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A COMPARATIVE MYOLOGICAL STUDY OF THREE SUBGENERA OF *PEROMYSCUS*

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THE study reported here was begun several years ago with two principal objectives. The more important of these was to provide a "yard-stick" of the degree of myological variation which corresponds with the generally accepted concepts of subgeneric status. Secondly, it was hoped that the study would reveal evidence bearing on the validity of the accepted classification.

Except for the inclusion of *Baiomys*, which is now considered to be a separate genus, Osgood's classification of 1909 has remained generally acceptable until recently. Hooper (1958), however, called for the elevation of the subgenus *Ochrotomys* to full generic rank, and presented evidence indicating that the classification was in need of review. Layne (1960) followed Hooper in giving *Ochrotomys* generic rank.

Originally it was my intention to treat all five subgenera of *Peromyscus* in one account. Since dissectable specimens of *Megadontomys* and *Podomys* have not been available, this account of representatives of three subgenera is presented with the hope that I may follow soon with the others.

MATERIALS AND METHODS

In addition to numerous specimens of *Peromyscus leucopus* personally collected by the author, the following specimens from the collection of the Museum of Zoology, University of Michigan, were dissected: *Peromyscus* (*Peromyscus*) *leucopus*, Michigan, Berrien Co., 3; *Peromyscus* (*Ochrotomys*) *nuttalli*, Virginia, Campbell Co., 3; *Peromyscus* (*Haplomylomys*) *eremicus*, Texas, Brewster Co., 3.

These specimens were the basis for the descriptions which follow.

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For various reasons, some dissection was done on two specimens of *Peromyscus difficilis* and several of *P. maniculatus*. Since these dissections provided no comparative data not already demonstrated by *P. leucopus*, no further consideration will be given to them.

The procedure followed was to do parallel dissections on representatives of the three species, comparing each muscle directly. In instances where it was appropriate to use measurements, these were taken with dial calipers reading to tenths of millimeters.

Most of the specimens had been fixed in formalin and later stored in 70 per cent alcohol. During the course of the dissections they were kept in the embalming solution currently used in the laboratories of the Department of Anatomy, University of Michigan (Woodburne and Lawrence, 1952). It was found that this improved the character of the specimens for dissection, making them more pliable, and thus the muscles were less apt to be torn during manipulation.

All dissection was done under a binocular microscope at magnifications of 10× and 20×.

I am indebted to those in charge of the mammal collection of the Museum of Zoology, University of Michigan, for their generosity in providing me with specimens. Emmet T. Hooper has been especially helpful by giving freely his time and encouragement.

COMPARISONS OF THE SPECIES

In the accounts which follow, I have avoided detailed formal descriptions of the muscles (see Rinker, 1954), and have focused on those muscles which differ interspecifically. In so doing, I exclude 28 muscles or muscle groups which for various reasons were not examined in detail and an additional 111 (of the 150 which were examined) which appear to be identical in all species. The muscles of this latter group are as follows:

Muscles Identical in the Three Species:

- Masseter superficialis
- Masseter medialis
- Pterygoideus externus
- Pterygoideus internus
- Mylohyoideus
- Transversus mandibulae
- Digastricus (anterior belly)
- Digastricus (posterior belly)
- Stylohyoideus
- Jugulohyoideus
- Stylopharyngeus
- Pectoralis major
- Cutaneus maximus
- Biceps brachii
- Brachialis
- Epitrochleoanconeus
- Flexor carpi ulnaris
- Palmaris longus
- Flexor carpi radialis
- Flexor digitorum superficialis
- Abductor pollicis brevis
- Flexor pollicis brevis

Sternomastoideus
Cleidomastoideus
Cleido-occipitalis
Acromiotrapezius
Spinotrapezius
Genioglossus
Hyoglossus
Styloglossus
Splenius
Extensor caudae medialis
Rectus capitis posterior major
Rectus capitis posterior minor
Obliquus capitis superior
Obliquus capitis inferior
Quadratus lumborum
Psoas minor
Geniohyoideus
Sternohyoideus
Sternothyroideus
Thyrohyoideus
Omohyoideus
Intertransversarius lateralis longus
Serratus posterior superior
Serratus posterior inferior
Sternocostalis
Intercostales externi
Levatores costarum
Rhomboideus posterior
Omocervicalis
Teres major
Subscapularis
Clavo-acromiodeltoideus
Spinodeltoideus
Teres minor
Supraspinatus
Infraspinatus
Triceps brachii
Anconeus
Dorsoepitrochlearis
Extensor carpi radialis longus
Extensor carpi radialis brevis
Extensor digitorum communis
Extensor indicis
Extensor digiti minimi
Extensor carpi ulnaris
Adductor pollicis
Adductor digiti secundi (manus)
Abductor digiti minimi (manus)
Flexor digiti minimi brevis (manus)
Adductor digiti minimi (manus)
Opponens digiti minimi (manus)
Lumbricales (manus)
Interossei (manus)
Palmaris brevis
Iliacus
Psoas major
Tensor fasciae latae
Gluteus maximus
Tenuissimus
Pyriformis
Gluteus minimus
Vastus lateralis
Vastus medialis
Vastus intermedius
Extensor hallucis longus
Tibialis anterior

Extensores breves
Peroneus longus
Peroneus brevis
Peroneus digiti quarti
Peroneus digiti minimi
Adductor magnus
Obturator externus
Obturator internus
Gemellus superior
Semimembranosus
Gastrocnemius
Soleus
Popliteus
Tibialis posterior
Flexor digitorum fibularis
Flexor digitorum brevis
Flexores breves accessorii
Abductor hallucis brevis
Abductor digiti minimi (pes)
Flexor digiti minimi brevis (pes)
Adductor hallucis
Lumbricales (pes)
Interossei (pes)

BRANCHIOMERIC MUSCULATURE

Masticatory Group

M. masseter lateralis profundus, pars anterior.—Relations are generally similar in the three forms. Variations worthy of note, however, relate to the conformation of the zygomatic process of the maxilla. *P. leucopus* and *eremicus* have well-developed zygomatic notches, as a result of the projection anteriad of the margin of the zygomatic plate. The most anterior fibers of *M. masseter lateralis profundus* arise from the outer margin of this projection, which thus intervenes between these fibers and those of the infraorbital portion of *M. masseter medialis* (Fig. 1, b). In *nuttalli,* no such projection exists, and the origin of the anteriormost fibers of *M. masseter lateralis profundus* extends almost to the base of the zygomatic process, thus, extending well medial to the margin of the zygomatic plate, overlying directly the infraorbital fibers of *M. masseter medialis.* The two situations described here are almost exact parallels of those found in the two subgenera of *Reithrodontomys* (Rinker and Hooper, 1950).

The superficial portion of *pars posterior* of this muscle appears to be more nearly discrete in *leucopus* than in the other two forms.

M. temporalis.—The only variation observed in this muscle is in the width (dorsoventral dimension) of the part arising from the lambdoidal crest—greater in *nuttalli* than in the other two forms. This is correlated with the relatively greater distance between the parieto-squamosal suture at the lambdoidal crest and the tip of the mastoid process of the squamosal.

Superficial Facial Group

Although detailed comparative study of the muscles of this group was not attempted because suitably preserved specimens were not available, a few features of the internal cheek pouch and its musculature were noted. The pouch was present in all specimens of *leucopus* and *nuttalli,* but absent in all examples of *eremicus.* In *leucopus,* its size was variable, possibly as a result of the degree of contraction of the related muscle fascicles at the time of fixation. In Figure 1, b, it is shown at the maximum observed size. In *nuttalli,* this pouch was found to be much larger; in all observed instances it was developed to nearly the same extent (Fig. 1, a).

The pouch is formed from an evagination of the mucosa opposite the diastemal region, and its musculature is provided by the parts of the buccinator complex which normally lie in that area, specifically

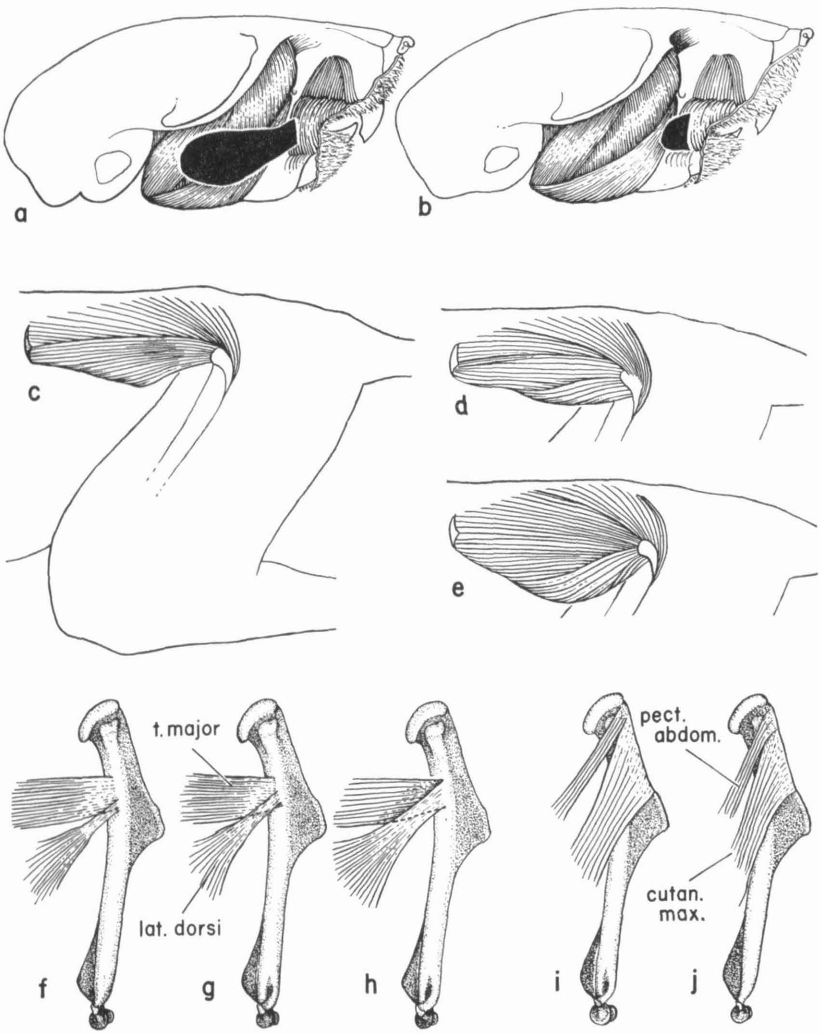

FIG. 1. Lateral view, showing development and relations of cheek pouch in *P. nuttalli* (a) and *P. leucopus* (b). Superficial portion of *M. gluteus medius* of *nuttalli* (c), *eremicus* (d), and *leucopus* (e). Insertional relations of *M. latissimus dorsi* and *M. teres major* in *nuttalli* (f), *eremicus* (g), and *leucopus* (h). Insertional tendons of *M. pectoralis abdominalis* and *M. cutaneus maximus* in *leucopus* and *eremicus* (i) and in *nuttalli* (j).

pars intermaxillaris and *pars mandibularis anterior* (cf. Rinker, 1954, fig. 5). In depth, the pouch lies deep to *M. platysma myoides pars buccalis* and to *M. zygomaticolabialis,* both of which approach this area from the posterior. In no instances were fibers of these muscles seen to attach to the pouch (to provide a retractor), and it would appear that no such apparatus exists in *Peromyscus*. On the other hand, the muscular investment of the pouch appears to be sufficient to provide for extrusion of any contents. Presence or absence of this pouch may prove to be a character of taxonomic value.

MYOTOMIC MUSCULATURE: DORSAL DIVISION

Sacrospinalis and Semispinalis Groups

Elements of these groups show numerous minor variations among the three species. These have generally to do with attachments to one vertebra or rib more or less. Since this degree of variation can and frequently does occur on two sides of a single individual, none of the observed differences is considered to be significant. Muscles of these groups which were dissected in detail are: *M. iliocostalis, M. longissimus, M. semispinalis,* and *M. extensor caudae medialis.*

Lateral Cervical Group

M. scalenus.—A different relationship between the slips of M. *scalenus* and *M. serratus anterior* occurs in each of the three species. While these were constant in the individuals dissected, they may not be truly interspecific differences. In nearly every species of cricetine, of which I have dissected several specimens, individual variations of this same character were found.

APPENDICULAR MUSCULATURE: MUSCLES OF THE PECTORAL GIRDLE AND LIMB (EXTENSOR SYSTEM)

Costo-spino-scapular Group

M. levator scapulae et M. serratus anterior.—Relationships of these muscles are similar in all three species. In *nuttalli,* however, no slip was found to arise from the ninth rib. This is not considered to be a significant variation in light of the fact that similar variation has been observed among individuals of *leucopus.*

M. rhomboideus anterior.—Origin in *leucopus* and *eremicus* involves the entire length of the nuchal ligament anterior to the spine of the first thoracic vertebra. In *nuttalli,* the cranial limit of origin is at the level of the spine of the atlas. Insertion is similar in all three species.

M. occipitoscapularis.—Origin is from the occipital crest, extending as far dorsally as the superior temporal line in *leucopus* and *eremicus,* but not quite so far in *nuttalli. P. leucopus* and *nuttalli* have the insertion no farther caudad than the middle third of the vertebral border of the scapula. In *eremicus,* insertion is shifted to a slightly more posterior position.

M. latissimus dorsi.—Some variation occurs in the insertion of this muscle, but relations at the origin are similar. The tendon of this muscle, as it passes onto the arm, goes deep to the brachial artery and associated nerves. A small aponeurotic slip leaves the main tendon before this, however, to pass superficial to the vessel and nerves and become continuous with the anterior border of *M. dorsoepitrochlearis.* This tendency is more pronounced in *nuttalli* and *eremicus,* and in these the slip actually contains a few muscle fibers.

In *leucopus* the main tendon of this muscle is somewhat wider at the insertion than in the other two species, and it inserts at the same level on the humerus as does *M. teres major* (Fig. 1, f–h). In *eremicus,* this tendon is approximately half the width of *M. teres major* at its insertion; it inserts on the level of the distal half of *M. teres major.* The tendon of *M. latissimus dorsi* is narrowest in *nuttalli* and inserts at such a level that only its proximal border overlaps *M. teres major.*

Extensor Group of Forearm

M. supinator.—Origin is similar in all three species, but there is a noticeable difference in the insertion. In *leucopus,* this muscle inserts along the proximal 55 per cent of the length of the radius. In *eremicus* 45 per cent of this length is involved, while attachment in *nuttalli* is to only the proximal 38 per cent.

M. extensor pollicis brevis et M. abductor pollicis longus.—Very little difference was observed. The tendons of these muscles appear to be slightly more discrete in *eremicus* and *nuttalli,* but insertions are similar in all.

Pectoral Group

M. pectoralis minor (pectoralis profundus).—Minor differences were observed in this muscle. Relations at the origin were similar in all three species. In the specimens of *eremicus* which were dissected, there was no tendency for the muscle to split into cranial and caudal parts, while in *leucopus* and *nuttalli* the muscle is slightly divided.

M. pectoralis abdominalis.—Relations at the origin are similar. In *leucopus* and *eremicus* the insertional tendon comes to lie parallel to and in the same plane as the anteromedial edge of *M. cutaneus maximus,* uniting with it just before insertion. In *nuttalli,* this tendon inserts somewhat more distally, and lies on the surface of *M. cutaneus maximus,* between this muscle and *M. pectoralis profundus.*

Flexor Group of Arm

M. coracobrachialis.—Origin and insertion are similar in the three species. The short part of this muscle (that portion proximal to the musculocutaneous nerve) differs in its degree of development. It is well developed in *eremicus*, considerably weaker in *leucopus*, and much reduced in *nuttalli.*

Flexor Group of Forearm

M. pronator teres.—This muscle is similar in the three species, but there is a slight difference in relations at the insertion. In *leucopus*, the insertion reaches almost exactly as far distad as does that of *M. supinator* (*q.v.*) while in the other two species it extends somewhat beyond that of *M. supinator.* This apparent difference seems to result entirely from the shorter *M. supinator* in these forms.

M. flexor digitorum profundus.—No differences were observed between *leucopus* and *eremicus.* In some specimens of *nuttalli,* however, the common tendon is formed from five tendons, rather than from three as in the former two species. The additional two tendons are derived from the radial portion of the radio-ulnar head of the muscle. Thus, in these individuals, in place of a single tendon from the radio-ulnar head, there are three, each distinctly separate. Of these, the one from the ulnar portion of the fleshy part of the muscle is the largest, approximating the combined size of the other two. Neither *leucopus* nor *eremicus* shows any indication of this separation.

M. pronator quadratus.—Relations are generally similar in the three species, except that the muscle occupies a relatively greater length of the forearm in *nuttalli* than in the other two. Relative to the total length of the ulna, the width of *M. pronator teres* is 27 per cent in *eremicus* and *leucopus,* and 33 per cent in *nuttalli.*

MUSCLES OF PELVIC GIRDLE AND LIMB (EXTENSOR SYSTEM)

Iliacus Group

M. pectineus.—Relations at the origin are similar in all three species, except that in *eremicus* the area of origin appears to be less. Insertion in *leucopus* is along the posterior lip of the crest of the lesser trochanter, reaching a point 35 per cent of the length of the femur from its proximal end. *P. nuttalli* differs considerably in that the insertion not only extends somewhat more distally (to a point 49 per cent of the length of the femur from the proximal end), but also encroaches well onto the posterior surface of the femur, even reaching the region of the posterior lip of the gluteal crest. *P. eremicus* exhibits an intermediate condition, with a few fibers spilling onto the posterior aspect of the lesser trochanteric crest. The last species is nearer *leucopus* than *nuttalli* in that the most distal extent of the insertion is 40 per cent of the length of the femur as measured from the proximal end.

Gluteal Group

M. femorococcygeus.—Origin in *leucopus* is by a thin aponeurosis opposite the level of the first and second caudal vertebrae. In *eremicus,* origin is a little wider, extending as far craniad as the caudal border of the fourth sacral vertebra. *P. nuttalli* exhibits generally similar origin, but the level is opposite the caudal half of the last sacral vertebra, the first caudal vertebra, and the cranial half of the second caudal vertebra.

The original aponeurosis of this muscle lies superficial to, and is partially fused with, the tendon of *M. caudofemoralis.* In *leucopus* and *eremicus* the entire origin is thus shared with *M. caudofemoralis,* while in *nuttalli* only the caudal half of the tendon of origin of *M. femorococcygeus* is fused with that of *M. caudofemoralis.*

The insertion of this muscle shows a considerable amount of variation. In *leucopus,* insertion is onto the shaft of the femur distal to the gluteal crest, extending continuously to the lateral condyle, passing then into the lateral patellar retinaculum. In *nuttalli,* the muscle divides into two slips. One of these, small and thin, inserts onto the proximal half of that length of the femur beyond the gluteal crest. The other much larger slip inserts onto the femur just above the lateral condyle and onto the lateral patellar retinaculum. This leaves a considerable length of the femur on which no part of this muscle inserts. *P. eremicus* resembles *leucopus* in that this muscle is undivided, but the most proximal point of insertion is more distal, beginning at a level well below the gluteal crest. Individual variation in relations of this muscle was observed on one side of one specimen of *eremicus* where the entire *M. femorococcygeus* inserted on the lateral condyle of the femur and the lateral retinaculum.

M. gluteus medius.—No significant variation was observed in the general area of origin, but there are rather distinct differences in the character of this muscle among the three species. In *leucopus* it appears to be most robustly developed, with a greater number of the fibers passing over the proximal end of the femur to insert on the posterior surface. *P. nuttalli* exhibits the weakest and simplest development of the superficial part of *M. gluteus medius.* The dorsal and ventral superficial portions are least distinct (Fig. 1, c, d, e), and fewer fibers insert on the posterior surface of the trochanter. In *eremicus* the conditions are almost exactly intermediate between those seen in *leucopus* and *nuttalli.* In *nuttalli* the deep part of this muscle becomes completely distinct from the superficial parts, to a degree which is greater than in any cricetine I have examined.

Quadriceps Femoris Group

M. rectus femoris.—There is a slight difference in the exact manner of origin of this muscle in each species. The direct head of origin is least developed in *leucopus,* slightly stronger in *eremicus,* and best developed in *nuttalli.* No differences were observed at the insertion.

Tibial Extensor Group

M. extensor digitorum longus.—This muscle is generally similar in the three species, but the terminal tendons are distinctly more firmly united by the oblique connecting bands in *nuttalli.*

Adductor Group

M. gracilis pars anterior.—In *leucopus* and *nuttalli,* only the anterior one-fourth to one-half of this muscle at its origin is concealed deep to *M. adductor longus.* In *eremicus,* the attachment appears to be situated farther cranially and nearly the entire width of the origin is hidden by *M. adductor longus.* This latter condition is owing primarily to the greater width of *M. adductor longus* in *eremicus.*

M. gracilis pars posterior.—Relations at the origin are similar in all three species. The tendon of insertion is considerably narrower in *eremicus* than in *leucopus* and *nuttalli.* Actual site of insertion is similar in *eremicus* and *nuttalli,* being slightly more distal than in *leucopus* such that the distal borders of the tendons of both parts of *M. gracilis* are on the same level. In *leucopus, pars posterior* inserts deep to the middle of the attachment of *pars anterior.*

M. adductor longus.—The origin of this muscle is similar in *leucopus* and *nuttalli,* but is much wider in *eremicus.* This greater width covers more of the underlying *M. gracilis pars anterior,* causing the latter muscle to appear to arise farther cranially than it actually does.

At the insertion, the tendon is at least twice as wide in *nuttalli* as in the other two forms. The lower margin of the insertional tendon is at the level of the middle of the femur. The relative narrowness of *M. pectineus* in *leucopus* is responsible for a considerable hiatus between insertion of this muscle and *M. adductor longus*. In *nuttalli* the distal margins of the two tendons are at the same level, while *eremicus* presents relationships intermediate between those of the other two species. It should be pointed out that the apparent difference in level of insertion of *M. adductor longus* is a function of differences in the insertion of *M. pectineus*. *M. adductor longus* actually inserts at the same relative level in all three species.

M. adductor brevis.—Origin is similar in *leucopus* and *nuttalli*, but is more extensive in *eremicus*. In the former two, only the pubic ramus, from the pectineal eminence to the cranial end of the symphysis, is involved, while in the last species the origin extends onto the cranial two-thirds of the symphysial region. Insertion is generally similar in the three forms, but begins slightly more distally on the femur in *leucopus*.

Ischiotrochanteric Group

M. gemellus inferior.—Although the difference is slight, origin extends farthest caudad on the ischium in *eremicus*, somewhat less far in *nuttalli*, and even less in *leucopus*. Other relations are similar.

M. quadratus femoris.—In *leucopus* and *nuttalli*, origin is from the dorsal one-third of the ischiopubic ramus. In *eremicus*, the origin is wider, involving the dorsal half of this ramus. Insertion is similar in all three species.

Hamstring Group

M. caudofemoralis.—Except for slight differences in relationship to the tendon of *M. femorococcygeus*, origin is similar in the three species. Some variation occurs in the site of insertion. In *leucopus*, insertion is onto the sesamoid in the tendon of origin of the medial head of *M. gastrocnemius* and onto the tendon just proximal to this sesamoid. In *nuttalli* insertion is onto this tendon and also for a short distance immediately superior onto the medial epicondylar ridge of the femur. Insertion in *eremicus* is similar to that in *nuttalli*, but extends slightly more proximad on the femur.

M. semitendinosus.—No differences were observed in relationships at origin or insertion. In *nuttalli* the muscle appears to be considerably thinner than in the other two species. This could be an artifact owing to positions of the limbs in the specimens dissected.

M. biceps femoris.—Relationships are generally the same in the three species. *P. leucopus* differs slightly from the other two in that the muscle is somewhat wider at the insertion.

Flexor Group of Leg

M. plantaris.—No differences were observed in relations at origin or insertion. In *nuttalli* this muscle is considerably less robust than in the other two species, with the fleshy part of the muscle making up only approximately half the total length. In *leucopus* and *eremicus* approximately two-thirds of the length is fleshy.

M. flexor digitorum tibialis.—Relations at attachments are similar in all three species. In *eremicus* the muscle belly is definitely relatively shorter and smaller than in the other two, and the contribution to the plantar aponeurosis is weak.

Flexor Group of Pes

M. abductor ossis metatarsi quinti.—In *leucopus* and *nuttalli* origin of this muscle is from the medial aspect of the calcaneus. In *eremicus* origin is partially from the plantar surface of this bone, immediately deep to the tendon of *M. plantaris.* No other differences were observed.

M. flexor hallucis brevis.—This muscle is apparently absent in *leucopus* and *nuttalli,* but is present and rather well developed in *eremicus.* Here the muscle originates from what appears to be a cartilaginous plate beneath the tubercle of the base of the first metatarsal, and it inserts on the proximal aspect of the medial sesamoid of the metatarsophalangeal joint. This is the first instance, among the Cricetinae, in which I have observed a well-developed muscle in this position (cf. Rinker, 1954: 113).

M. adductor digiti secundi.—The general relations of this muscle are quite similar in all three forms. In *leucopus* less of the total length of the muscle appears to be fleshy than in the other two, but the entire muscle is so thin that this may not be a valid judgment.

M. adductor digiti quinti.—Remarks under *M. adductor digiti secundi* apply equally well here.

DISCUSSION

In this discussion I use the term "primitive" to mean similar to the condition presumably found in a common ancestral stock. "Advanced" is used to indicate evolutionary change in any direction from the character of the assumed stem form.

Among the 150 muscles or muscle complexes studied, only 35 were found to demonstrate noticeable interspecific variation. These 35 may be grouped into four categories which distinguish (1) each of the three species; (2) *nuttalli* from *eremicus* and *leucopus*; (3) *leucopus* from *nuttalli* and *eremicus*; and (4) *eremicus* from *nuttalli* and *leucopus*. These are listed in Table 1.

Among the twelve muscles of the first group there are two that exhibit a type or degree of variation which I consider insignificant. These are *Mm. scalenus* and *occipitoscapularis*. To reject these muscles from consideration is not to deny the possibility that differences therein might be significant, but is rather a move toward conservatism. It has been observed that *M. scalenus* tends to vary to a considerable extent not only between individuals but even on the two sides of the same individual. For this reason, I can not be certain that the observed variation of this muscle is interspecific.

A rather peculiar situation is illustrated by *M. occipitoscapularis*. If one considers the origin of this muscle, then similarity is found between *leucopus* and *eremicus*, while *nuttalli* differs to a slight degree. On the other hand, the insertion is similar in *leucopus* and *nuttalli*, but has shifted to a more posterior position in *eremicus*. In either case the difference is very small, and I hesitate to consider it significant.

M. caudofemoralis shows variation in the three species, but the shift in the site of insertion is slight. Since the insertion of this muscle is primitively on the shaft of the femur, it might be said that even these small differences indicate a trend, with *eremicus* being least advanced and *leucopus* the most.

The remaining muscles of this group are believed to show variation dependably indicating divergence of the stocks. Four of these, *Mm. femorococcygeus, coracobrachialis, gluteus medius*, and *rectus femoris*, also show trends which may indicate the relative degree of change from the more primitive conditions. It is reasonable to accept the primitive insertion of *M. femorococcygeus* as being on the proximal half of the femur (Appleton, 1928). The insertion of this muscle in *leucopus* shows the least shift from this, *eremicus* somewhat more, and *nuttalli* the most. In reduction of the proximal part of *M. coracobrachialis, eremicus* shows least reduction, *leucopus* is intermediate, and *nuttalli* has progressed farthest. In regard to specialization of *M. gluteus medius* two factors must be considered. The superficial part is most primitive in *nuttalli*, slightly changed in *eremicus*, and most advanced in *leucopus*. The deep part of this muscle is completely discrete in *nuttalli*, however, and hardly separable from the superficial part in the other two forms. Considering the entire muscle, I rank

TABLE 1

MUSCLES WHICH PRESENT UNIQUE RELATIONSHIPS IN EACH OF THREE SPECIES OF *Peromyscus*

Muscles unique in each species (12)	Muscles unique in *nuttalli*, similar in the other to (11)	Muscles unique in *leucopus*, similar in the other two (5)	Muscles unique in *eremicus*, similar in the other two (8)
Scalenus[1]	*Masseter lateralis profundus*	*Extensor pollicis brevis et abductor pollicis longus*[1]	*Pectoralis minor*
Latissimus dorsi	*Temporalis*	*Biceps femoris*[1]	*Gracilis anterior*[1]
Occipitoscapularis[1]	*Rhomboideus anterior*	*Adductor digiti II*[1]	*Adductor longus*
Supinator	*Levator scapulae et serratus anterior*[1]	*Adductor digiti V*[1]	*Adductor brevis*
Coracobrachialis	*Pectoralis abdominalis*		*Quadratus femoris*
Pectineus	*Flexor digitorum profundus*[1]		*Flexor digitorum tibialis*
Femorococcygeus	*Pronator quadratus*		*Abductor ossis metatarsi V*
Gluteus medius	*Extensor digitorum longus*		*Flexor hallucis brevis*
Rectus femoris	*Semitendinosus*[1]		
Gracilis posterior	*Plantaris*		
Gemellus inferior			
Caudofemoralis			

[1] These muscles not considered valid indices of divergence of stocks.

nuttalli as most advanced, *eremicus* as least. The origin of *M. rectus femoris* shows a progressive suppression of the reflected head with greater development of the direct head. In this, *leucopus* is most primitive, *eremicus* intermediate, and *nuttalli* most advanced.

Turning to the second group of muscles listed in Table 1, three of the ten should be rejected from consideration. These three are: *Mm. levator scapulae et serratus anterior, semitendinosus,* and *flexor digitorum profundus.* The observed variation of the first falls within the limits of possible individual variation; differences noted in the second might well be apparent rather than real; and inconstancy of variation of the third removes it from consideration. The variations shown by the remaining seven muscles are probably valid indicators of divergence of the species. As a group, however, they do not aid in an analysis of the degree of specialization.

Examination of the five muscles in the third category of Table 1 will reveal that none should be given consideration. The differences observed in *Mm. extensor pollicis brevis et abductor pollicis longus, biceps femoris, adductor digiti secundi* and *adductor digiti quinti* represent nearly the minimum which could be detected, and are not of the type or extent upon which dependable conclusions might be based.

The last group of muscles comprises those in which *eremicus* differs from the other two species. *M. gracilis pars anterior* should be omitted from consideration because its apparent variation depends primarily on the increased width of *M. adductor longus,* at its origin. The remaining seven muscles present variations which seem to be reasonably dependable. *Mm. adductor longus, adductor brevis,* and *quadratus femoris* are distinctly better developed in *eremicus* than in the other two species. Because of the rather close functional relation of these muscles, it would appear that this concomitant variation is the result of a specific adaptive trend in *eremicus,* or in both *leucopus* and *nuttalli.* I can not, however, come to a decision as to which condition represents an advance.

The division of *M. pectoralis minor* into anterior and posterior parts is assumed to indicate a specialization. In this, *eremicus* has maintained the undivided condition; the other two species show a tendency toward division. Of greater certainty as an indication of more primitive character is the retention of *M. flexor hallucis brevis* by *eremicus* while it has been lost in *leucopus* and *nuttalli.* I am unable to judge the relations shown by the other two muscles as to primitive versus advanced character.

After this culling of the muscles (Table 1), it is evident that only a meager number remains to form the basis for any conclusions. Ten remain in column 1, seven in column 2, none in column 3, and seven in column 4.

If one assumes that these remaining muscles are valid indices of divergence of the stocks, then it is seen that *nuttalli* is unique in 17 instances (cols. 1 and 2, Table 1); *leucopus* is unique in 10 (cols. 1 and 3); and *eremicus* is unique in 17 (cols. 1 and 4). It is also apparent that *nuttalli* differs from *leucopus* in 17 muscles (cols. 1, 2, and 3), *nuttalli* from *eremicus* in 24 muscles (cols. 1, 2, and 4), and *eremicus* from *leucopus* in 17 (cols. 1, 3, and 4).

Thus, even after rejecting several differences in the interest of a conservative approach, *nuttalli* and *eremicus* can be shown to differ from *leucopus* to approximately the same degree, but each in an individual manner, so that they differ considerably more from one another than either does from *leucopus.*

To find such a small amount of variation in the muscles of these species which represent different subgenera may be surprising to those who accept the present arrangement of the genus as rather clear-cut. In my earlier study of four genera of cricetines (1954), the genera *Neotoma* and *Peromyscus* were found to differ significantly in only 35 muscles, and *Sigmodon* and *Oryzomys* in only 37. With this in mind, perhaps it is not going too far to state that there is real significance in one-half to two-thirds that number of variant muscles between subgenera. Since no better "yard-stick" is available, I am inclined to accept this evidence of divergence of the subgenera.

With respect to the position of the three species on the "primitive-advanced" scale, even less evidence is available from myology. Of the muscles in which differences were found, there are only eight which I feel safe in using. These are listed in Table 2, and indicate my judgment of the positions of the species. *P. eremicus* is most primitive in the character of five muscles, *leucopus* most primitive in three. It may be very significant that *nuttalli* shows the most advanced condition in five of the eight muscles and shares an advanced condition with *leucopus* in two others. While this alone is far from conclusive, it does lend some support to the opinion that *Ochrotomys* should be accorded full generic rank.

The inconclusive nature of the discussion above may well be the basis for the most important conclusions to be drawn from this study. Myologically, the segment of the genus *Peromycus* which is represented by the species studied is a very closely related unit, with few features separating the subgenera as they are now known. This is not to say that these groupings are invalid or unnatural. It may merely reflect the fact that here is a genus which is either rather conservative

TABLE 2

MUSCLES IN WHICH AN EVOLUTIONARY TREND IS EVIDENT AMONG THREE SPECIES OF *Peromyscus*

Muscle	Primitive	Advanced	Most Advanced
Coracobrachialis	*P. eremicus*	*P. leucopus*	*P. nuttalli*
Caudofemoralis	*P. eremicus*	*P. nuttalli*	*P. leucopus*
Gluteus medius	*P. eremicus*	*P. leucopus*	*P. nuttalli*
Femorococcygeus	*P. leucopus*	*P. eremicus*	*P. nuttalli*
Pectoralis minor	*P. eremicus*	*P. leucopus and nuttalli*	....
Pectineus	*P. leucopus*	*P. eremicus*	*P. nuttalli*
Rectus femoris	*P. leucopus*	*P. eremicus*	*P. nuttalli*
Flexor hallucis brevis	*P. eremicus*	*P. leucopus and nuttalli*	....

in its evolutionary rate, or that it is a relatively new genus which is only now in the process of radiation from a stem form.

Whatever may be the situation in that respect, it is obvious that the muscular system provides minimal evidence which could be of taxonomic value. I am of the belief that such a group as this represents the lower limit of the range of taxonomic categories to which this type of study can be applied profitably. This approach is better limited to the study of intergeneric and higher level relationships.

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