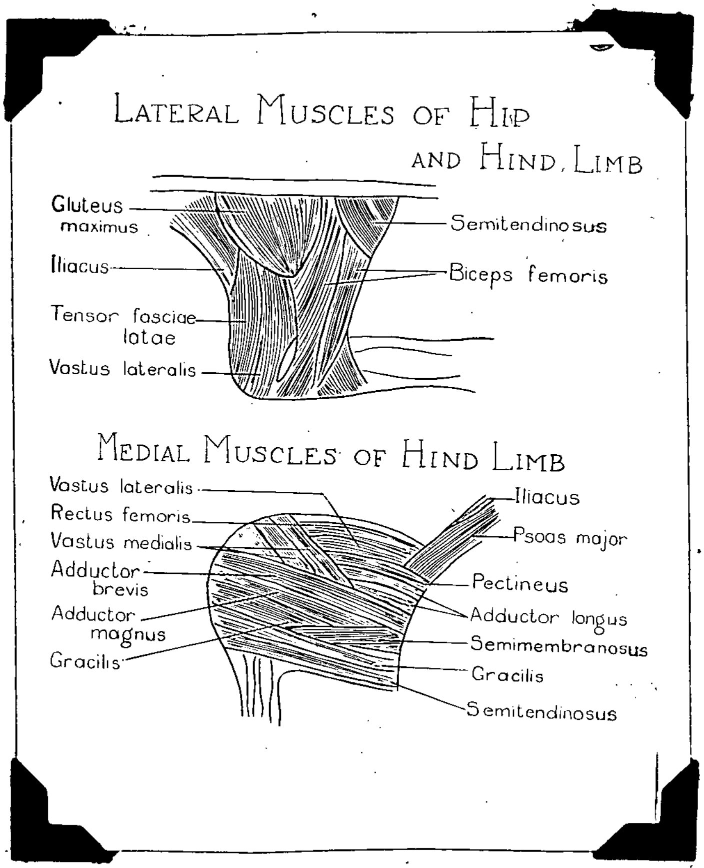

LATERAL MUSCLES OF HIP
AND HIND LIMB
Gluteus
maximus
Iliacus
Tensor fasciae
latae
Vastus lateralis
Semitendinosus
Biceps femoris
MEDIAL MUSCLES OF HIND LIMB
Vastus lateralis
Rectus femoris
Vastus medialis
Adductor
brevis
Adductor
magnus
Gracilis
Iliacus
Psoas major
Pectineus
Adductor longus
Semimembranosus
Gracilis
Semitendinosus

Fig. 20

Literature Cited

Edgeworth

1916 - Cranial Muscles of Vertebrates

Cambridge University Press.

1911 - Morphology of Cranial Muscles in Some Vertebrates

Quart. Jour. Micro. Sci., 56: 167-316, 100 figs. in text.

Greene, E.C.

1935 - Anatomy of the Rat

American Philosophical Society Transactions

University of Pennsylvania Press, 1-370, 339 figs. in text.

Gregory W.K. and Camp, C.L. - see p. 2.

Hill, J.E.

1937 - Morphology of the Pocket Gopher. Mammalian Genus Thomomys

Univ. of Calif. Publications in Zoology, 42: 81-172,

26 figs. in text.

Howell, A.B.

1924 - Individual and Age Variations in *Microtus Montanus Yosemite*

Jour. Agric. Research 28, No. 10, Dec. 4: 997-1015.

1926 - Anatomy of the Wood Rat

Williams and Wilkins Co., Baltimore

i-x, 1-225, pls. 1-3, 37 figs. in text.

1936 - Phylogeny of the Distal Musculature of the Pectoral Girdle

Jour. of Morphology 60: 287-315, 3 figs. in text.

1936 - The Phylogenetic Arrangement of the Muscular System

Anat. Record 66: 295-316.

Lewis, W.K.

1910 - The Development of the Muscular System

In Keibel and Mall, Manual of Human Embryology

1-ch. 12: 454-522, 55 figs. in text.

McMurrich, J.P.

1902(b) Phylogeny of the fore-arm flexors

Amer. Jour. of Anat. 2: 177-209 (mammals 186-209)

Parsons, F.G.

1894(b) On the Morphology of Tendon Achilles

Jour. Anat. Physiol. 28: 414-418, 2 figs. in text.

Gregory, W.K. and Camp, C.L.

1918 - Studies of Comparative Myology and Osteology

Bull. Amer. Mus. Nat. Hist.

38: 447-563, pls. 39-50, 16 figs. in text.