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MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 176

Comparative Myology and Phylogenetic Systematics of the Heteromyidae (Mammalia, Rodentia)

by
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ABSTRACT

Ryan, James M. 1989. Comparative Myology and Phylogenetic Systematics of the Heteromyidae (Mammalia, Rodentia). Misc. Publ. Mus. Zool. Univ. Michigan, 176:1–103, figs. 1–26.—The phylogenetic relationships among heteromyid and geomyid rodents are investigated. Complete anatomical descriptions are given for 224 muscles, including origin, insertion, and innervation. In addition, the condition of the muscle in heteromyids is compared with that of other rodent groups (where information is available). Based on 40 muscle characters, the most parsimonious hypothesis contains several well-supported clades. Thirteen synapomorphies support the monophyly of the Geomyoidea. Geomyids have four synapomorphies and are the primitive sister group of the Heteromyidae. The Heteromyidae is characterized by seven synapomorphies. Few characters are available to diagnose the Heteromyinae or Perognathinae. The sister-group relationship between perognathines and dipodomyines is based on a single character, a reduced temporalis. *Microdipodops* and *Dipodomys*, the only bipedal heteromyids, form a clade diagnosed by fourteen synapomorphies. Recent hypotheses suggesting a paraphyletic Heteromyidae are refuted.

Key words: *Cladistics, Geomyoidea, Heteromyidae, Geomyidae, phylogeny, anatomy, myology.*

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INTRODUCTION

The present study describes the muscular variation within the Heteromyidae, makes comparisons with other rodent groups, and uses myological characters in a cladistic analysis to test the hypotheses of heteromyid relationships discussed below.

The New World family Heteromyidae includes the kangaroo rats and mice (Dipodomyinae), the pocket mice (Perognathinae), and the spiny mice (Heteromyinae). The closely related Geomyidae includes the various pocket gophers (Geomyinae). The Heteromyidae and Geomyidae are each others closest relatives and form the superfamily Geomyoidea (McLaughlin, 1984), which is based on a suite of shared characters (Wahlert, 1985), most notably the presence of large external cheek pouches. The geomyoid rodents underwent their major radiation beginning in the Oligocene of North America (but see Li, 1974, for a description of a possible Miocene geomyid from Shangtung, China). Hafner and Hafner (1983) and Wahlert (1985) have recently reviewed the extensive taxonomic history of the Geomyoidea and only the salient points will be reviewed below.

The systematics of the Geomyoidea is controversial and involves problems at three separate taxonomic levels: superfamilial relationships, monophyly of the Heteromyidae, and the monophyly of the subfamily Dipodomyinae.

The phylogenetic position of the superfamily Geomyoidea in relation to other rodent superfamilies (e.g. Muroidea, Sciuroidea) has been debated for nearly a century. Tullberg (1899), Matthew (1910), Miller and Gidley (1918), and Simpson (1945) placed geomyoids in the paraphyletic suborder Sciuromorpha along with castorids and sciurids, based on their shared sciuromorphous masseter arrangement. Alternatively, Brandt (1855), Coues (1877), Romer (1966), Wood (1965), and Wahlert (1978) advocated ignoring the primitive masseter morphology and placed geomyoids in the Myomorpha based on a variety of shared derived dental and skeletal characters. Lastly, Thaler (1966) erected a new suborder, Geomorpha, for geomyoids.

Recently, Wahlert (1978, 1985) provided a cladistic analysis of geomyoid cranial characters and like Wilson (1949) considered geomyoids and muroids to be sister groups (but see Fahlbusch, 1985). He considered the sciuromorphous masseter to have evolved in parallel in sciuroids and geomyoids (Wahlert, 1985), and listed several cranial characters uniting geomyoids and muroids. Although the evidence uniting geomyoids with muroids is limited, the alternative classification defines a paraphyletic assemblage (Sciuromorpha).

The systematic evidence offered to date indicates that the Geomyoidea is a monophyletic group which contains two clades, Geomyidae and Heteromyidae (but see Brylski, 1985). Some workers placed all extant geomyoids in a single family, variously called Saccomyidae, Geomyidae, or Heteromyidae (Carus, 1868; Gray, 1868; Alston, 1876; and Lindsay, 1972). The current classification with separate Geomyidae and Heteromyidae is supported by Merriam (1895), Wood (1931, 1935), Rensberger (1971, 1973), Hafner (1982), Hafner and Hafner (1983), and Wahlert (1985). Geomyids are highly fossorial and share with heteromyids a series of synapomorphies including: bilophodont molars, evergrowing cheek teeth, a dorsally flattened skull, and small incisive foramina enclosed by the premaxilla (McLaughlin, 1984; Wahlert, 1985) among others.

The family Heteromyidae has a fossil record dating from the Oligocene (Chadronian; Wilson, 1949). Members of this family are primarily North American, but some extend into northern South America. They are terrestrial and range from quadrupedal to bipedal. Wood (1931) initially erected three subfamilies: Heteromyinae (*Heteromys* and *Liomys*), Dipodomyinae (*Microdipodops* and *Dipodomys*), and Perognathinae (*Perognathus* and *Chaetodipus*). In 1936, Wood erected a fourth subfamily, the Florentiamyinae, for the Miocene genus *Florentiamys*. The subfamily Florentiamyinae was later assigned to the Geomyidae by Rensberger (1973) and Fahlbusch (1985). However, Wahlert (1983) included a second genus, *Sanctimus,* and recognized the family Florentiamyidae based on cranial and dental characters.

Three hypotheses on the interrelationships of heteromyid rodents have been proposed (Fig. 1). The traditional view is that the Heteromyidae is monophyletic and contains three clades (each containing two genera) corresponding to the subfamilies Heteromyinae, Perognathinae, and Dipodomyinae. The heteromyines (*Heteromys* and *Liomys*) are conservative with respect to many (but not all) morphological features and are considered the sister group of perognathines and dipodomyines. Recently Brylski (1985) and Rensberger (1971) challenged the monophyly of the Heteromyidae (Fig. 1b). They suggested that the heteromyines (*Heteromys* and *Liomys*) and geomyids (pocket gophers) form a monophyletic group independent of the dipodomyine-perognathine clade. If this hypothesis is correct the Heteromyidae, as currently recognized, is paraphyletic. Paraphyly of the Heteromyidae was also proposed by Shotwell (1967) and Lindsay (1972), but they concluded that dipodomyines and geomyids are each others closest relatives. With the exception of Brylski's (1985) two characters (a reduced stapes and lack of the stapedial artery), all of these challenges are based on dental and, to a lesser extent, cranial characters.

The Dipodomyinae includes 23 living species in two genera, *Dipodomys* and *Microdipodops*. The phylogenetic position of the genus *Microdipodops* with respect to *Dipodomys* and the other heteromyids is also controversial. Male reproductive tract anatomy (Hafner and Hafner, 1983) and various other morphological characters (Reeder, 1956; Lindsay, 1972; Brylski, 1985) support the monophyly of *Dipodomys* and *Microdipodops* (i.e. Dipodomyinae), but some authors (Wood, 1935; Hafner, 1976, 1978) attribute a subset of these similarities to parallelism. *Microdipodops* is derived from a perognathine ancestry according to some workers (Wood, 1935; Hafner, 1978; but see Brylski, 1985). The Perognathinae was recently reorganized

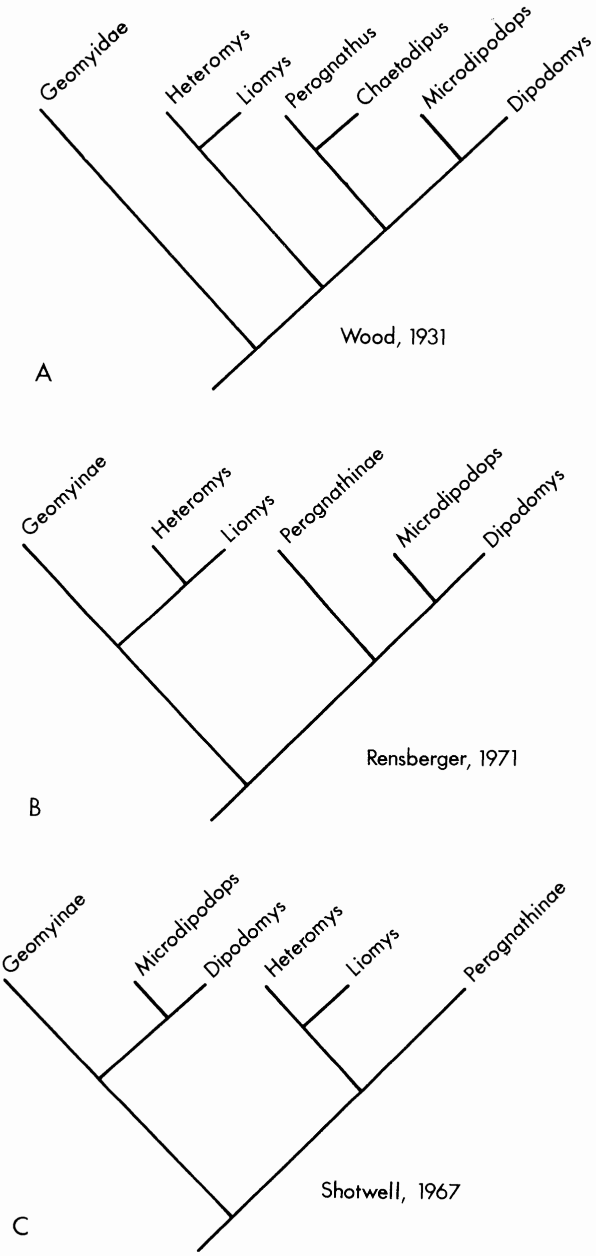

FIG. 1. Three alternative phylogenies of geomyoid relationships based primarily on dental evidence from A) Wood, 1931, B) Rensberger, 1971, and C) Shotwell, 1967. None of these hypotheses are consistent with the myological data presented herein.

to include two genera, *Perognathus* and *Chaetodipus* (Hafner and Hafner, 1983) and exclude *Microdipodops* (*contra* Hafner, 1978).

Paleontologists have been unable to agree on the phylogenetic relationships of the geomyoid rodents largely because of the difficulties in polarizing dental characters and the sparse fossil record for some genera. Study of the morphology of extant forms is not only desirable as a test of the paleontological hypotheses, but mandatory if systematists are to unravel geomyoid evolution.

Myological characters have been used as valuable morphological characters in several studies of phylogenetic relationships among rodents (Rinker, 1954; Klingener, 1964; 1970; Woods, 1972; Woods and Hermanson, 1985). While homologies of many muscles have been demonstrated using relative position, innervation, and embryology in a variety of rodent groups (Cheng, 1955; Lance Jones, 1979), few studies (e.g. Woods and Hermanson, 1985; Dunlap *et al.*, 1985) have attempted to place such characters in a cladistic framework. Cladistic methodology allows systematists to test hypotheses of relationship on the basis of shared derived characters. Given the controversial nature of the dental and skeletal data relating to heteromyid systematics and the substantial number of conflicting hypotheses presented over the last 100 years, it is appropriate to reanalyze the phylogenetic relationships of the Heteromyidae using an independent character set.

MATERIALS AND METHODS

Specimens

Table 1 presents a partial classification of rodents and the specimens examined during this study. The family Heteromyidae as currently recognized (McLaughlin, 1984) consists of six genera: *Heteromys* (10 spp.); *Liomys* (5 spp.); *Perognathus* (9 spp.); *Chaetodipus* (16 spp.); *Microdipodops* (2 spp.); and *Dipodomys* (21 spp.). Because myological variation is minimal below the generic level (Rinker, 1963), representative species from each of the five heteromyid genera were chosen based primarily on availability. Exceptions were made to ensure the inclusion of representatives of four-toed and five-toed species of *Dipodomys*.

The musculature of *Heteromys* is taken as a standard for comparison. Members of the subfamily Heteromyinae (*Heteromys* and *Liomys*) possess many plesiomorphic characters and are thought to be the monophyletic sister group to the remaining heteromyid rodents (Wood, 1931). For each muscle described, unless otherwise indicated in the section on "Remarks," the condition in *Liomys, Perognathus, Chaetodipus, Microdipodops,* and *Dipodomys* is similar enough to that of *Heteromys* to require no additional description.

TABLE 1
CLASSIFICATION AND LIST OF SPECIMENS EXAMINED

Taxa	Specimen Number*
Sciuroidea	
Sciuridae	
Sciurinae	
Tamias striatus	UMA 3186, 3187
Eutamias minimus	UMA 3199, 3196, 3197,1088
Geomyoidea	
Geomyidae	
Geomyinae	
Thomomys talpoides	UMA 3207, UMMZ 110120, 110121
Geomys bursarius	USNM 547921
Heteromyidae	
Heteromyinae	
Heteromys desmarestianus	USNM 520360, 520355, 520348, 520359 520356, 520357, UMMZ 113141, 113142
Heteromys lepturus	UMMZ 116314, 116315
Liomys pictus	UMMZ 80703, 80704, 111735, 111734
Perognathinae	
Perognathus fallax	USNM 93548, 93552, 93553, 93556
Perognathus parvus	UMA 3200
Chaetodipus hispidus	UMMZ 74926, 74931, 74932
Dipodomyinae	
Dipodomys panamintinus	UMA 3212, 3210, 3211
Dipodomys microps	UMA 3209
Dipodomys merriami	UMMZ 58338, 58347, 58348, 78445, 78446, UMA 3716
Dipodomys ordii	UMA 3147, UMMZ 81486, 58349, 58364
Microdipodops megacephalus	UMA 3201, 3204
Muroidea	
Muridae	
Cricetinae	
Phodopus sungorus	UMA 3834, 3835, 3836, 3837, 3838
Mesocricetus auratus	UMA 3533
Cricetus cricetus	UMMZ 108462
Cricetulus barabensis	UMMZ 103724, 103735
Gliroidea	
Gliridae	
Glirinae	
Glis glis	USNM 319217

*UMA = University of Massachusetts, Amherst.
UMMZ = Museum of Zoology, University of Michigan.
USNM = United States National Museum.

Only adults fixed in 10% buffered formalin or 70% ethanol were dissected. Skeletons of most of the genera listed in Table 1 were also studied.

The entire muscular system (with the exception of the extrinsic ocular muscles, diaphragm, muscles of the larynx, and ear pinna) was dissected in four or more specimens of each genus of Heteromyidae, except *Liomys* and *Microdipodops,* for which only two specimens each were available. Questionable points were checked with additional specimens, which were not completely dissected. Non-heteromyid genera were not completely dissected, but were used to verify undescribed muscular conditions or statements from the literature.

Hereafter the species listed in Table 1 are referred to by their generic names. All dissections and drawings were made with the aid of either a Wild M5 dissecting microscope equipped with a camera lucida or a Bausch and Lomb Stereozoom dissecting microscope. Proportional dividers were used to enlarge the original drawings to scale.

Superficial facial muscles lie directly beneath, and in many cases insert onto, the dermis of the skin. Dissections of superficial facial muscles were made by first shaving the fur and vibrissae from the head and shoulders, then working the skin off from the shoulder to the rostrum. Fiber direction was determined by observation or with the aid of iodine muscle stain (Bock and Shear, 1972).

In describing the muscles of heteromyids I have followed Klingener's (1964) nomenclature. Because frequent comparison is made with Howell's (1932) study of *Dipodomys* and dipodoid rodents, I have provided synonyms for muscle names that differ from Howell's usage. Howell's (1932) description of musculature in *Dipodomys* is incomplete and in some cases (i.e. superficial facial muscles) erroneous. The accuracy of Hill's (1937) study of the anatomy of *Thomomys* has been verified herein. However, his description of several important muscle groups is also incomplete. The papers of Rinker (1954, 1963), Stein (1986), and Kesner (1986) were useful for comparison with murid rodents, as was Woods (1972) for "hystricomorphs," Klingener (1970) and Fry (1961) for *Aplodontia,* and Bryant (1945) for sciurids. Meinertz's (1932, 1935a, 1935b, 1941, 1943a, 1943b, 1944, 1951) numerous papers were extremely useful for the superficial facial musculature. The monographs by Greene (1935) on the anatomy of the rat and Cooper and Schiller (1975) on the guinea pig were not used because of numerous errors and inconsistencies between text and figures.

Groupings of muscles used here are based on adult position and innervation. These groupings do not always reflect embryonic derivation (Cheng, 1955; Lance Jones, 1979), but are justified because using them makes comparison with other rodents groups easier and because there are few ontogenetic studies of rodent muscles. Within each grouping, muscles are listed from superficial to deep or anterior to posterior.

Phylogenetic Methods

The goal of phylogenetic systematics is to recover the genealogical history of the taxa involved (Wiley, 1981, refers to this as the "history of speciation"). Genealogical history is defined as descent from a common ancestor and, as a result, only those characters that are shared by two or more taxa and also found in their common ancestor provide evidence of genealogy. Such characters are termed shared derived homologies or synapomorphies (Wiley, 1981). In contrast, characters that are structurally or functionally similar (homoplasies), but which are thought to have evolved independently in the group under study, do not provide evidence of genealogical relationships. Likewise, characters shared by all members of the study group and members of the outgroup (e.g., shared primitive characters) are uninformative. Thus, only shared derived characters are useful in recovering the group's "history" of descent.

The criteria used to establish homology of the myological characters used in this study included: topographic position, constancy of innervation, and ontogenetic similarity (Wiley, 1981). In addition, Cheng (1955), Lance Jones (1979), and Rowe (1986) have described the myological transformations and established the homology of many vertebrate muscle groups.

Of the various methodologies offered to date to classify organisms, only phylogenetic systematics (cladistics) is restricted to the use of shared derived characters (Hennig, 1966; Wiley, 1981; and references therein). The specifics of cladistic methodology are best left to recent texts on the subject (Wiley, 1981; Nelson and Platnick, 1981; Eldredge and Cracraft, 1980). It is important to note that contradictory hypotheses of phylogeny can occur because of homoplasy (or synapomorphies that contradict one another) in the character set. This conflict is resolved by choosing the hypothesis supported by the most evidence (i.e. the simplest hypothesis of relationships is favored). This parsimony argument, as it is usually called, "requires the fewest *ad hoc* explanations to protect it (the phylogeny) from contradictory evidence" (Novacek, 1986:9). That instances of character convergence or parallelism occur in nature does not invalidate the method.

Determining the synapomorphies for the group(s) under study is accomplished by outgroup and ontogenetic criteria (see Maddison *et al.*, 1984 for a discussion of the outgroup method). The most useful outgroup for determining character polarity is the sister group of the group under study. The outgroups used for the analysis of the Heteromyidae include its hypothesized sister group the Geomyidae. I accept Wahlert's (1974, 1985) and Luckett's (1985) conclusion that the Sciuridae are the primitive sister group of the Myomorpha, and I include the Sciuridae in my outgroup analysis. The choice of more than one outgroup recognizes that characters are primitive, not taxa. Not all appropriate outgroup taxa were available for dissection. In such cases, literature descriptions were used when available. As a result, not all muscle character states could be polarized. Only muscle characters that could be polarized were used in the PAUP analysis. The polarity and character number of each muscle used is described in the "Remarks" section of that muscle.

Phylogenetic trees were generated by Swofford's PAUP program (version 2.2; Fink, 1986) running on an IBM Model 30 with 640k RAM and an 8087 math coprocessor. PAUP analysis (ALLTREES) yields the most parsimonious tree(s), with minimum branch lengths and a consistency index closest to one.

DESCRIPTION OF MUSCLES

BRANCHIOMERIC MUSCLES

Masticatory Group (Figs. 2, 3)

In most rodents the masseter is divisible into three parts, the superficial, medial, and lateral. In some lineages, including the Heteromyidae, the lateral and medial parts are further divided into anterior and posterior components. Divisions of the masseter are recognized on the basis of differences in fiber direction. Schumacher and Rehmer (1962) and Becht (1953) used terminology that is difficult to synonymize with that of other workers. Only recently has there been an attempt to standardize rodent masseter nomenclature. The terminology used here follows that of Hill (1937) for *Thomomys,* Klingener (1964) for dipodoids, and Rinker (1954) for murids. Hill (1937) provided a useful list of synonyms for use with the older rodent literature. In addition, Edgeworth (1916, 1935) and Adams (1919) provided masseter synonymies for other mammals. Innervation of the masseter, temporalis, and external pterygoideus is via the masticatory nerve.

M. masseter superficialis (Fig. 2)

ORIGIN.—By a narrow tendon on the maxilla ventral to the anterior margin of the infraorbital foramen.

INSERTION.—On the ventral border of the mandible from the anterior angular process to the area below the incisor root. Some fibers run under the mandible to insert on its medioventral edge.

REMARKS.—In heteromyids the insertion of the superficial masseter is difficult to separate from the lateral masseter. The origin is completely distinct. In *Dipodomys, Perognathus,* and *Microdipodops,* the origin is from the posteroventral margin of the infraorbital foramen, the tendon continues further posteriorly, and the insertion is shifted further posteriorly on the mandible. In *Microdipodops* this part of the masseter is reduced in size. In dipodoids the superficial masseter is incompletely differentiated from the lateral masseter at its insertion (Klingener, 1964). The condition of the superficial masseter in muroids is similar to that in heteromyids and geo-

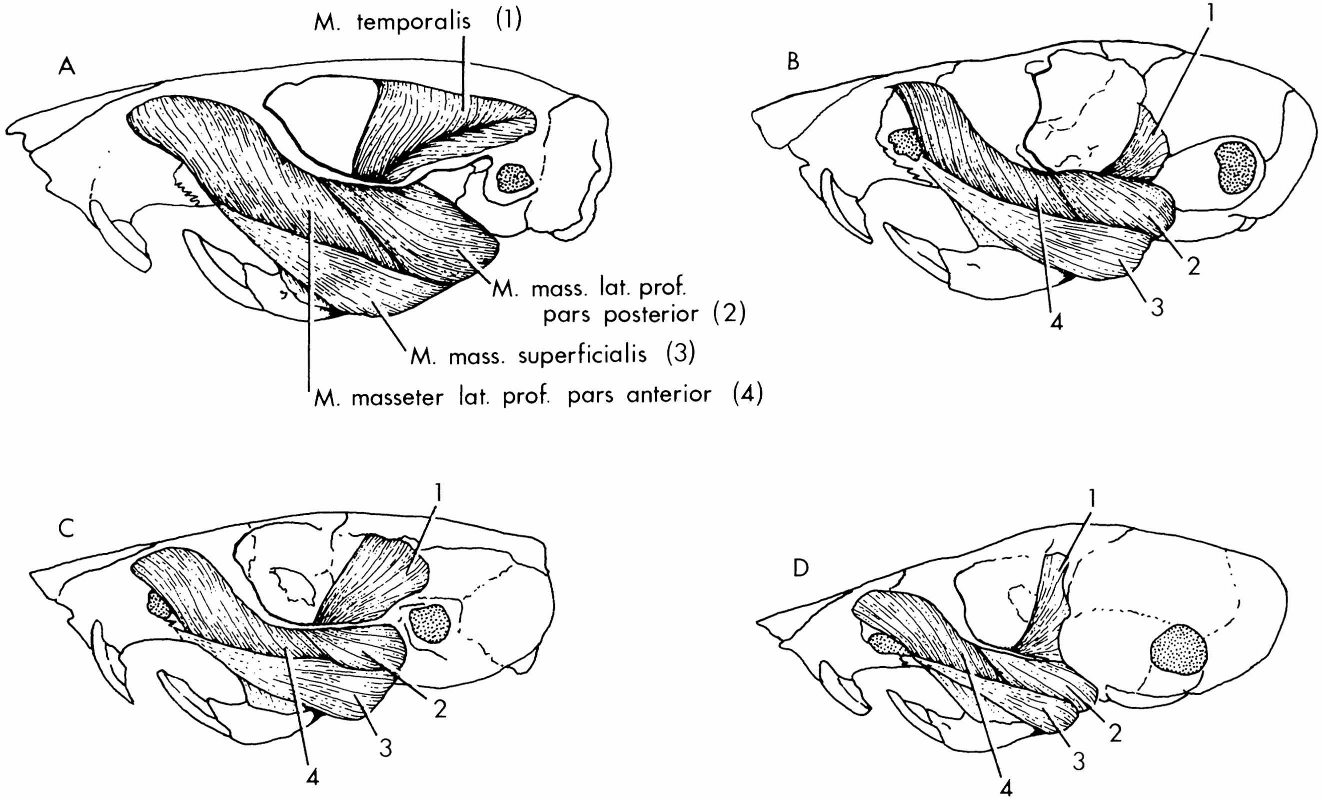

FIG. 2. Masticatory muscles of heteromyid rodents: A) *Heteromys,* B) *Dipodomys,* C) *Perognathus,* D) *Microdipodops.*

myids (Hill, 1937; Rinker, 1954). In *Thomomys* the tendon also originates from the posteroventral margin of the infraorbital foramen (Hill, 1937). Some fibers pass ventrally onto the medial side of the mandible in sciurids, *Aplodontia,* and murids, as well as in heteromyids (Hill, 1937; Bryant, 1945; Rinker, 1954). A similar condition was reported for *Ctenodactylus, Anomalurus,* and *Pedetes* by Tullberg (1899). The reflected superficial masseter is extremely well developed in New and Old World "hystricomorph" rodents and led Tullberg to erect the tribe Hystricognathi. A medially reflected superficial masseter is also found in the microtines *Clethrionomys, Phenacomys,* and *Arborimus.* It is present but reduced in *Microtus, Pitymys, Arvicola,* and *Neofiber,* but absent in *Ondatra* (Kesner, 1980).

M. masseter lateralis profundus pars anterior (Fig. 2)

ORIGIN.—From the zygomatic plate, anteriorly from the posterior margin of the bulge created by the incisor root and posteriorly along the zygomatic arch to a point just ventral to the eye.

INSERTION.—On the lateral mandible deep to the superficial masseter; along the lower border of the masseteric fossa.

REMARKS.—In geomyoids the lateral masseter is divisible into anterior and posterior parts. In *Dipodomys* the origin is shifted caudad along the rostrum and does not completely cover the infraorbital foramen. In *Perognathus, Dipodomys,* and *Microdipodops* the lateral masseter is not reduced, but begins further posteriorly on the rostrum so that the infraorbital foramen is exposed. The anterior insertion of this muscle is covered by a tendinous sheet in *Dipodomys, Microdipodops,* and *Perognathus.* In *Perognathus* the tendinous sheet is more extensive. In microtines only a single M. masseter lateralis profundus is present (Kesner, 1980).

M. masseter lateralis profundus pars posterior (Fig. 2)

ORIGIN.—From the zygomatic arch ventral to the eye.

INSERTION.—The fibers run ventrocaudad to insert on the dorsal and lateral margins of the angular process.

REMARKS.—The origin in *Dipodomys* includes the dorsal margin of the zygoma, while the insertion is primarily on the medial and lateral surfaces of the angular process including the groove created by the condyle and the angular process. *Perognathus* and *Microdipodops* are similar to *Heteromys* except that the origin is partly tendinous. This muscle is the smaller of the two parts of M. masseter lateralis. In *Aplodontia* this muscle represents the bulk of the masseter complex (Klingener, 1970; Hill 1937). Based on outgroup comparisons, the origin from the dorsal zygoma is considered derived (character 1).

M. masseter medialis pars anterior (Fig. 3)

ORIGIN.—From the medial zygoma below the eye and from the orbital side of the zygomatic plate.

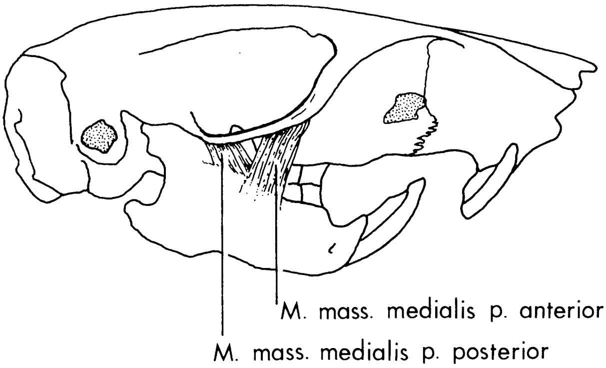

FIG. 3. Deep masticatory muscles in *Heteromys*.

INSERTION.—On the anterior and lateral margin of the coronoid process and dorsolaterally on the mandible at the level of the posterior molars.

REMARKS.—In *Perognathus, Microdipodops,* and *Dipodomys* the fibers converge to form a tendon dorsal to their insertion on the lateral surface of the mandible ventral to M_2. In *Eutamias* and other sciurids the anterior part is reduced (Bryant, 1945; Hill 1937). In *Aplodontia* the orbital part is large, and a few fibers pass into the infraorbital foramen from the orbital side (Coues and Allen, 1877). This "proto-hystricomorph" condition was disputed by Hill (1937), but led Eastman (1982) to speculate that the "hystricomorphous" masseter is the primitive condition for rodents (but see Wilson, 1986, for a discussion of this slip). In "myomorph" rodents this slip of the masseter runs into the expanded infraorbital foramen from the orbital side.

M. masseter medialis pars posterior (Fig. 3)

ORIGIN.—From the medial side of the posterior zygoma near the squamosal.

INSERTION.—Fibers run cranioventrad to insert on the mandible in the region of the notch created by the condyle and the coronoid process.

REMARKS.—Fibers run anteroventrad to the mandible and are penetrated by the masticatory nerve as in *Thomomys* (Hill, 1937). This muscle is reduced in *Dipodomys* and is probably synonymous with the ventral part of the temporalis of Howell (1932). In *Dipodomys* the origin is from the squamosal just anterior to the temporomandibular joint. The fibers run craniad to insert on the lateral aspect of the condyle and slightly on the medial surface of the angular process.

M. temporalis (Fig. 2)

ORIGIN.—From the dorsal margin of the squamosal, posterior to the jugal, and from the nuchal and sagittal ridge and the temporal fossa.

INSERTION.—On the medial surface of the coronoid process ventral to the posterior margin of the molar tooth row and slightly on the anterolateral surface of the coronoid.

REMARKS.—In *Dipodomys* this muscle is greatly reduced, even in comparison with *Microdipodops* (which also has inflated auditory bullae). In geomyids the temporalis is large. In heteromyines, and to a lesser extent in other heteromyids, a tendon separates the dorsomedial and ventrolateral parts of the temporalis. These may be homologous to Rinker's (1954) superficial and deep parts of M. temporalis. In the dipodoid *Jaculus* the temporalis is also greatly reduced. Klingener (1964) suggested that reduction in the anterior part of the temporalis is associated with a shift to a grinding dentition. If so, the condition in *Dipodomys* parallels that of *Jaculus:* the anterodorsal temporalis is absent and grinding dentition has evolved. Reduction in the temporalis is considered the derived character (character 2).

M. pterygoideus externus (not figured)

ORIGIN.—From the alisphenoid bone and the lateral surface of the pterygoid plate.

INSERTION.—On the medial surface of the condyloid process of the mandible.

REMARKS.—The origin and insertion sites do not differ in heteromyids, but the muscles vary in size and shape because of differences in the position and relative size of the pterygoid and alisphenoid bones.

Internal Pterygoid Group (Fig. 4)

This muscle group is innervated by the medial branch of the mandibular nerve.

M. pterygoideus internus (Fig. 4A)

ORIGIN.—From the lateral walls of the pterygoid fossa.

INSERTION.—On the medial surface of the angular process of the mandible.

M. tensor tympani (not figured)

ORIGIN.—From the internal surface of the anterior lateral wall of the ectotympanic.

INSERTION.—On the medial surface of the manubrium of the malleus.

REMARKS.—The tensor tympani runs from the ectotympanic, around a right angle created by the cochlearform process, and across the middle ear to its insertion. See Webster and Webster (1975) for details.

M. tensor veli palatini

This muscle was not dissected.

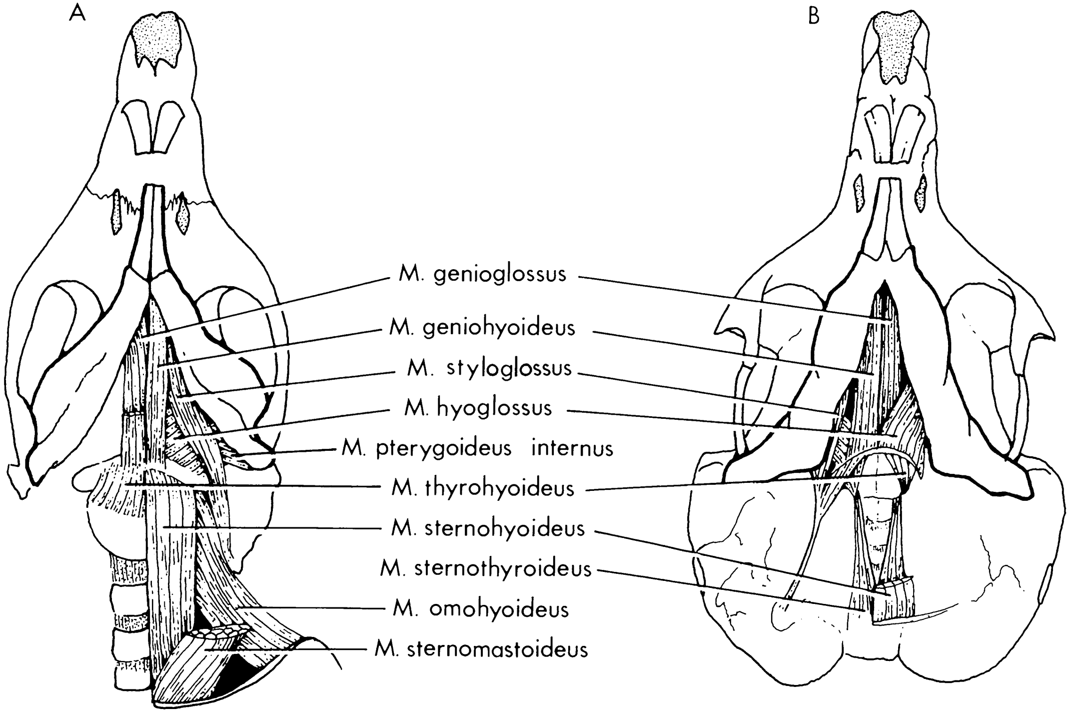

FIG. 4. Ventral views of the muscles of the hyoid region. The right side of each skull is a superficial view and the left side a deeper view: A) *Heteromys*, B) *Dipodomys*.

Mylohyoid Group (Fig. 5)

Innervation of these muscles is via the mylohyal branch of the mandibular nerve.

M. mylohyoideus (Fig. 5)

Origin.—From the medial surface of the mandible, ventral to the molar tooth row.

Insertion.—Onto the median raphe and the corresponding fibers from the opposite side and fascially onto the body of the hyoid.

Remarks.—This muscle is visible between the right and left digastrics. In *Dipodomys,* this muscle is shifted posteriorly and is attached to the hyoid arch along most of its length. In the mole rat, *Tachyoryctes,* this muscle is reduced to a small area between the mandibles (Bereke, 1983).

M. transversus mandibulae (Fig. 5)

Origin.—From the ventral and medial edge of the mandible, deep to the anterior digastric and anterior to the mylohyoideus.

Insertion.—Into the corresponding fibers from the opposite side of the mandible.

Remarks.—In *Dipodomys* and *Microdipodops* this muscle extends further posteriorly and is more robust than in *Perognathus* or *Heteromys.* This muscle is drastically reduced in many "hystricomorph" rodents (Woods, 1972). Parsons (1894) was mistaken in reporting the absence of this muscle as a character separating the "Sciuromorpha" from "Hystricomorpha."

M. digastricus (Fig. 5; anterior belly)

Origin.—As a direct continuation of the tendon of the posterior digastric and from the anterior surface of the tendinous arch over the hyoid.

Insertion.—Along the ventral edge of the mandible posterior and lateral to the mandibular symphysis.

Remarks.—Geomyoids have an hystricomorphine-type digastric (Parsons, 1894), a type which Hill (1937) regarded as derived. The right and left anterior bellies do not contact in the midline in the "hystricomorphine" digastric (Parsons, 1894). Dipodoids and muroids (Klingener, 1964; Rinker, 1954) have a sciuromorphine digastric, in which the two anterior bellies are partly fused along the ventral midline, covering the mylohyoideus. With the exception of *Erethizon* (Woods, 1972) and *Coendou* (Parsons, 1894), the anterior and posterior bellies of the "hystricomorph" digastric are not separated by a tendon as they are in geomyoids, bathyergids, muroids, and dipodoids (Parsons, 1894; Rinker, 1954; Klingener, 1964). In microtines the digastric is unique. The anterior belly originates from the tendon of the posterior belly and from a "tendinous arcade" over the hyoid bone. The condition in microtines is highly variable, with the underlying mylohyoideus completely hidden in *Ondatra* and *Lemmus.* In *Lemmus,* fibers from the right and left anterior bellies intermingle at the level of the "tendinous

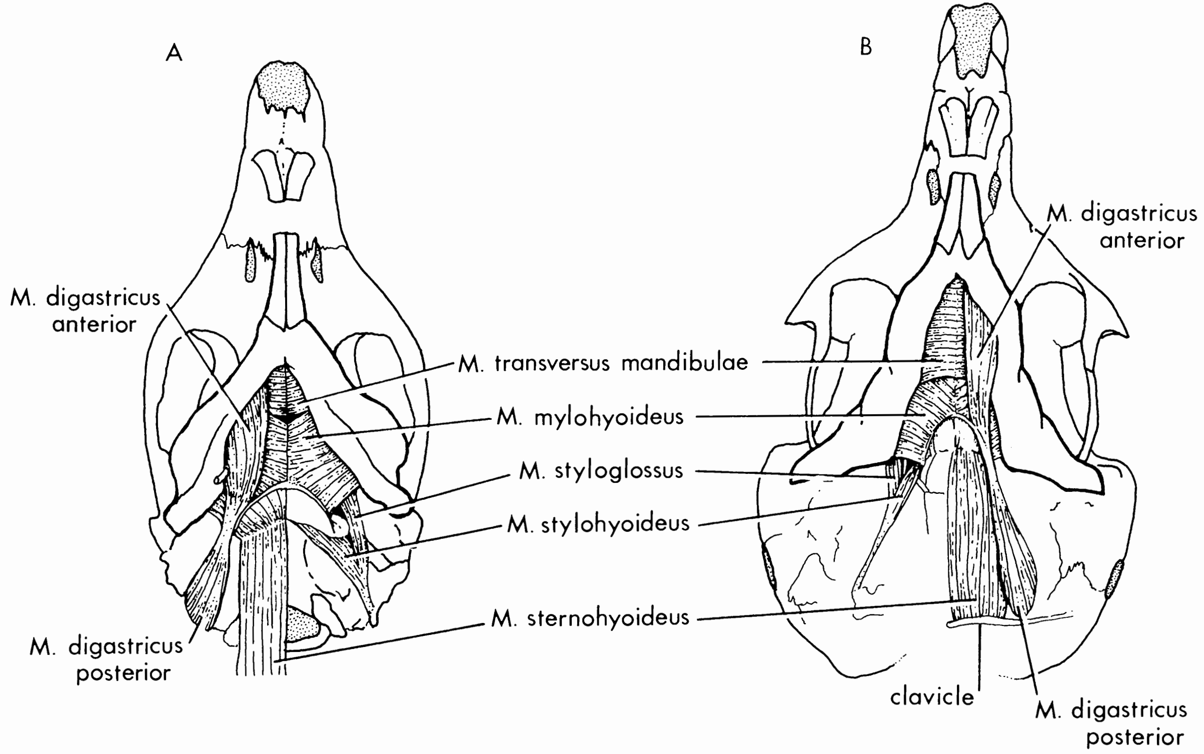

Fig. 5. Ventral views of the muscles of the hyoid region: A) *Heteromys*, superficial muscles on the left, deeper muscles on the right; B) *Dipodomys*, superficial muscles on the right.

arcade." However, in *Dicrostonyx, Lagurus,* and *Arborimus* the right and left bellies do not overlap along their midlines (Kesner, 1980). The sciuromorphine digastric is considered primitive for rodents (character 3; Hill, 1937).

Superficial Facial Group (Figs. 6–10)

The superficial facial muscles are innervated by the facial nerve. Huber (1930, 1931) discussed in detail the evolution of superficial facial muscles in mammals. Most rodents lack the sphincter colli superficialis; however Schrieber (1929) described a reduced sphincter colli superficialis in the agouti and paca. His sphincter colli superficialis is probably the pars palpebralis of the sphincter colli profundus sheet. Lagomorphs have a true sphincter colli superficialis (Meinertz, 1935b).

M. platysma myoides (Figs. 6 and 7)

ORIGIN.—From the dorsal midline caudal to the occiput and extending posteriorly to the area between the scapulae. Pars auricularis originates from the anterior surface of the auricular cartilage and runs anterad superficial to the "intermediate plate" (see description below).

INSERTION.—In three parts: Pars auricularis inserts into the orbicularis oculi fibers ventral to the eye; pars buccalis inserts along the junction of orbicularis oris pars sacculi and the anterolateral pouch wall; and pars mentalis inserts into fibers of buccinatorius pars orbicularis near the mandibular symphysis.

REMARKS.—The three divisions of M. platysma myoides is a typical pattern in rodents. All three divisions occur in some "hystricomorphs," sciurids, dipodoids, and muroids. This muscle is reduced in *Dipodomys* and *Microdipodops* and no pars auricularis is present. In these two genera the origin does not extend over the shoulder, perhaps due to the shortened neck. Reduction in superficial facial muscles is considered a derived character for rodents (character 4). M. platysma myoides pars auricularis is found is all rodents studied and is considered primitive for rodents (character 5). In *Marmota* (but not *Sciurus* or *Eutamias*), the pars mentalis slip is completely separate and runs partially deep to pars buccalis (Meinertz, 1943b). A similar situation is found in heteromyids where pars mentalis is separate from pars buccalis and runs deep to pars buccalis posterior to the pouch.

M. platysma cervicale (Figs. 6B and 7A)

ORIGIN.—From the nuchal midline deep to platysma myoides and anteriorly deep to the cervico-auricular muscles.

INSERTION.—Into the M. platysma myoides and the pouch retractor muscle from below (along a "fusion-zone" running between the ear and the shoulder).

REMARKS.—In *Dipodomys* and *Microdipodops* the origin is reduced. The insertion is unique to geomyoids. In most other rodents the platysma

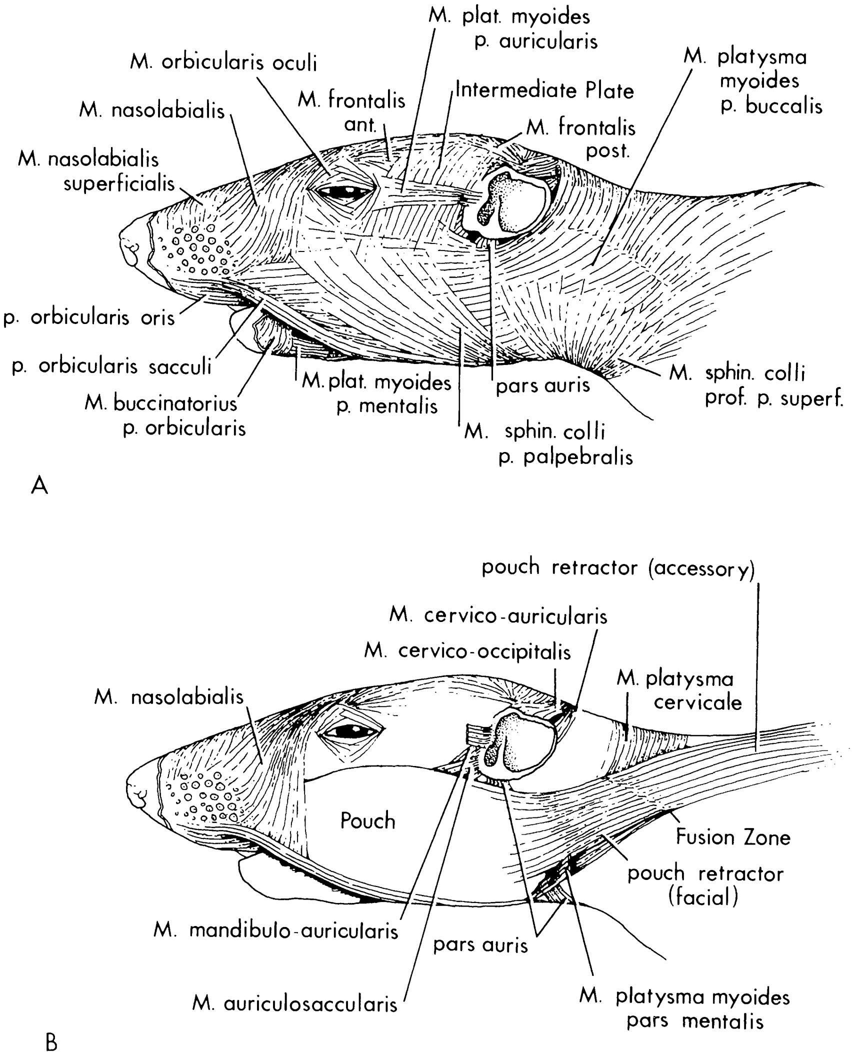

FIG. 6. Superficial facial muscles of *Heteromys:* A) superficial muscles. M. sphincter colli profundus pars intermedia dorsalis and pars intermedia ventralis make up the "intermediate plate." B) Deep view of the superficial facial muscles associated with the cheek pouch. The pouch retractor muscle is dually innervated. The anterior M. retractor sacculi pars facialis is derived from superficial facial musculature and innervated by the facial nerve. The posterior M. retractor sacculi pars trapezius is innervated by the accessory nerve. The "fusion zone" indicates the region where these two portions of the pouch retractor meet.

cervicale runs deep to M. platysma myoides to insert into the skin along the throat. In sciurids, however, the platysma cervicale inserts into connective tissue between pars auris and platysma myoides pars buccalis (Meinertz, 1943b). Insertion into M. retractor sacculi pars facialis is considered the derived condition for rodents (character 6).

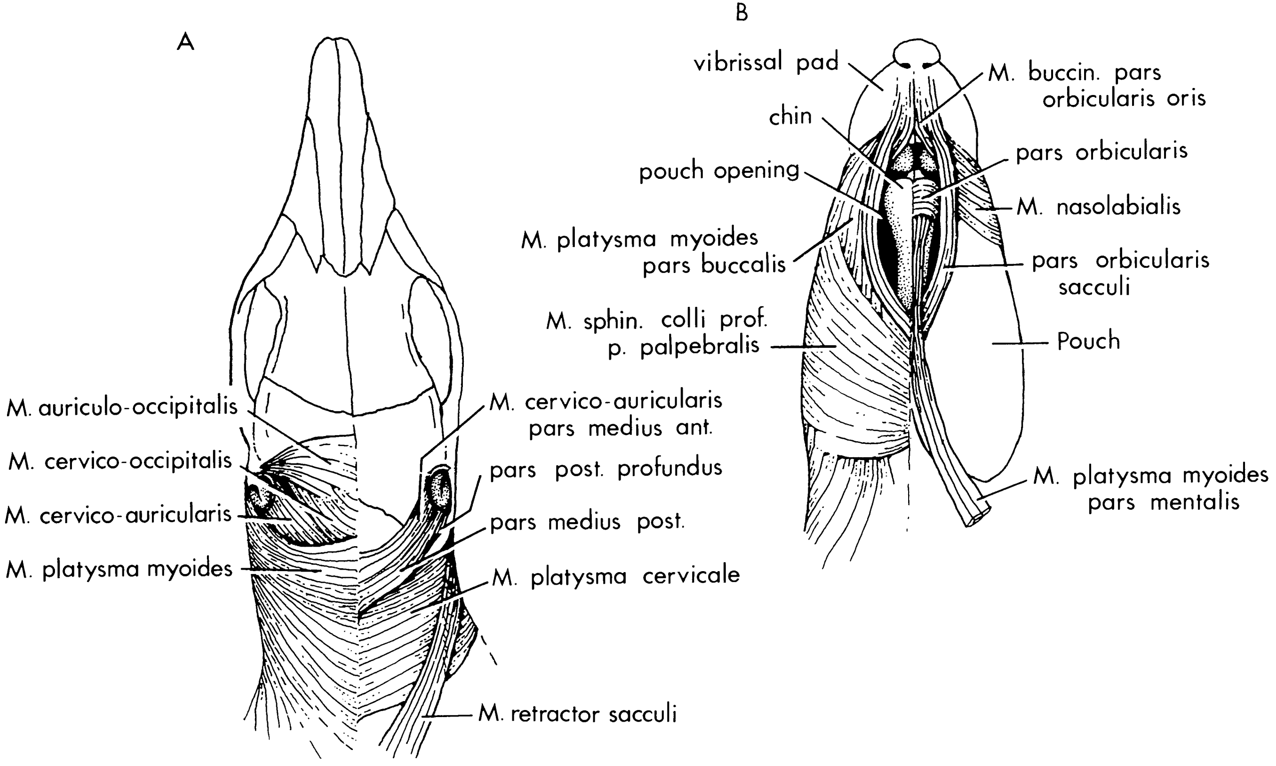

FIG. 7. Superficial facial muscles in *Heteromys:* A) dorsal view, superficial muscles on the left and deeper muscles on the right; B) ventral view, superficial muscles on the left and deeper muscles on the right.

M. retractor sacculi pars facialis (Figs. 6B and 7A)

Origin.—From the fibers of the trapezial retractor at the "fusion-zone" with the platysma cervicale.

Insertion.—Onto the laterodorsal and medial walls of the posterior one-third of the cheek pouch.

Remarks.—The retractor is thinner in dipodomyines. Heteromyids (and geomyids) possess a dually innervated retractor, with the anterior portion innervated by the facial nerve, and the posterior portion innervated by the accessory nerve (Hill, 1935). This shared condition represents a synapomorphy for the Geomyoidea (character 7). In sciurids that have cheek pouches, the retractor is innervated solely by the facial nerve, and the origin is from the scapular spine and from the sternum. In cricetine hamsters, the pouch retractor is innervated by the accessory nerve and the origin is from the lumbar vertebrae (see Ryan, 1986, for a review of cheek pouch evolution in rodents).

M. cervico-auricularis (Figs. 6B and 7A)

Origin.—From the ligamentum nuchae along the dorsal midline posterior to the occiput and deep to M. platysma myoides.

Insertion.—On the caudal and dorsomedial aspects of the ear cartilage via three distinct slips (not to be confused with M. cervico-auricularis medius anterior).

Remarks.—In *Heteromys* there appear to be three slips. The anterior slip inserts on the anterior and dorsal auricular cartilage. The median slip passes deep to a small bundle of auricular muscles to insert on the posterodorsal auricular cartilage. The posterior slip inserts posterior to the ear cartilage. In *Dipodomys* the posterior origin of this muscle lies superficial to the platysma myoides. In many rodents this muscle inserts on the auricular cartilage by a number of slips, usually two (Meinertz, 1941). In dipodoids (Klingener, 1964) the cervico-auricularis and cervico-occipitalis are not separable. In sciurids only a single M. cervico-auriculo-occipitalis muscle is present (Meinertz, 1943a; 1943b) and this condition is considered primitive (character 8). In geomyoids and muroids the superficial retroauricular muscles are divided into a separate M. cervico-auricularis and M. cervico-occipitalis (Klingener, 1964; Rinker, 1954).

M. cervico-auricularis medius anterior (Fig. 7A)

Origin.—From the ligamentum nuchae, deep to M. cervico-occipitalis and continuous at origin with medius posterior.

Insertion.—On the dorsomedial surface of the auricular cartilage deep to the anteriormost of the three M. cervico-auricularis slips.

Remarks.—This muscle shares a common origin with pars medius posterior in *Heteromys, Liomys,* and *Perognathus,* but pars medius anterior and pars medius posterior are distinct slips throughout their lengths in *Dipodomys*. In *Marmota* and *Sciurus* the M. cervico-auricularis medius is not divisible into posterior and anterior slips (Meinertz, 1943a, 1943b). In dipodoids and muroids the two muscles are completely separate at the origin (Klingener, 1964; Rinker, 1954). Meinertz (1941) found no medial layer in the Greenland lemming, *Dicrostonyx*. Both slips are apparently present in *Hydrochoerus* and *Cavia* (Meinertz, 1932, 1944). The three slips of M. cervico-auricularis are not to be confused with this deeper layer of cervico-auricular muscles.

M. cervico-auricularis medius posterior (Fig. 7A)

ORIGIN.—From the ligamentum nuchae, deep to M. cervico-auricularis and continuous with the origin of medius anterior.

INSERTION.—On the caudal surface of the auricular cartilage deep to the posteriormost of the three M. cervico-auricularis slips.

M. cervico-auricularis posterior profundus (Fig. 7A)

ORIGIN.—From the ligamentum nuchae and fascially from M. cervico-auricularis medius posterior.

INSERTION.—On the posteroventral surface of the auricular cartilage partially covered by medius posterior.

REMARKS.—Not found in *Dipodomys* or *Perognathus*. This muscle is the homolog of the posterior division found in carnivores (Huber, 1930, 1931). Meinertz (1941) believed this deepest layer was derived from the M. platysma cervicale (or vice versa) because of their common innervation via a branch of ramus auricularis posterior.

M. cervico-occipitalis (Figs. 6B and 7A)

ORIGIN.—From the ligamentum nuchae along the dorsal midline posterior to the occiput and deep to the M. platysma myoides. This muscle is an anterior continuation of M. cervico-auricularis.

INSERTION.—On the surface of the skull deep to M. auriculo-occipitalis, dorsal portions of the "intermediate plate," and the auricular part of M. frontalis.

M. mandibulo-auricularis (Fig. 6B)

ORIGIN.—From the edge of the mandible in the groove created by the condylar process and the angular process.

INSERTION.—On the anterodorsal surface of the auricular cartilage.

M. sphincter colli profundus

This muscle is divided into five parts: pars auris, pars intermedia, pars palpebralis, pars oris, and pars cervicalis (Huber, 1930, 1931). In rodents, however, the pars oris is included in the buccinatorius group, and the pars palpebralis is traditionally included with the pars intermedia group. In all but "hystricomorphs" the pars cervicalis is absent (Meinertz, 1941).

M. sphincter colli profundus pars auris (Figs. 6 and 10A; M. sterno-auricularis of Hill, 1937)

ORIGIN.—From the ventral midline of the manubrium sterni.

INSERTION.—On the ventral surface of the auricular cartilage.

REMARKS.—In the sciurid *Eutamias* pars auris fibers course dorsad and insert partially into the descending fibers of pars intermedia ventralis. This condition is found in some "hystricomorphs" (Meinertz, 1941, 1944). See also the remarks under pars auriculosaccularis (below).

M. sphincter colli profundus partes intermedia ventralis et palpebralis (Fig. 6A)

These fibers make up the greater part of the sphincter colli profundus. The pars palpebralis and pars intermedia ventralis form a continuous sheet in heteromyids. Klingener (1964) stated that the pars intermedia ventralis fibers pass deep to M. platysma myoides in dipodoids. Rinker (1954) found these fibers to be continuous anteriorly with those of pars palpebralis, which is superficial to M. platysma myoides in muroids. In heteromyids both muscles form one sheet which passes superficial to M. platysma myoides. Pars intermedia ventralis runs dorsad over the pouch and inserts into the descending fibers of the pars intermedia dorsalis at the dorsal margin of the pouch. Although there is no clear separation, pars palpebralis inserts into the skin over the pouch ventral to the eye without interdigitating with fibers of pars intermedia dorsalis.

M. sphincter colli profundus pars auriculosaccularis (Fig. 6B; M. sternoauricularis of Hill, 1937)

ORIGIN.—From the anterior surface of the auricular cartilage superficial to M. mandibulo-auricularis.

INSERTION.—On the medial pouch wall ventral to the eye.

REMARKS.—Hill (1937) called this slip M. sternoauricularis and considered it to be part of the pars auris. I consider this muscle to be derived from the "intermediate plate" (see description below) based on its innervation. Pars auris is innervated by the ramus colli of the facial nerve, while the pars auriculosaccularis is innervated by ramus platysmaticus superficialis (also a branch of the facial nerve). It is possible that the pars auriculosaccularis in heteromyids is homologous to the M. zygomaticolabialis, which was not found in heteromyids. If true, this would require major shifts in both origin and insertion. This muscle is a synapomorphy for geomyoid rodents (character 9).

M. sphincter colli profundus pars intermedia dorsalis (Fig. 6A)

This sheet is called "intermediate plate" by Rinker (1954). It is found in all heteromyids, where it originates fascially on the dorsum of the cranium superficial to M. frontalis. It passes ventrad between the eye and ear and runs deep to M. platysma myoides pars auricularis and pars buccalis, to interdigitate with the ascending fibers of pars intermedia ventralis. In other rodents the intermediate plate varies in the extent of its development. Sciurids have a reduced intermediate plate, but it is also reduced in the dipodoids *Jaculus* and *Alactagulus* (Klingener, 1964) as well as in the dipodomyines. "Hystricomorph" rodents also exhibit a strongly reduced intermediate plate (Meinertz, 1941, 1944). Meinertz (1941) described a transition from a well developed intermediate plate to a much reduced condition he referred to as M. depressor helicus.

M. auriculo-occipitalis (Fig. 7A)

ORIGIN.—From the surface of the posterior parts of M. frontalis, pars auricularis and the "intermediate plate."

INSERTION.—Into the skin of the cranium superficial to M. cervico-auricularis.

REMARKS.—In rodents this muscle is highly variable in the extent to which it covers the dorsum of the cranium. It is small in sciurids; this is presumably the primitive condition (Meinertz, 1943a,b).

M. auricularis anterior superior et inferior

Absent in the Heteromyidae.

M. frontalis (Fig. 6A; anterior part)

ORIGIN.—From the orbital surface of the frontal bone at the anterior margin of the eye.

INSERTION.—Into fibers of the posterior (auricular) part of M. frontalis between the eye and ear.

M. frontalis (Fig. 6A; posterior part)

ORIGIN.—From the anterodorsal surface of the auricular cartilage.

INSERTION.—Into fibers of the orbital part of M. frontalis posterior to the eye, after running deep to the intermediate plate.

REMARKS.—The posterior frontalis does not extend as far anterior in *Dipodomys* and is reduced in *Microdipodops*. Klingener (1964) stated that in dipodoids "this muscle runs forward deep to the intermediate plate, as in *Sigmodon* and *Oryzomys*." In *Peromyscus, Neotoma, Rattus, Mesocricetus,* and *Dicrostonyx* this muscle lies superficial to the intermediate plate (Meinertz, 1941; Rinker, 1954; Wineski, 1985). Meinertz (1941) stated that M. frontalis in *Arvicola* "breaks through" the intermediate plate to lie on its deep side.

M. nasolabialis (Figs. 6 and 7B)

ORIGIN.—From the orbital surface of the frontal bone, dorsal to the origin of M. frontalis.

INSERTION.—Into the skin on the rostrum and into the mystacial pad. Posterior fibers run deep to pars buccalis to insert at the junction of the anterior pouch wall and M. buccinatorius pars orbicularis sacculi.

REMARKS.—The nasolabialis fans out ventrally just anterior to the eye. The fibers form a broad sheet which terminates in the orbicularis sacculi along the lateral pouch opening, deep to platysma myoides pars buccalis.

Rostrally these fibers fan out into the mystacial pad. The muscle is reduced in *Microdipodops* and slightly reduced in *Dipodomys* relative to the other heteromyids. Contraction of M. nasolabialis may function to raise the anterolateral pouch wall.

M. nasolabialis superficialis (Fig. 6A)

ORIGIN.—Fascially from the nasal bone.

INSERTION.—Into the mystacial pad.

M. orbicularis oculi (Fig. 6)

This muscle consists of fibers that surround the eye and insert into the skin of the eyelid and surrounding skin. Fibers are difficult to separate anteriorly from those of M. nasolabialis and posteriorly from the intermediate plate. M. retractor anguli oculi lateralis is absent in heteromyids.

M. zygomaticolabialis

Not present in heteromyids, but see remarks under pars auriculosaccularis (above).

The following muscles represent the anterior reorganization of the sphincter colli profundus. This can be seen in lagomorphs where the pars oris muscles are continuous with the pars palpebralis.

M. maxillolabialis (Fig. 9A)

ORIGIN.—From the maxilla ventral to the infraorbital foramen and posterior to the suture between the premaxilla and maxilla.

INSERTION.—Into the mystacial pad.

REMARKS.—The fibers of this muscle run anteriorly along the medial and dorsal surface of the pouch to insert among the bases of the individual vibrissae.

M. dilator nasi (Fig. 8)

ORIGIN.—From the dorsal surface of the zygomatic plate anterior to the eye.

INSERTION.—Via a thin tendon into the dorsolateral portion of the nasal cartilage.

REMARKS.—This muscle originates deep to M. nasolabialis but inserts superficial to pars media superior. In *Dipodomys* the origin is narrower and insertion is less tendinous. The dilator nasi is tendinous at the insertion in dipodoids (Klingener, 1964), muroids (Rinker, 1954; Meinertz, 1941, 1951), and sciuroids (Meinertz, 1943a,b; but see Bryant, 1945, p. 314). In "hystricomorphs" and bathyergids the dilator nasi does not become tendinous (Meinertz, 1941, 1951). Based on their innervation, Meinertz (1941) believed that this muscle and M. maxillolabialis are derived from a single muscle. As evidence supporting this idea, Meinertz (1943a) noted that these two muscles are connected along part of their length in *Sciurus*.

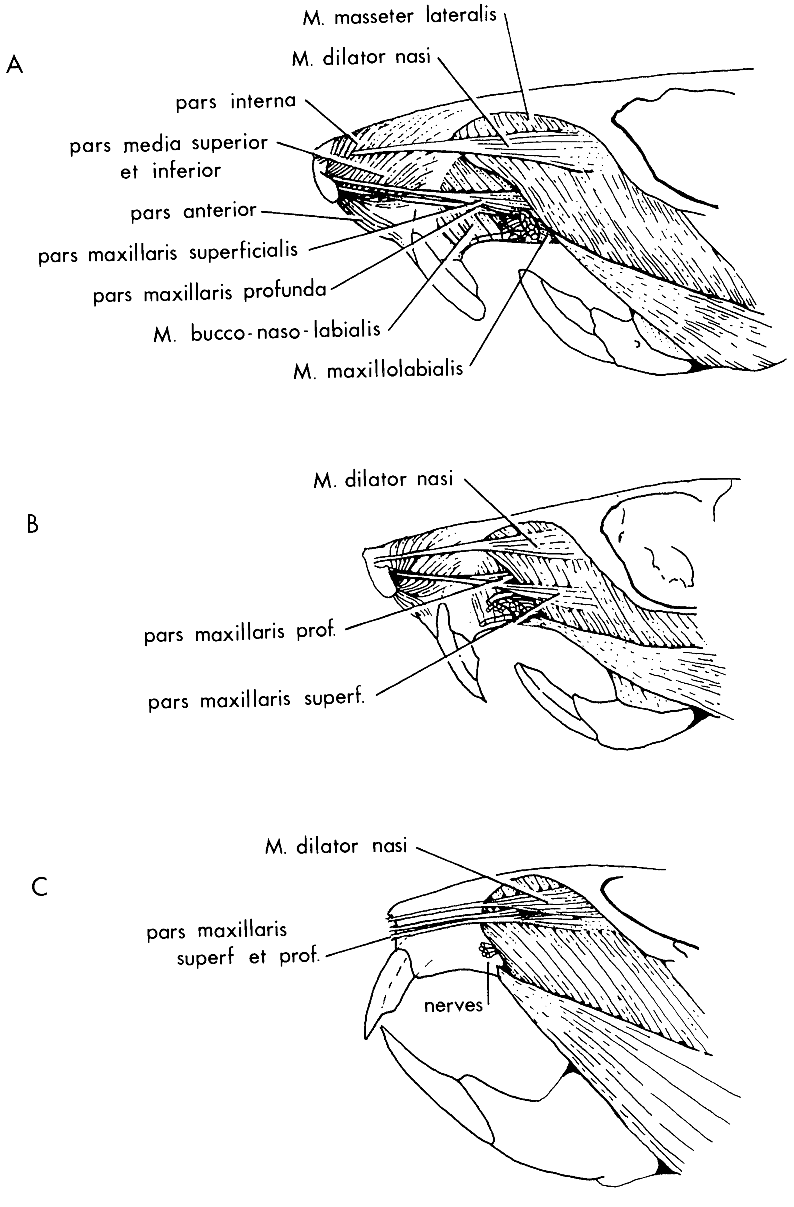

FIG. 8. Lateral views of the deep rostral muscles in A) *Heteromys,* B) *Perognathus,* and C) *Thomomys.* Unless otherwise indicated, the muscles are slips of M. nasolabialis profundus.

M. nasolabialis profundus

This muscle is composed of several parts.

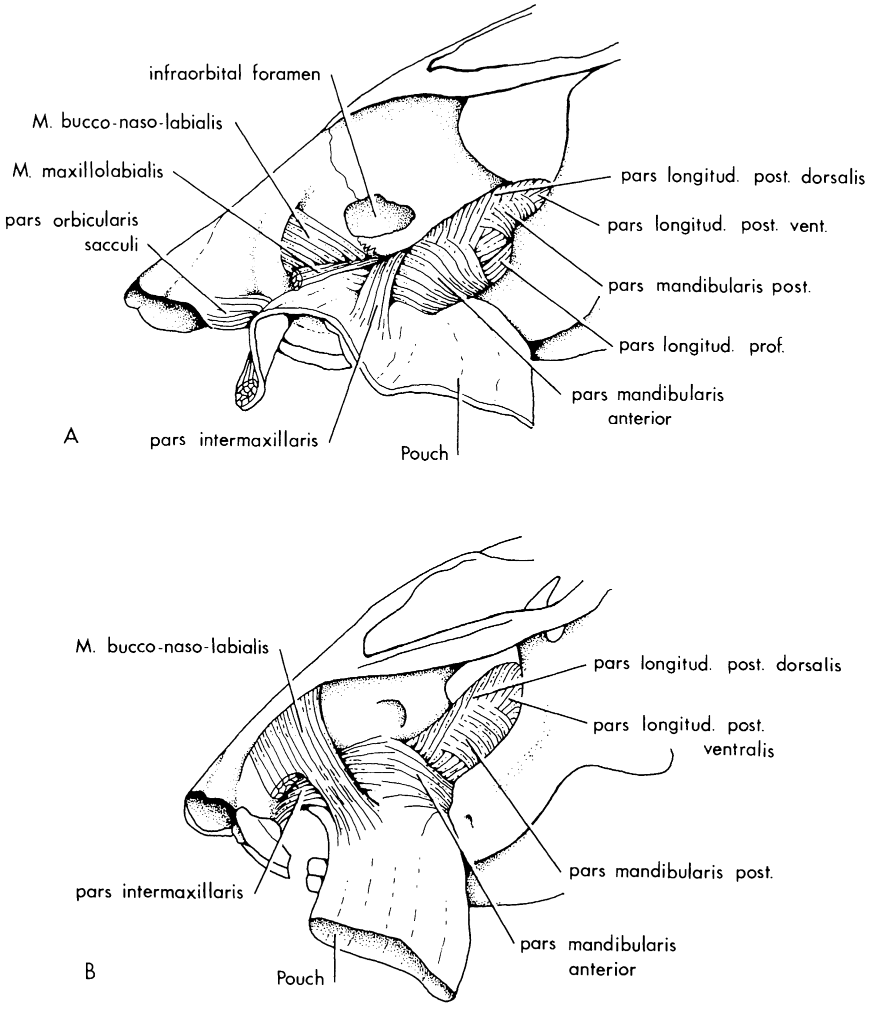

FIG. 9. Oblique lateral views of the muscles associated with the anterior cheek pouch in rodents. The pouch has been cut and reflected anteriorly. The remaining muscles have been removed for clarity. A) *Heteromys*, B) *Eutamias*.

M. nasolabialis profundus pars interna (Fig. 8A)

ORIGIN.—From the dorsolateral nasal cartilage.

INSERTION.—Into the skin over the nasal bones after being pierced by the tendon of M. dilator nasi.

REMARKS.—As in dipodoids (Klingener, 1964), this muscle is divided into two parts. A smaller deep part inserts into the dilator nasi at its insertion. The larger superficial part runs posterodorsad over the dilator nasi onto the dorsal rostrum. Both parts are reduced and hard to separate in perognathines and dipodomyines.

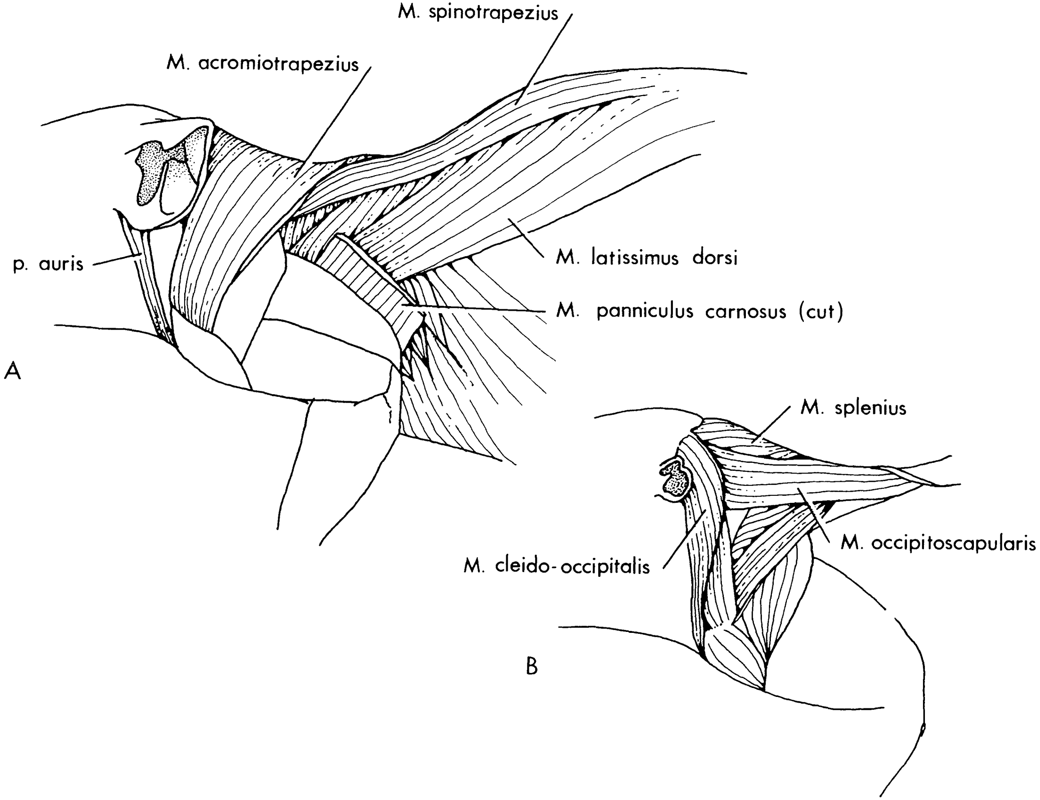

FIG. 10. Lateral views of the anterior half of the body of *Heteromys:* A) superficial muscles of the pectoral limb, B) deeper muscles of the shoulder region.

M. nasolabialis profundus pars media superior (Fig. 8A)

Origin.—From the premaxilla above and between the incisors, superficial and anterior to the origin of pars media inferior.

Insertion.—Into the skin of the rostrum posterior to the insertion of pars interna.

Remarks.—This muscle is reduced in dipodomyines.

M. nasolabialis profundus pars media inferior (Fig. 8A)

Origin.—From the premaxilla above and between the incisors and ventral to the origin of pars media superior.

Insertion.—Into the anteroventral part of the mystacial pad.

Remarks.—Fibers of this muscle fan out caudally to wind among the bases of the vibrissae. The tendons of partes maxillaris superficialis and profunda run through this muscle on their way to the nasal cartilage.

M. nasolabialis profundus pars anterior (Fig. 8A)

Origin.—From the premaxilla between the incisors.

Insertion.—Into the anterior margin of the upper lip, with a few fibers inserting into orbicularis oris.

M. nasolabialis profundus pars anterior profunda

This small muscle was not found in heteromyids.

M. nasolabialis profundus pars maxillaris superficialis (Fig. 8)

Origin.—From the internal lateral wall of the infraorbital foramen.

Insertion.—Into the lateral rhinarium dorsal to the insertion of pars maxillaris profunda.

Remarks.—There is much variation in the condition of this muscle in heteromyids. In the heteromyines and dipodomyines the fibers originate from inside the infraorbital foramen. Wahlert (1985) lists as a shared derived character for the Heteromyidae the presence of a "large perforation in the wall of the rostrum anterior to the infraorbital foramen." This muscle originates from this area and the "perforation" may represent the constraints placed on the bone by the presence of the partes maxillaris superficialis and profunda. Perognathines differ in that the pars maxillaris superficialis originates on the lateral masseter and fuses with the pars profunda anterior to the infraorbital foramen. In the geomyids both partes maxillaris superficialis and profunda originate from the lateral masseter and zygomatic plate and only nerves pass through the infraorbital foramen. The lack of an infraorbital origin of the pars maxillaris superficalis in geomyids is consistent with Wahlert's (1985) rostral perforation, which is found only in heteromyids. The condition in perognathines appears intermediate between other heteromyids and geomyids.

In muroids and dipodoids, the origin is from the anteroventral border of the zygomatic plate and maxillary bone ventral to that (Rinker, 1954; Klingener, 1964; Meinertz, 1941). Although Priddy and Brodie (1948) did not find either partes maxillaris superficialis or profunda in *Cricetus* or *Mesocricetus,* I found both in *Mesocricetus* and *Phodopus.* I also found this muscle present in the gliroid *Glis glis.* Here the pars maxillaris profunda is absent or tightly fused to the pars maxillaris superficialis. In *Glis* the origin is from the lateral margin of the outside of the infraorbital foramen. The insertion is onto the dorsolateral rhinarium close to that of M. dilator nasi. Both partes maxillaris superficialis and profunda are absent in sciuroids, castoroids, "hystricomorphs," and bathyergids (Meinertz, 1932, 1941, 1943a,b, 1944, 1951). Absence of M. nasolabialis profundus partes maxillaris profunda and superficialis is primitive for rodents (character 10). Within geomyoids the primitive condition is found in geomyids. Perognathines possess an intermediate character state between that found in geomyids and both heteromyines and dipodomyines.

M. nasolabialis profundus pars maxillaris profunda (Fig. 8)

ORIGIN.—From the internal lateral wall of the infraorbital foramen ventral to the origin of pars maxillaris superficialis.

INSERTION.—Into the lateral rhinarium ventral to the insertion of pars maxillaris superficialis.

REMARKS.—In perognathines this muscle originates from inside the infraorbital foramen as in other heteromyids, but the pars maxillaris superficialis does not (see remarks above). The pars maxillaris superficialis fuses with this muscle at the level of the bulge created by the incisor root, and the two continue anteriorly together.

M. bucco-naso-labialis (Figs. 8A and 9; M. buccinatorius of Howell, 1932)

ORIGIN.—From the premaxilla ventral to the bulge created by the incisor root.

INSERTION.—Into the anterodorsal margin of the upper lip and into the anteromedial pouch wall.

REMARKS.—In dipodomyines the anterior origin is from the leading edge of the bulge created by the incisor root, but the posterior two-thirds of the origin is from the ventral edge of the bulge, and is considered the derived condition (character 11). In all other rodents studied, the origin is from the ventral margin of the incisor root. The fibers extend further posteriorly, covering the anterior portion of the infraorbital foramen. The perognathines are similar to *Heteromys.* In dipodoids (Klingener, 1964) the origin is from the ventral edge of the bulge created by the incisor root.

M. buccinatorius

In *Dicrostonyx groenlandicus,* which lacks a pouch, Meinertz (1941) subdivided this muscle into over 14 divisions. Here I divide this muscle into nine distinct parts, following Hill (1937) and Klingener (1964).

M. buccinatorius pars intermaxillaris (Fig. 9)

ORIGIN.—From the median raphe of the premaxilla just anterior to the incisive foramen on the palate.

INSERTION.—Into the medial pouch wall after running deep to M. maxillolabialis and posterior to M. bucco-naso-labialis.

REMARKS.—There is little variation in the heteromyids. In the sciurids, cricetines, dipodoids (Klingener, 1964), and murids (Rinker, 1954), the pars intermaxillaris retains the primitive origin further anterior on the palate, just posterior to the incisors (character 12). The posterior origin in geomyoids is derived and likely results from the externalization of the pouch (movement of the embryonic pouch laterally to form the external pouch of the adult).

M. buccinatorius pars intermaxillaris superficialis

This muscle is absent in heteromyids.

M. buccinatorius pars mandibularis anterior (Fig. 9; pars mandibularis of Klingener, 1964)

ORIGIN.—From the dorsomedial surface of the mandible, at the diastema, just posterior to the symphysis.

INSERTION.—Into the medial pouch wall anteriorly and into the lining of the oral cavity posteriorly, where fibers interdigitate with fibers of pars longitudinalis posterior dorsalis.

REMARKS.—The zygomaticolabialis penetrates this muscle in dipodoids (Klingener, 1964).

M. buccinatorius pars mandibularis posterior (Fig. 9)

ORIGIN.—From the dorsolateral mandible, lateral to the molar tooth row.

INSERTION.—Into fibers of M. buccinatorius pars longitudinalis posterior dorsalis and ventralis.

M. buccinatorius pars orbicularis (Figs. 6A and 7B)

ORIGIN.—From the dorsal surface of the mandibular symphysis.

INSERTION.—Into the skin of the lower lip at the ventral symphysis.

M. buccinatorius pars orbicularis oris (Figs. 6A and 7B)

ORIGIN.—From the skin of the upper lip.

INSERTION.—Into the skin of the lower lip and into pars orbicularis.

REMARKS.—This muscle forms the anteromedial border of the pouch opening. This contrasts with sciurids and cricetids, in which it forms the lateral border. In heteromyids the pars orbicularis sacculi is derived from the orbicularis oris of the lips.

M. buccinatorius pars orbicularis sacculi (Figs. 6A, 7B, and 9A; sphincter of the pouch of Hill, 1937)

Origin.—Continuous with the pars orbicularis oris in the upper lip, but diverging laterally from it at the level of the upper incisor.

Insertion.—Into the corresponding muscle from the other side of the head, below and behind the mouth.

Remarks.—This muscle is a synapomorphy for geomyoids (character 13). It is derived from the pars orbicularis oris and forms a band around the lateral pouch opening. It functions to close the pouch opening. This muscle has been termed the "sphincter muscle of the pouch" and "constrictor orifice of the pouch" by Hill (1937). Here I choose to follow Howell (1932) in calling this a separate slip of M. buccinatorius pars orbicularis oris because of the distinct insertion. This muscle does not, however, form a true sphincter around the pouch. Rather, it forms only the lateral border of the pouch opening. At the level of the insertion of pars orbicularis sacculi a slender slip of M. platysma myoides pars mentalis passes superficial to the pars orbicularis sacculi insertion and inserts into pars orbicularis ventrally. Thus, the incomplete "sphincter" surrounding the pouch opening is formed by three separate muscles: M. platysma myoides pars mentalis, M. buccinatorius pars orbicularis sacculi, and pars orbicularis oris. M. buccinatorius pars orbicularis sacculi is not found in any other rodents studied to date.

M. buccinatorius pars longitudinalis posterior dorsalis (Fig. 9)

Origin.—From the maxilla lateral to the alveoli of the molar tooth row.

Insertion.—Into the posterior fibers of M. buccinatorius pars mandibularis anterior and slightly into fibers of pars orbicularis oris.

Remarks.—This muscle, along with the M. buccinatorius pars longitudinalis posterior ventralis, separates the buccal cavity from the medial wall of the pouch. There is little variation in the forms studied. In heteromyids the fibers run anteriad and slightly ventrad and are difficult to separate from pars longitudinalis posterior ventralis.

M. buccinatorius pars longitudinalis posterior ventralis (Fig. 9)

Origin.—From the lateral margin of the alveoli of the molar tooth row on the mandible and deep to pars mandibularis posterior.

Insertion.—Into the posterior fibers of pars mandibularis anterior and pars orbicularis oris.

Remarks.—The fibers pass anteriad and slightly dorsad into the fibers of mandibularis anterior.

M. buccinatorius pars longitudinalis profundus (Fig. 9A)

Origin.—From the dorsal surface of the anterior margin of the masseteric ridge.

Insertion.—Into the lining of the medial pouch wall deep to pars mandibularis anterior and into fibers of pars orbicularis oris at the angle of the mouth.

Remarks.—This muscle was not described for dipodoids by Klingener

(1964) or for murids by Rinker (1954). Meinertz described this muscle in the arvicoline *Dicrostonyx* (Meinertz, 1941).

Hyoid Constrictor Group (Fig. 5)

M. digastricus (Fig. 5; posterior belly)

ORIGIN.—From the jugular (= paroccipital) process.

INSERTION.—Via a small round tendon into the anterior belly of the digastricus and fascially onto the hyoid.

REMARKS.—In *Dipodomys* and *Microdipodops,* in which the bullae are greatly inflated, the origin is from the exoccipital bone anterior to the mastoid, and the insertion is onto the tendinous arch over the hyoid. Fibers of the tendon at insertion run anteriorly along the hyoid but do not fan out to the extent described for dipodoids (Klingener, 1964) or muroids (Rinker, 1954). The condition in *Heteromys* more closely resembles that seen in *Neotoma* (Rinker, 1954). The posterior belly attaches to the hyoid fascially and therefore is not a strong insertion. The heteromyid digastric is characterized as an hystricomorphine-type by Parsons (1894). Hill (1937) regarded this type as derived. Sciurids and *Aplodontia* show the sciuromorphine-type digastric. In microtine rodents there is a separate medial portion that inserts into the posteromedial "tendinous arcade." However, the medial slip is not present in cricetines (Kesner, 1980). "Hystricomorphs" do not have a tendon separating anterior and posterior bellies, and there is no attachment to the hyoid bones (Woods, 1972). Origin from the exoccipital is considered a synapomorphy for dipodomyines (character 14).

M. stylohyoideus (Fig. 5)

ORIGIN.—From a long thin tendon over the paroccipital process.

INSERTION.—On the posterior thyrohyal bone.

REMARKS.—There is no stylohyal cartilage like that found in dipodoids (Klingener, 1964) and murids (Rinker, 1954). Woods (1972) did not find this muscle in any of the "hystricomorphs" he dissected. Edgeworth (1935) stated that this muscle is also absent in bathyergids. The outgroup, Sciuridae, retain the stylohyal cartilage. Loss of this cartilage in geomyoids is considered derived (character 15).

M. jugulohyoideus

This muscle was not found in heteromyids, probably due to the absence of the stylohyal cartilage.

M. stapedius (not figured)

ORIGIN.—From the bony wall of the horizontal semicircular canal and from the mastoid bone over the facial nerve.

INSERTION.—By a thin tendon onto the posterior aspect of the neck of the stapes.

Remarks.—Webster and Webster (1975) described in detail the postnatal development and functional morphology of the ear in heteromyids.

Glossopharyngeal Group

Muscles in this group are supplied by the glossopharyngeal nerve.

M. stylopharyngeus
Hill (1937) reported that this muscle is present in *Thomomys*. I did not find this muscle in heteromyids.

Trapezius Group (Figs. 4, 6, 10–12)

This group of muscles is innervated by the spinal accessory nerve and the second and third cervical nerves. I have included the posterior portion of the cheek pouch retractor muscle here because it is innervated by the accessory nerve.

M. retractor sacculi pars trapezius (Fig. 6B)

Origin.—From the last few lumbar vertebrae.

Insertion.—Into the fibers of the facial part of the retractor at the "fusion-zone" with the insertion of the platysma cervicale.

Remarks.—See comments under the pouch retractor pars facialis (character 7).

M. sternomastoideus (Figs. 4A and 11B)

Origin.—From the anterior margin of the manubrium sterni.

Insertion.—Onto the posterior rim of the external auditory meatus.

Remarks.—The insertion is not tendinous as it is in dipodoids (Klingener, 1964). This muscle is more robust than the surrounding trapezial muscles. In *Dipodomys* the insertion is onto the bulla ventral and slightly anterior to the external auditory meatus and includes part of the depression created by the meatus.

M. cleidomastoideus (Fig. 11B)

Origin.—From the clavicle medial to the origin of the cleido-occipitalis and deep to the origin of the sternomastoideus.

Insertion.—In common with the sternomastoideus on a small tubercle on the posterior rim of the external auditory meatus.

Remarks.—This muscle is not tendinous and lies deep and between the sternomastoideus and cleido-occipitalis. In dipodomyines this muscle is absent, or its fibers are not separable from those of the sternomastoideus (character 16). Klingener (1964) and Howell (1932) found this muscle to be absent in *Jaculus* (also a highly bipedal form).

M. cleido-occipitalis (Figs. 10B and 11B; M. clavotrapezius of Howell, 1926)

Origin.—From the middle third of the clavicle deep to the acromiotrapezius and lateral to the cleidomastoideus.

Insertion.—On the lambdoidal crest of the skull after passing deep to the acromiotrapezius; a few fibers may also insert into the occipitoscapularis.

Remarks.—At its insertion this muscle extends from the dorsal margin of the auricular cartilage to the dorsalmost level of the temporalis. In *Dipodomys* the insertion is on the posteroventral aspect of the bulla behind and below the external auditory meatus after passing deep to acromiotrapezius, but does not extend dorsal to the meatus or the temporalis as in *Heteromys*. Howell (1926) incorrectly identified the cleido-occipitalis as the clavicular part of the trapezius. Hill (1937) pointed out that the cleido-occipitalis and acromiotrapezius are separated by the auricular nerve.

M. acromiotrapezius (Figs. 10A and 12A)

Origin.—From the dorsal midline of the neck posterior to the level of the dorsalmost scapular spine.

Insertion.—Onto the anterior surface of the scapular spine, from the tip of the tubercle distad along the spine and acromion, and onto the dorsal surface of the clavicle.

Remarks.—The fibers run cranioventrad and are closely tied with the inserting fibers of the spinotrapezius. The fibers are thicker at the center of the muscle and taper toward the edges. In *Dipodomys* the origin is from the interbullar suture at the level of the dorsal auricular cartilage and posteriorly as far as the last cervical vertebra.

In *Neotoma* and *Peromyscus* the fibers do not insert onto the clavicle (Rinker, 1954). In the dipodoids the clavicular insertion is small as in heteromyids (Klingener, 1964). In some "hystricomorphs" the insertion includes the anterior spinotrapezius (Woods, 1972). Insertion on the clavicle is considered the derived condition for geomyoids (character 17).

M. spinotrapezius (Fig. 10A)

Origin.—Fascially from the dorsal midline over lumbar vertebrae one to three.

Insertion.—Onto the caudal surface of the scapular spine ventrally as far as the tip of the tubercle.

Remarks.—In *Dipodomys* the origin is from the dorsal midline over lumbar vertebrae one and two and may include the last thoracic vertebra. The muscle fibers do not extend to the midline, but rather continue as fascia. The insertion is onto a common tendon with the acromiotrapezius dorsally; ventrally the muscle inserts onto the caudal surface of the scapular spine.

The auricular slip described by Klingener (1970) for dipodoids was not found in geomyoids. It is likely that the auricular slip has been incorpo-

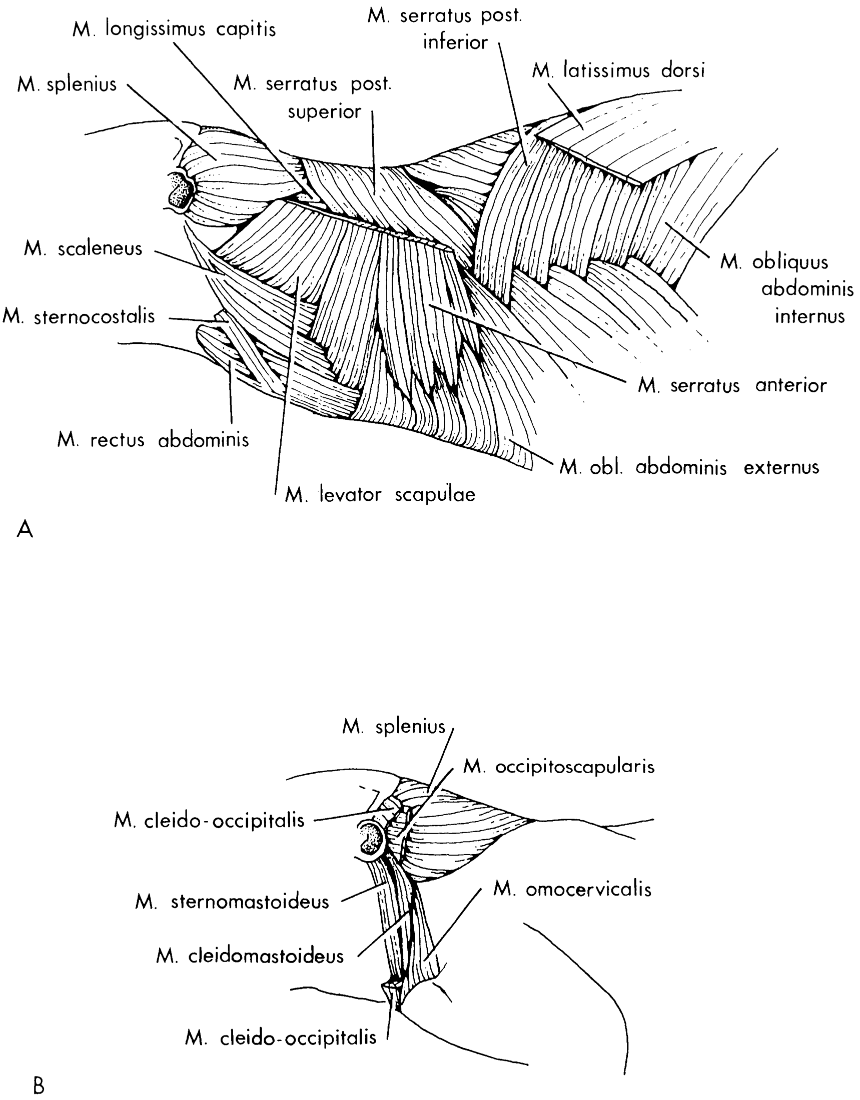

FIG. 11. Lateral views of the anterior half of the body of *Heteromys:* A) appendicular and axial muscles after removal of the scapula, B) deep muscles of the shoulder and neck region.

rated into the trapezial portion of the cheek pouch retractor. Klingener (1970) described the enlarged auricular slip in *Aplodontia* and speculated that this represents the primitive condition for rodents. An auricular slip of this type could have been "preadapted" to forming the pouch retractor in geomyoids (Klingener, 1970). Thus, the auricular slip would have become fused to the facial muscles attached to the posterior cheek pouch forming the dual retractor. Auricular slips of one sort or another are found in some sciurids, dipodoids, muroids, "hystricomorphs," and bathyergids (Klingener, 1970; Ryan, 1986; Woods, 1972). Woods (1972)

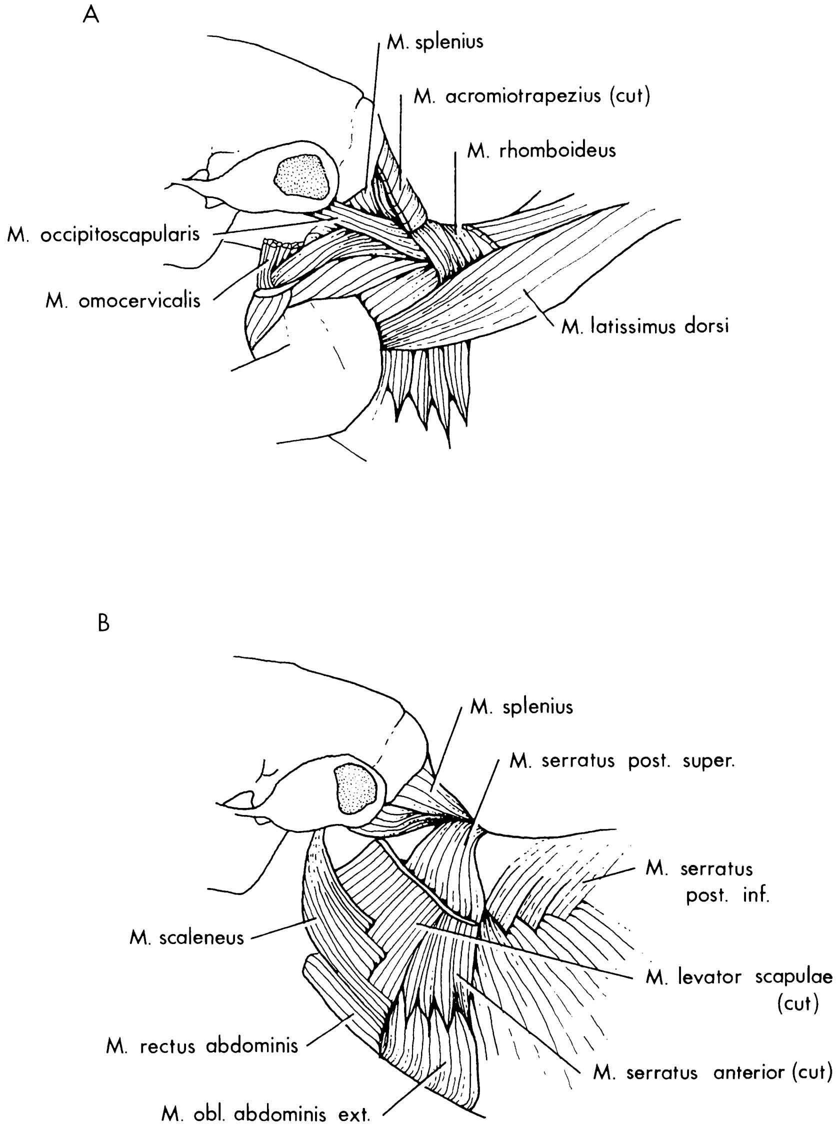

FIG. 12. Lateral views of the anterior half of the body of *Dipodomys:* A) superficial muscles of the pectoral limb, B) appendicular and axial muscles after removal of the scapula.

described an enlarged auricular slip, like that found in *Aplodontia,* in the caviomorph *Ctenomys* (a fossorial rodent convergent on geomyids).

Myotomic Muscles

Lingual Group (Figs. 4, 5)

M. genioglossus (Fig. 4)

Origin.—From the medial surface of the mandibular symphysis in common with the geniohyoideus.

Insertion.—On the anterior surface of the basihyal and part of the thyrohyal deep to the origin of the hyoglossus and into the medial portion of the tongue.

M. hyoglossus (Fig. 4)

Origin.—From the anterior surfaces of the basihyal and thyrohyal bones.

Insertion.—Into the lateral portion of the body of the tongue.

Remarks.—This muscle lies deep to geniohyoideus at its origin and fuses with the styloglossus at its insertion into the tongue. Woods (1972) reported an additional slip of this muscle originating from the stylohyal cartilage in "hystricomorphs."

M. styloglossus (Figs. 4 and 5)

Origin.—From a common tendon with the stylohyoideus on the paroccipital process and from the bullar fascia.

Insertion.—Into the lateral portion of the body of the tongue.

Remarks.—In *Dipodomys* the origin comes from deep to the stylohyoideus, and the fibers run anteriad under the mandible to reappear lateral to the hyoglossus. In the "hystricomorph" rodents the styloglossus has shifted its origin to the tip of the pterygoid process (Woods, 1972).

Superficial Spino-occipital Group (Figs. 10–12)

M. splenius (Figs. 10B, 11, and 12)

Origin.—From the ligamentum nuchae, from just posterior to the occiput to a point over the first few thoracic vertebrae.

Insertion.—Onto the lateral part of the suture between the parietal and interparietal and along the lambdoidal crest medially.

Remarks.—In *Dipodomys* the insertion is via an aponeurosis onto the bullar inflation medial and posterior to the external auditory meatus. This muscle is not well developed in dipodomyines.

Sacrospinalis Group (Figs. 11, 13, 14)

Slijper (1946) discussed in detail the axial musculature in mammals. The sacrospinalis group lies lateral to the zygapophyses of the vertebrae and extends out into the medial transversospinalis column. This group includes two columns of deep epaxial muscles, M. longissimus and M. iliocostalis. In many rodents (and other mammals) the iliocostalis and longissimus are fused in the lumbar region, forming the sacrospinalis. These two muscles are separable, however, in the cervical and thoracic regions. The medial part of the M. extensor caudae lateralis, of the sacral and caudal regions, is a continuation of the M. longissimus. These muscles are divisible into their component parts by sheets of aponeuroses formed by the fusion of flat tendons which run anterolaterad from the zygapophyses of the vertebrae. In the sacral region the transversospinalis is separated from the extensor caudae lateralis by the metapophyseal aponeuroses. In the posterior lumbar region the metapophyseal aponeuroses separate the transversospinalis from the deeper longissimus. The spinal aponeuroses cover the intrinsic back muscles superficially.

In the anterior lumbar region the aponeuroses separate the deeper sacrospinalis into its two major components, the longissimus and iliocostalis. These muscles are further separable and these divisions are described below.

M. *iliocostalis lumborum* (Fig. 13)

ORIGIN.—From the lateral surface of the lumbosacral aponeurosis along the posterior lumbar region but not reaching the sacrum (stops 4 - 5 mm from the sacrum).

INSERTION.—Onto the posterior surfaces of ribs ten to twelve, some fibers continuing anteriorly on the surface of M. iliocostalis dorsi to the level of rib seven but not inserting onto ribs.

REMARKS.—This muscle is difficult to separate from iliocostalis dorsi and the separation may be somewhat arbitrary. The origin from the ilial spine of the pelvis, in dipodomyines, is considered the derived condition (character 18). *Perognathus* is similar to *Heteromys*. Apparently in *Thomomys* the iliocostalis lumborum inserts on the last six ribs (Hill, 1937).

M. *iliocostalis dorsi* (Fig. 13)

ORIGIN.—Extremely difficult to separate from other iliocostalis, but begins at the level of ribs four through six.

INSERTION.—Onto the anterior surfaces of ribs nine to eleven.

REMARKS.—In *Thomomys* the insertion is onto ribs three through six (Hill, 1937). In *Dipodomys* this part seems reduced. The origin is via a narrow tendon from rib six, with insertion onto ribs ten to twelve.

M. *iliocostalis cervicis* (Fig. 13)

ORIGIN.—From the anterodorsal surface of ribs four through nine.

INSERTION.—Onto the transverse processes of the last three cervical and first thoracic vertebrae and on the proximal part of the first rib.

REMARKS.—This muscle is completely separable from longissimus dorsi and partially separable from iliocostalis dorsi. In *Dipodomys* there is no insertion on the first rib. In *Thomomys* the insertion is on the first rib and the last three cervical vertebrae (Hill, 1937). The iliocostalis muscles appear reduced in dipodomyines as first suggested by Howell (1932). Pars cervicis

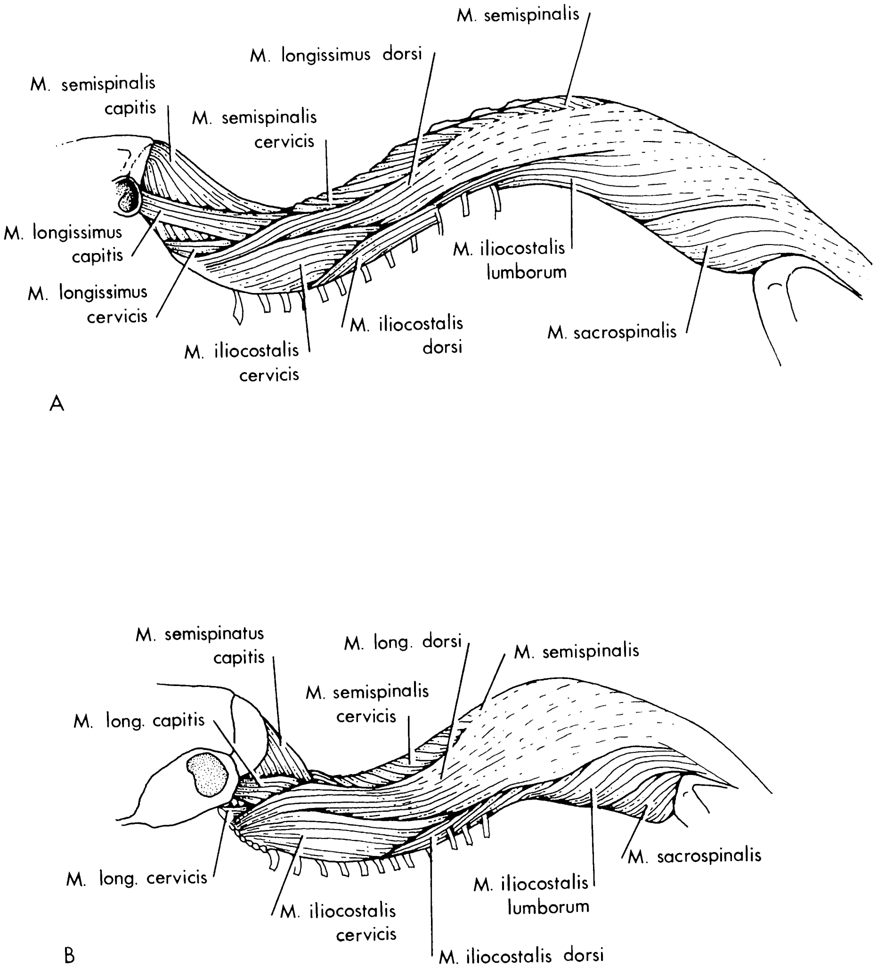

FIG. 13. Lateral views of the deep epaxial muscles: A) *Heteromys,* B) *Dipodomys.*

is separable from pars dorsi in *Sicista* but not other dipodoids (Klingener, 1964). As in heteromyids, the M. iliocostalis is reduced in bipedal dipodoids.

M. longissimus dorsi (Fig. 13)

ORIGIN.—As a continuation of part of the M. sacrospinalis in the lumbar region, and from tendons arising from the metapophyses of the last two thoracic through second lumbar vertebrae.

INSERTION.—Onto all ribs except the first, on accessory processes of the lumbar and last few thoracic vertebrae, on the fused metapophyses and accessory processes of thoracic vertebrae six to nine, and on the transverse processes of the last three cervical and first thoracic vertebrae.

REMARKS.—In *Dipodomys* this muscle is thicker and more robust and the insertion includes the last four or five cervical vertebrae. This muscle is also enlarged in *Jaculus* (Klingener, 1964).

M. longissimus cervicis (Fig. 13)

ORIGIN.—From the tubercles of ribs two through five.

INSERTION.—Onto the transverse processes of the third through fifth cervical vertebrae.

REMARKS.—This muscle is slender and lies deep (medial) to the anterior part of longissimus dorsi. In *Dipodomys* the insertion includes the axis vertebra. In *Thomomys,* the longissimus cervicis inserts on the transverse processes of all cervical vertebrae. In sciurids the insertion is restricted to the last three, and in *Aplodontia* it is restricted to the fourth and fifth cervical vertebrae (Hill, 1937).

M. longissimus capitis (Figs. 11A, 13; M. trachelomastoideus of Howell, 1932)

ORIGIN.—From ribs five through eight.

INSERTION.—Onto the lower lambdoidal crest posterior and slightly ventral to the external auditory meatus.

REMARKS.—In *Dipodomys* the origin is from ribs six through eight. This muscle is more triangular in *Dipodomys* owing to the curvature of the neck.

M. extensor caudae lateralis (Fig. 14A,B,D)

This muscle is divided into three parts following Howell (1932), but nomenclature follows that of Klingener (1964). The pars superficialis (pars ectalis of Howell, 1932) originates on the caudal surface of the ilial aponeurosis and from the transverse processes of the sacral vertebrae. The pars intermedia (pars intermedius of Howell, 1932) originates from the iliac spine and crest. Pars medialis (pars entalis of Howell, 1932) is the deepest of the three and originates as a continuation of M. longissimus. Insertion of these muscles is via long tendons that run on the dorsal chevron bones of the tail.

Semispinalis Group (Fig. 14)

M. transversospinalis et M. extensor caudae medialis (Fig. 14)

Slijper (1946) discussed in great detail the intrinsic back muscles. This is an exceedingly complex muscle group and the nomenclature used here follows that of Slijper (1946) and Klingener (1964). The primitive condition in rodents is found in quadrupedal dipodoids (Klingener, 1964) and cricetids, in which M. transversospinalis is restricted to the area between the neural spines and the zygapophyses. The posterior continuation of M. transversospinalis as the extensor caudae medialis is also thought to be primitive for rodents.

In the lumbosacral region M. transversospinalis is composed of fibers running between neural spines (spinales and interspinales) and fibers run-

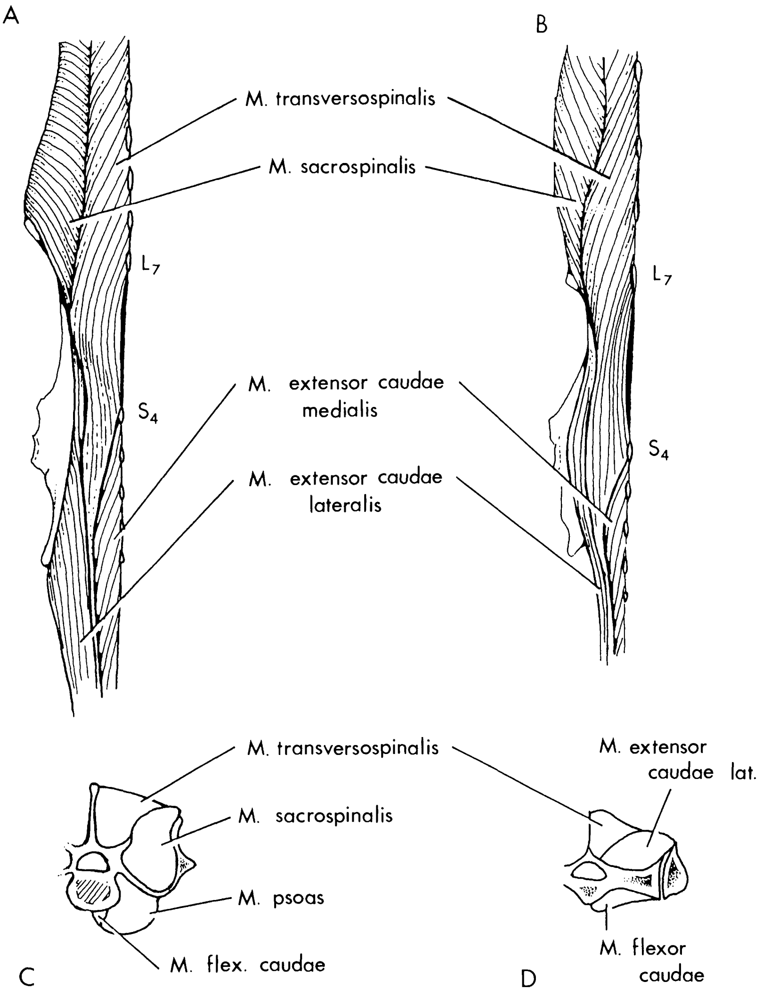

FIG. 14. Dorsal views (A,B) and transverse sections (C,D) of the epaxial muscles of the lumbosacral region: A) *Heteromys*, B) *Dipodomys*, C) transverse section through the anterior sacral region of *Heteromys*, D) transverse section through the posterior sacral region of *Heteromys*.

ning between transverse processes (intertransversarii). In heteromyid rodents the spinales fibers occur from the last two lumbar vertebrae to the fourth and fifth sacral vertebrae. In *Heteromys* the lumbosacral transversospinalis is continuous anteriorly with the rest of M. transversospinalis, but at the level of the last lumbar vertebra it broadens to meet the iliac spine. In the bipedal dipodomyines this expansion is more pronounced and begins at the level of the fifth lumbar vertebra. In these bipeds the expanded transversospinalis extends laterad almost to the anterior ilium, covering almost all of M. extensor caudae lateralis. Lateral expansion of the transversospinalis muscles is considered a synapomorphy for dipodomyines (character 19). In heteromyids the transversospinalis narrows and terminates onto the postzygapophyses of sacral vertebra four and slightly into a narrow tendon that extends out onto the caudal vertebrae. In *Dipodomys* this muscle is also expanded at the level of the fourth sacral vertebra. M. extensor caudae medialis tends to be reduced in heteromyids. It is further posterior in heteromyids owing to the reduction of the neural spines on the anterior sacral vertebrae. Hatt (1932) discussed the loss of these neural spines in bipedal rodents. As a result of their loss, M. extensor caudae medialis is displaced posteriorly to the fourth and fifth sacral vertebrae. Between lumbar vertebra seven and sacral vertebra four is a median space bordered by the spinales fibers. The expansion of M. transversospinalis in the sacral region and the reduction of the neural spines of the anterior sacral vertebrae has probably evolved independently in bipedal heteromyids and dipodoids.

Along the anterior lumbar vertebrae M. transversospinalis can be separated into distinct muscle slips. M. semispinalis capitis originates from the tubercles of ribs two to eight, from the transverse processes of the first six thoracic vertebrae, and from the last four cervical vertebrae. This muscle inserts on the occipital crest superficial to the rectus muscles. In *Dipodomys* the origin is from the tubercles of ribs two to nine, the transverse processes of the thoracic vertebrae, and (contrary to Howell, 1932) from the last few cervical vertebrae. M. semispinalis cervicis is an anterior extension of M. semispinalis, extending as a thick band along the vertebral column from the thoracic to the cervical vertebrae. In *Dipodomys* this muscle inserts onto the fused second and third cervical vertebrae. In general the fibers originate on the transverse processes and insert on the spine of the vertebra anterior to the vertebra of origin. As Howell (1932) observed, the transversospinalis is expanded in the thoracic region. There does not appear to be a separation into a horizontal and ventral component of M. semispinalis cervicis in *Dipodomys*. Hatt (1932) correlated this separation with the sharp flexion of the neck in *Jaculus*. It is thus curious that *Dipodomys* does not possess this division.

Mm. intertransversarii dorsales (not figured)

These muscles run from the sides of the cervical vertebrae anterolaterad to the adjacent vertebra. They are situated deep to M. levator scapulae and M. longissimus cervicis, and superficial to M. semispinalis capitis.

Suboccipital Group (Fig. 15)

M. rectus capitis posterior major (Fig. 15A,B)

ORIGIN.—From the tip of the axial spine.

INSERTION.—Onto the supraoccipital region dorsal to rectus capitis posterior minor.

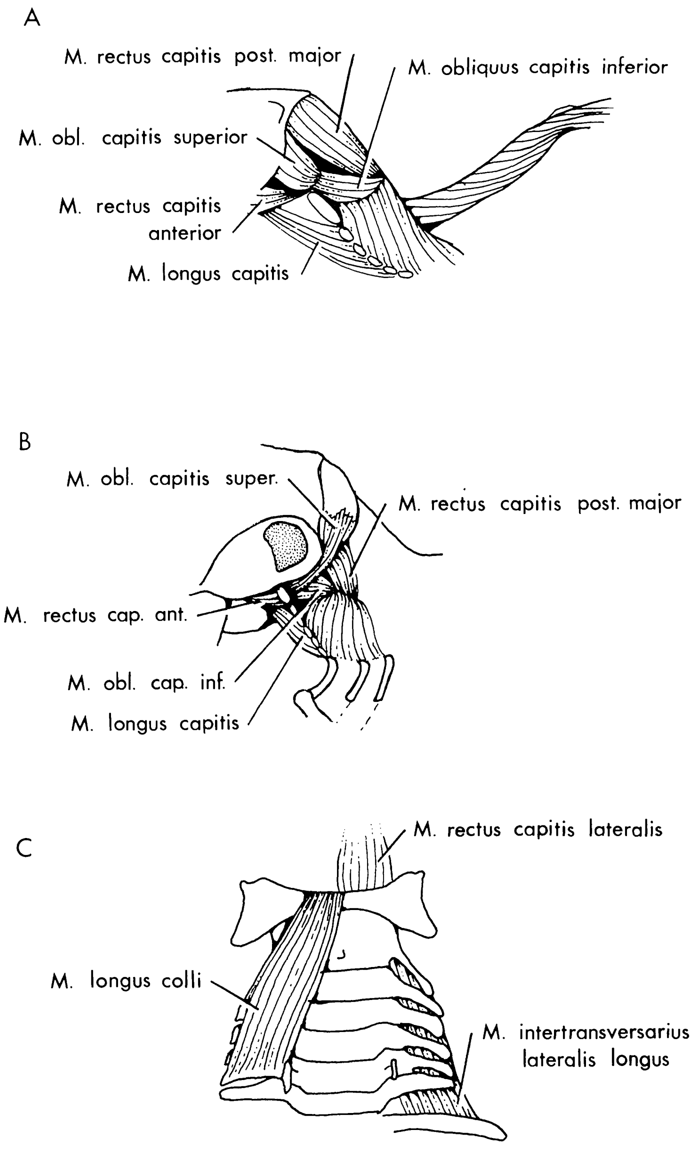

Fig. 15. Lateral and ventral views of the muscles of the neck region in heteromyids: A) deep neck muscles in *Heteromys,* B) deep neck muscles in *Dipodomys,* C) ventral view of the cervical vertebrae and deepest muscles of the neck in *Dipodomys.*

Remarks.—In *Dipodomys* the insertion is reduced owing to the enlarged auditory bulla.

M. rectus capitis posterior minor (not figured)

Origin.—From the anterior and dorsal surfaces of the atlas.

Insertion.—Onto the supraoccipital region deep to the pars posterior major.

M. obliquus capitis superior (Fig. 15A,B)

ORIGIN.—From the transverse process of the atlas.

INSERTION.—Onto the occipital region of the skull, lateral to the insertion of the rectus capitis posterior major.

REMARKS.—Howell (1932, 1926) described two slips of this muscle. I found only one muscle in the heteromyids I dissected. Both Howell (1932) and Hill (1937) refer to this muscle as M. rectus capitis lateralis.

M. obliquus capitis inferior (Fig. 15A,B)

ORIGIN.—From the lateral surface of the axial spine.

INSERTION.—Onto the posterior surface of the transverse process of the atlas.

Cervical Prevertebral Group (Fig. 15)

M. rectus capitis anterior (Fig. 15A,B)

ORIGIN.—From the atlas along the anterior margin of the transverse process.

INSERTION.—Onto the ventral surface of the basioccipital.

M. longus colli (Fig. 15C)

There are two divisions of this muscle in geomyoids (Hill, 1937). The inferior (thoracic) division takes origin from the ventral surfaces of the anterior four thoracic vertebrae and last two cervical vertebrae. It inserts onto the carotid tubercle and the bodies of the posterior cervical vertebrae. The superior division (cervical) takes origin from the carotid tubercle and the bodies of cervical vertebrae two to six, and inserts onto the body of the axis and slightly onto the atlas. In *Dipodomys* the inferior division takes origin from the first five thoracic vertebrae. In *Thomomys* the inferior division takes origin from the heads of the first two ribs and the first three thoracic and last cervical vertebrae (Hill, 1937). In dipodoids and muroids the two divisions are difficult to separate (Klingener, 1964; Rinker, 1954).

M. longus capitis (Fig. 15A,B)

ORIGIN.—From the lateral carotid tubercle and the ventral surfaces of cervical vertebrae three through seven.

INSERTION.—Anteriorly on the basioccipital near the occipitosphenoidal suture.

REMARKS.—In *Dipodomys* the origin includes the expanded dorsal part of rib one and is only fascial from the cervical vertebrae.

Lumbar Prevertebral Group (Fig. 14)

M. quadratus lumborum (not figured)

ORIGIN.—By short tendons from the transverse processes of the first sacral and last four lumbar vertebrae.

Insertion.—Onto the ventral bodies of the first two lumbar and last two thoracic vertebrae.

Remarks.—In *Dipodomys* the insertion is on the last three thoracic vertebrae. Howell (1932) included the last rib in the insertion of this muscle in *Dipodomys.* I found no such insertion on the last rib. Hill (1937) described the insertion on the last two ribs in *Thomomys* and the last three ribs in sciurids and *Aplodontia.* In murids the eleventh rib is included also (Rinker, 1954).

M. psoas minor (= M. psoas on Fig. 14C)

Origin.—From the ventral bodies of lumbar vertebrae four through six.

Insertion.—Via a thin tendon on the iliopectinal eminence.

Remarks.—In *Dipodomys* the origin is from the second and third lumbar vertebrae. In *Thomomys* the origin is from the first five lumbar vertebrae (Hill, 1937). In dipodoids the origin is from the third lumbar vertebra except in *Jaculus,* in which it includes the first three lumbars. This latter condition is similar to that found in murids (Rinker, 1954).

Caudal Flexor Group (Fig. 14)

M. flexor caudae lateralis (not figured; M. flexor caudae externus of Howell, 1932)

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

Insertion.—By tendons on the ventral surfaces of the caudal vertebrae.

Remarks.—This muscle is complex and made up of many divisions, each of which ends in a tendon, making the exact limits of this muscle difficult to follow. Howell (1932) did not include the last two lumbar vertebrae in his description of *Dipodomys.* Hill (1937) included the last lumbar vertebra in his description of *Thomomys.* In *Aplodontia* the lumbar vertebrae are not included in the origin (Hill, 1937).

M. flexor caudae medialis (Fig. 14C,D; M. flexor caudae internus of Howell, 1932)

Origin.—From the bodies and transverse processes of the fifth lumbar through second caudal vertebrae.

Insertion.—On the ventral surfaces of the caudal vertebrae.

Remarks.—Howell (1932) divided this muscle into three parts, partes antica, media, et postica. The divisions of this muscle are complex and I have not described it in its entirety. Hill (1937) described the origin as including only the sacral and caudal vertebrae in *Thomomys.* This muscle is also very difficult to separate from flexor caudae lateralis.

Medial Ventral Cervical Group (Figs. 4, 5)

Edgeworth (1916) showed that the muscles in this group developed from a single condensation in mammals.

M. geniohyoideus (Fig. 4)

ORIGIN.—From the medial surface of the mandibular symphysis, in common with M. genioglossus.

INSERTION.—Onto the anterior basihyal and thyrohyal bones, superficial to M. hyoglossus.

REMARKS.—Hill (1937) found this muscle to be robust and inseparable from its counterpart at the insertion in *Thomomys*. Parsons (1894) used the separation of the right and left halves of this muscle as an "hystricomorph" character. However, Woods (1972) found the halves to be inseparable in the "hystricomorphs" he dissected.

M. sternohyoideus (Figs. 4 and 5)

ORIGIN.—From the second costal cartilage, in common with the origin of M. sternothyroideus.

INSERTION.—Onto the posterior surface of the basihyal.

REMARKS.—Howell (1932) described the origin in *Dipodomys* as including part of the first sternebra. Hill (1937) provided a similar description for *Thomomys*.

M. sternothyroideus (Fig. 4B)

ORIGIN.—In common with M. sternohyoideus, along its deep surface.

INSERTION.—On the thyroid cartilage.

REMARKS.—In *Dipodomys* the insertion is onto the lateral laryngeal cartilage. The muscle tapers sharply at insertion to a narrow insertion deep to M. sternohyoideus.

M. thyrohyoideus (Fig. 4)

ORIGIN.—From the ventrolateral aspect of the thyroid cartilage of the larynx.

INSERTION.—Onto the posterior basihyal bone, deep to the insertion of M. sternohyoideus and partially deep to M. omohyoideus.

REMARKS.—In *Dipodomys* the origin is from the lateral thyroid cartilage, and the shape is much more triangular. Hill (1937) described a lateral origin for this muscle in *Thomomys*. Apparently sciurids have a thyrohyoideus similar to that of *Heteromys,* in which the origin covers the majority of the ventral thyroid cartilage (Bryant, 1945; pers. obs.). Woods (1972) felt that this represented the primitive condition for rodents.

M. omohyoideus (Fig. 4A)

ORIGIN.—From the anterior edge of the scapula near the coracoid.

INSERTION.—Onto the posterior lateral surface of the hyoid, deep to the insertion of M. sternohyoideus and superficial to M. thyrohyoideus.

REMARKS.—Howell (1932) reported that this muscle was absent in *Zapus;* however Klingener (1964) found it in all dipodoids. Hill (1937) stated that this muscle is enlarged in *Aplodontia* and *Thomomys*. Parsons (1896) showed that there is a tendency toward reduction or loss of this muscle in "hystricomorphs." This observation was supported by Woods (1972).

Lateral Cervical Group (Figs. 11, 12, 15)

M. rectus capitis lateralis (Fig. 15C)

ORIGIN.—From the anterior surface of the ventral arch of the atlas.

INSERTION.—Onto the posterior aspect of the paroccipital (jugular) process.

M. scalenus (Figs. 11A and 12B)

ORIGIN.—From the transverse processes of the cervical vertebrae.

INSERTION.—Onto ribs one through four.

REMARKS.—In *Dipodomys* the origin is chiefly on the atlas, with minor attachments to cervical vertebrae. The dorsal slip splits and runs deep to the posterior part of M. levator scapulae. The next slip runs superficial to M. levator scapulae, but deep to M. serratus anterior, and inserts on rib five (not four, as in *Heteromys*). The ventral part of the same slip runs deep to M. obliquus abdominis internus before inserting on rib five. The last major division of M. scalenus runs superficial to the anterior margin of M. serratus anterior, passes deep to a part of M. obliquus abdominis internus and M. rectus abdominis, and inserts on ribs two through five. Contrary to Howell (1932), I found a small slip hidden deep to the bulk of M. scalenus which inserts on the first rib. This entire muscle lies dorsal to the brachial plexus, as in dipodoids (Klingener, 1964). Rinker (1954) stated that there was so much variation in the individual slips of M. scalenus that it is probably not a useful character for phylogenetic analyses.

M. intertransversarius lateralis longus (Fig. 15C)

ORIGIN.—From the transverse processes of the last three or four cervical vertebrae, and from the first rib.

INSERTION.—Onto the transverse processes of the anterior cervical vertebrae.

REMARKS.—The anterior tendons are not separable from those of M. scalenus.

Medial Thoracoabdominal Group (Figs. 11, 12)

M. rectus abdominis (Figs. 11A and 12B)

ORIGIN.—From the pubis and the ventromedial inguinal ligament.

INSERTION.—Onto the posterolateral surfaces of the manubrium sterni and the first rib.

REMARKS.—Posteriorly, M. rectus abdominis is in two separate parts. The medial part takes origin from the pubis, where its fibers mingle with its counterpart from the other side. It broadens anteriorly and diverges from the midline only to converge on it again anterior to the xiphisternum and prior to its insertion on the manubrium sterni and the first rib. The lateral part takes origin from the inguinal ligament and is difficult to separate from M. obliquus abdominis externus. The two parts become joined over the rib cage.

The phylogenetic distribution of the lateral part of M. rectus abdominis appears phylogenetically informative. In addition to its presence in heteromyids, Hill (1937) found it in *Thomomys* and *Geomys*. Klingener (1964) found both medial and lateral parts in dipodoids. No lateral part was found in *Aplodontia* or sciurids (Hill, 1937; Bryant, 1945). Presence of the lateral part of M. rectus abdominis is considered derived (character 20).

The medial part is enclosed by M. obliquus abdominis internus et externus and M. transversus abdominis.

M. pyramidalis

This muscle was not found in heteromyids.

Lateral Thoracoabdominal Group (Figs. 11, 12)

M. serratus posterior superior (Figs. 11A and 12B)

ORIGIN.—From the ligamentum nuchae deep to M. rhomboideus.

INSERTION.—Onto ribs five through ten.

REMARKS.—This muscle is reduced and thinner in dipodomyines. It runs ventral to M. levator scapulae and M. serratus anterior to insert on the anterior surfaces of ribs six through nine.

M. serratus posterior inferior (Figs. 11A and 12B)

ORIGIN.—From the dorsal midline over the posterior thoracic vertebrae, via aponeurosis.

INSERTION.—Onto the last four ribs.

REMARKS.—As is common in rodents (Rinker, 1954; Klingener, 1964), the posterior margin is continuous with M. obliquus abdominis internus.

M. sternocostalis (Fig. 11A)

ORIGIN.—Via aponeurosis over the ventral midline of the sternum at the level of ribs three and four.

INSERTION.—Onto the posterior margin of the first rib, including the costochondral junction and the costal cartilage.

REMARKS.—This muscle passes superficial to M. rectus abdominis as in murids (Rinker, 1954) and dipodoids (Klingener, 1964).

Mm. intercostales externi (not figured)

The fibers of this muscle run slightly posteroventrad between adjacent ribs. The fibers take their origin along each rib from the tubercle to just below the costochondral junctions. A few fibers that originate on the first rib insert on ribs three and four. These fibers lie deep to Mm. levatores costarum dorsally.

Mm. levatores costarum (not figured)

ORIGIN.—From the anapophyses and transverse processes of the thoracic vertebrae.

INSERTION.—Onto the proximal angles of the ribs.

M. obliquus abdominis externus (Figs. 11A and 12B)

ORIGIN.—From the aponeurosis of M. obliquus abdominis internus and from the posterior seven or eight ribs.

INSERTION.—Into the linea alba along the ventral midline, on the symphysis of the pubis, and onto the tendon that runs from the iliac spine of the pelvis to the pubic symphysis.

REMARKS.—This muscle is well developed in heteromyids and is superficial to M. rectus abdominis. Anteriorly this muscle interdigitates with the fibers of M. serratus anterior. Posteriorly, these fibers are difficult to separate from the deeper M. rectus abdominis.

M. obliquus abdominis internus (Fig. 11A)

ORIGIN.—Via aponeuroses along the dorsal midline over the lumbar vertebrae and from the anterior iliac spine, including the inguinal border.

INSERTION.—Onto the posterior margins of the last few ribs.

REMARKS.—This muscle is continuous with M. serratus posterior inferior and difficult to separate from it. It lies deep to M. rectus abdominis.

Mm. intercostales interni (not figured)

The fibers of these muscles run anteroventrad between the angles of adjacent ribs to the sternum.

Mm. subcostales (not figured)

These muscles are highly variable within individuals and were not dissected in detail in heteromyids.

M. transversus thoracis (not figured)

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

INSERTION.—Onto costal cartilages two through seven.

M. transversus abdominis (not figured)

ORIGIN.—From the caudal margin of the rib cage, from the dorsal aponeurosis in common with the origin of M. obliquus abdominis internus, and from the posterior inguinal ligament.

INSERTION.—Into the linea alba along the ventral midline.

M. cremaster (not figured)

The fibers of this muscle are derived from a slip of M. obliquus abdominis internus and a slip of M. transversus abdominis; together these form a two-layered sheath whose fibers run at right angles to one another. This muscle forms the sheath of the testis in males and is difficult to discern unless the testes are scrotal.

Perineal Group (not figured)

M. iliococcygeus (M. iliocaudalis of Howell, 1932)

ORIGIN.—From the interior of the ilium anterior to the pubis and continuing caudad to a point posterior to the sacroiliac joint.

INSERTION.—Onto the transverse processes of the caudal vertebrae.

REMARKS.—This muscle forms approximately six tendons that insert on the tail.

M. pubococcygeus (M. pubocaudalis of Howell, 1932)

ORIGIN.—From the internal ramus of the pubis almost to the iliopectinal eminence.

INSERTION.—Onto the transverse processes of caudal vertebrae one through four and onto the tendons of M. iliococcygeus.

M. coccygeus (M. sacrospinosus of Howell, 1932)

ORIGIN.—From the dorsal and internal surface of the ilium just anterior to the acetabulum.

INSERTION.—Onto the transverse processes of the first few caudal vertebrae.

M. ischiocavernosus

ORIGIN.—From the posterior margin of the inferior ischial ramus.

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

M. bulbocavernosus

This muscle was not dissected in heteromyids.

M. sphincter ani externus

This muscle was not dissected in heteromyids.

PECTORAL GIRDLE AND LIMB

Costo-spino-scapular Group (Figs. 10–12)

M. levator scapulae et M. serratus anterior (Figs. 11A and 12B; M. serratus magnus and M. atlantoscapularis of Howell, 1932)

ORIGIN.—From ribs one through eight and from the transverse processes of the cervical vertebrae.

Insertion.—Onto the medial side of the vertebral border of the scapula below the insertion of M. rhomboideus.

Remarks.—The two components are not separable except by innervation. As a result they have been treated together by Bryant (1945), Rinker (1954), Klingener (1964), Kesner (1980), Stein (1986), and Woods (1972) for a wide diversity of rodent genera. Howell (1932) mistakenly referred to M. levator scapulae as the "depressor scapulae," part of M. serratus magnus. Howell's (1932) M. atlantoscapularis superior is really a part of this complex arising from the transverse process of the atlas. The part from the atlantal transverse process is present in all heteromyids, dipodoids (Klingener, 1964), and geomyids (Hill, 1937), but not in murids (Rinker, 1954).

In *Dipodomys* and *Perognathus* the posterior insertion is in common with the posterior M. rhomboideus, and the posteriormost part of M. serratus anterior inserts via a small tendon on the laterodorsal aspect of the scapula. In all heteromyids the anterior portion of this muscle is deep to M. scalenus. Posterior to rib four, however, M. serratus anterior lies superficial to M. scalenus.

M. rhomboideus (Fig. 12A; M. rhomboideus dorsi of Howell, 1932)

Origin.—From the surface of M. splenius beginning posterior to the sagittal crest and from the nuchal ligament.

Insertion.—Onto the entire vertebral border of the scapula, including the posterior three-quarters of the supraspinous border and the entire infraspinous border.

Remarks.—As stated above, the posterior M. rhomboideus inserts onto the posterior scapula via a small tendon in common with M. serratus anterior in *Dipodomys*. Contrary to Howell (1932), this muscle is not divisible into two separate parts as in murids (Rinker, 1954; Stein, 1986). Hill (1937) also found this muscle to be single in pocket gophers; however in *Geomys* it is continuous with M. occipitoscapularis. A single M. rhomboideus is found in *Aplodontia* (Lewis, 1949), dipodoids (Klingener, 1964), and in many sciurids (Bryant, 1945; Parsons, 1894).

M. occipitoscapularis (Figs. 10B, 11B, and 12A; M. rhomboideus capitis of Howell, 1932)

Origin.—From the lambdoidal crest, at the level of the temporalis, ventral to the lower margin of the external auditory meatus.

Insertion.—On the ventral border of the scapula, covering the supraspinous region but not the infraspinous region.

Remarks.—In *Dipodomys* the origin is from the bulla immediately ventral and posterior to the external auditory meatus. Fibers run in a narrow band caudad to insert onto the vertebral border of the scapula, including the anteriormost section of the infraspinous fossa. There is no medial inflection in heteromyids. Apparently in *Sigmodon* a portion of this muscle is reflected onto the medial scapula (Rinker, 1954). In *Thomomys* this muscle is quite large and its insertion includes the scapular spine, much as in *Aplodontia* (Hill, 1937).

M. omocervicalis (Figs. 11B and 12A; M. atlantoscapularis inferior of Howell, 1932)

ORIGIN.—From the ventral body of the atlas.

INSERTION.—Onto the dorsal margin of the acromion and the lateral clavicle, overlapping M. acromiotrapezius.

REMARKS.—Hill (1937) stated that the primitive origin is the transverse process of the atlas and the primitive insertion is the acromion. Parsons (1896) described *Heteromys* as retaining both primitive origin and insertion. In all heteromyids I dissected, the insertion included a portion of the clavicle. In geomyids the insertion is restricted to the clavicle (Hill, 1937). In sciurids (Bryant, 1945) and murids (Rinker, 1954; Stein, 1986), the insertion is on the metacromion. In dipodoids the insertion includes a portion of the clavicle (Klingener, 1964). Woods (1972) disagreed with Hill's (1937) interpretation and instead believed that the primitive insertion is on the metacromion.

Latissimus-subscapular Group (Figs. 10, 11, 12, 16, 17)

M. latissimus dorsi (Figs. 10A, 11A, 12A, 16A, and 17A)

ORIGIN.—From a broad area of aponeurosis over the anterior six lumbar vertebrae, deep to the origin of M. spinotrapezius.

INSERTION.—Onto the medial aspect of the humerus in common with the M. teres major tendon.

REMARKS.—The insertion onto the ventral tendon of M. teres major (not directly onto the humerus) is a synapomorphy for dipodomyines (character 21). In *Aplodontia* (Hill, 1937) and microtines (Stein, 1986) the latissimus dorsi inserts onto the tendon of M. teres major as in *Dipodomys*. Hill (1937) described a condition similar to that of *Heteromys* for geomyids. In dipodoids (Klingener, 1964), as in murids (Rinker, 1954), the insertion is directly onto the humerus. In the "hystricomorphs" the insertion has two slips to the humerus, one ventral to M. teres major and a second that inserts in common with M. teres major. In many "hystricomorphs" there is a separate slip called the latissimus Achselbogen which inserts on the pectoralis minor near the deltoid ridge (Woods, 1972). Woods (1972) described a dual innervation for these slips of the latissimus, which led him to conclude that the latissimus Achselbogen is formed by components of latissimus dorsi and cutaneus maximus.

M. teres major (Figs. 16A and 17A)

ORIGIN.—From the lateral and medial surface of the posterior angle of the axillary ridge of the scapula, and from the surface of M. infraspinatus.

INSERTION.—Via a tendon onto the medial humeral ridge deep to M. coracobrachialis profundus.

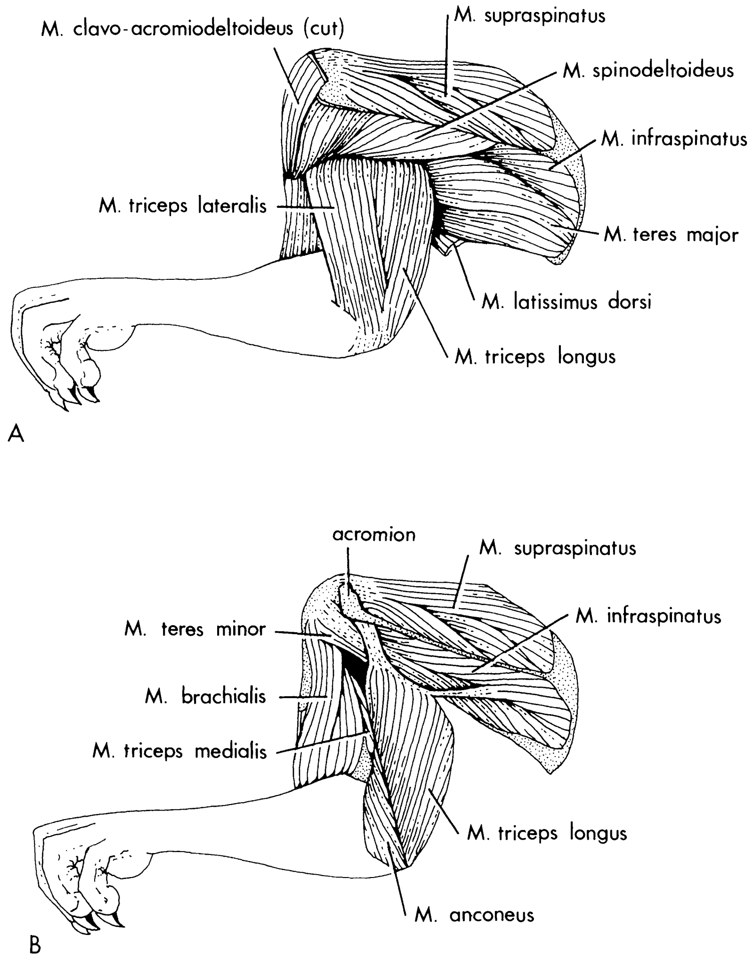

FIG. 16. Lateral views of the pectoral limb in *Heteromys:* A) superficial muscles, B) deeper muscles.

REMARKS.—The tendon of insertion is continuous with that of M. latissimus dorsi. In *Dipodomys* the origin from the lateral surface of the scapula is similar but slightly larger, extending dorsally a third of the way to the vertebral border of the scapula. The insertion also differs from that of *Heteromys* in that the tendon of M. latissimus dorsi inserts directly into the tendon of M. teres major at an angle of approximately 90 degrees. In *Heteromys* these two tendons join in a nearly parallel fashion. In *Aplodontia* the insertion is fleshy (Hill, 1937). In tree squirrels, M. teres major is more robust than in ground squirrels (Bryant, 1945). Dipodoids (Klingener, 1964) and muroids (Rinker, 1954; Stein, 1986) have a condition similar to *Heteromys*. In *Erethizon* the teres major tendon inserts separately deep to the tendon of M. latissimus dorsi (Woods, 1972).

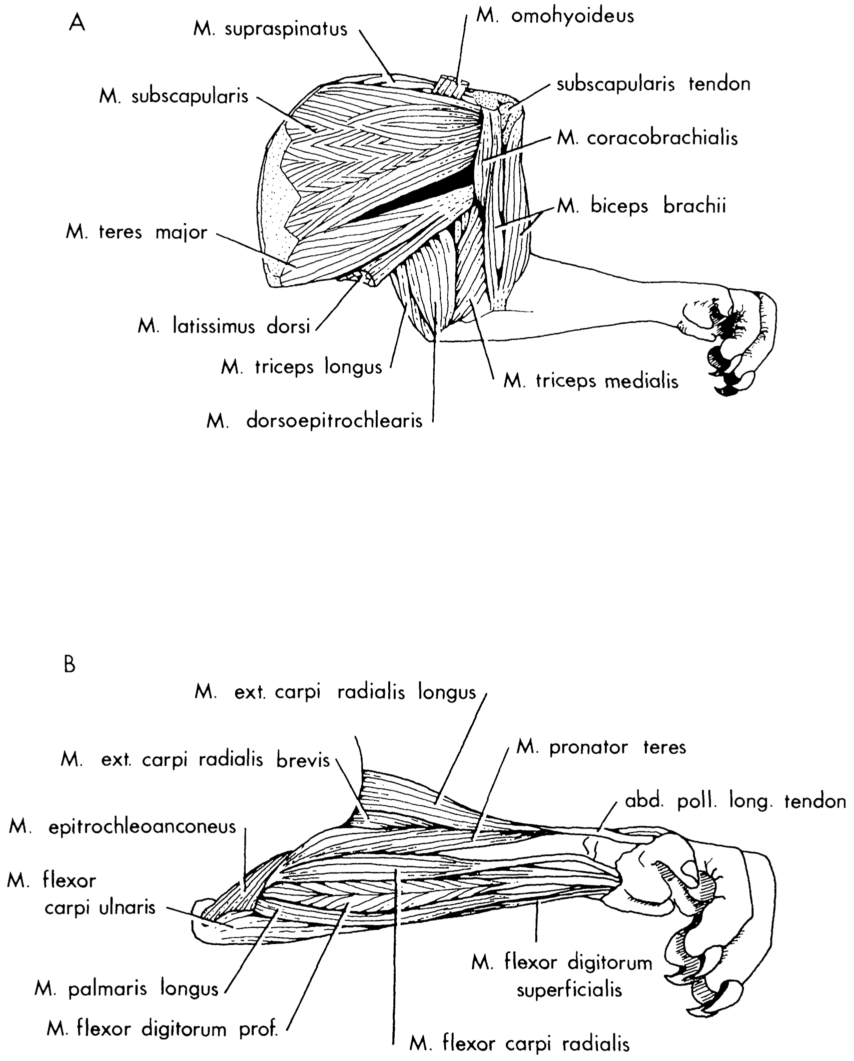

FIG. 17. Medial views of the pectoral limb in *Heteromys:* A) proximal muscles, B) forearm muscles.

M. subscapularis (Fig. 17A)

ORIGIN.—From the entire surface of the subscapular fossa. Dorsally the fibers originate from the dorsal border of the scapula and from the fascia over part of M. supraspinatus. Ventrally the fibers originate from the medial and ventral border of the scapula and almost run onto the lateral surface.

INSERTION.—Deep to the proximal coracobrachialis on the dorsal and medial surfaces of the lesser tuberosity of the humerus.

REMARKS.—This muscle is large and multipinnate. The insertional tendon lies deep to M. coracobrachialis. However, in dipodomyines M. subscapularis is reduced and less pinnate, consisting of only three fascicles. Reduction in M. subscapularis is considered a synapomorphy for dipodomyines (character 22). In sciurids and *Aplodontia,* but not in *Thomomys,* the muscle is also less subdivided into fascicles (Hill, 1937). In *Thomomys* and *Geomys* there are four bipinnate fascicles (Hill, 1937).

Deltoid Group (Fig. 16)

M. clavo-acromiodeltoideus (Fig. 16A)

ORIGIN.—From the lateral half of the clavicle and the ventral border of the acromion proximal to the origin of M. spinodeltoideus.

INSERTION.—On the distal tip of the lateral crest (deltoid crest) of the humerus along the medial and cranial margins (clavicular part) and on the craniolateral margin of the humerus (acromial part).

REMARKS.—The acromial and clavicular parts are slightly separable in heteromyids and not at all in geomyids (Hill, 1937). In dipodoids (Klingener, 1964) and microtines (Stein, 1986) the two parts are completely fused. In sciurids (Bryant, 1945) and many "hystricomorphs" (Woods, 1972) the two parts are distinct.

M. spinodeltoideus (Fig. 16A)

ORIGIN.—From the caudal border of the scapular spine, extending from the tuberosity of the spine distad to the acromion.

INSERTION.—Onto the posterior surface of the lateral (deltoid) crest of the humerus.

REMARKS.—In all heteromyids, fibers of the acromial part of M. clavo-acromiodeltoideus overlap those of M. spinodeltoideus at their origin. In dipodomyines, the origin is shifted slightly further distad and the insertion is tendinous.

M. teres minor (Fig. 16B)

ORIGIN.—From the distal third of the axillary border of the scapula deep to M. infraspinatus.

INSERTION.—Onto the greater tuberosity of the humerus distal to the insertion of M. infraspinatus.

REMARKS.—In heteromyids this small muscle is not tendinous. In the geomyid *Thomomys* the insertion is caudal to that of the infraspinatus (Hill, 1937). In dipodoids (Klingener, 1964) and many "hystricomorphs" (Woods, 1972), the insertion is tendinous.

Subscapular Group (Figs. 16, 17)

M. supraspinatus (Figs. 16 and 17A)

ORIGIN.—From the dorsal border and the cavity of the supraspinous fossa, from the cranial border of the scapular spine, and on the medial surface of the scapula.

INSERTION.—Onto the dorsocranial surface of the greater tuberosity of the humerus.

REMARKS.—The portion of this muscle coming from the scapular spine joins the cranial portion along a tendon situated between the two bellies. Klingener (1964) reported a similar condition in dipodoids, as did Rinker (1954), Stein (1986), and Howell (1926) for muroids.

M. infraspinatus (Fig. 16)

ORIGIN.—From the infraspinous fossa and the caudal surface of the scapular spine.

INSERTION.—Onto the lateral and caudal surface of the greater tuberosity of the humerus.

REMARKS.—This muscle is multipinnate and runs deep to the tendon of M. triceps longus at insertion. As in many other rodents, the infraspinous fossa is larger than the supraspinous fossa. If Cheng (1955) is correct and the two muscles of this group represent the reptilian supracoracoideus, then they would be more appropriately discussed under the ventral muscles. Howell (1926) considered this muscle to belong to the pectoral group. In "hystricomorphs" the origin is enlarged and covers most of the caudal surface of the scapula (Woods, 1972).

Triceps Group (Figs. 16, 17)

M. dorsoepitrochlearis (Fig. 17A)

ORIGIN.—From the ventral margin of M. teres major.

INSERTION.—Fascially onto the medial aspect of the olecranon process.

REMARKS.—In *Aplodontia* the origin includes the surface of M. latissimus dorsi (Hill, 1937). *Thomomys* has a similar condition, but in *Geomys* and sciurids the origin includes part of the scapula. In microtine rodents the origin is solely from the medial latissimus dorsi (Stein, 1986). "Hystricomorph" rodents also exhibit an origin from both M. latissimus dorsi and M. teres major (Woods, 1972). An origin from M. latissimus dorsi is widespread in mammals, but an origin on the scapula or M. teres major is more widespread in rodents (Woods, 1972). There is some disagreement over innervation of this muscle. Howell (1932) reported innervation via the radial nerve, while Cheng (1955) claimed the innervation (in the opossum) to be via the subscapular nerves in common with M. latissimus dorsi. The exact homology of this muscle remains in dispute.

M. triceps brachii, caput lateralis (Fig. 16A)

Origin.—Via tendons from the proximolateral deltoid crest, and the lateral and caudal surfaces of the greater tuberosity; and a fibrous origin from the head of the humerus posterior to the greater tuberosity.

Insertion.—Onto the lateral olecranon and fascially on the surface of the forearm.

Remarks.—This muscle is tendinous at insertion and is smaller than the long head. In *Dipodomys* the origin from the deltoid crest is lacking.

M. triceps brachii, caput medialis (Figs. 16B and 17A)

Origin.—From the posteromedial surface of the distal two-thirds of the humerus, just distal to the insertion of M. latissimus dorsi.

Insertion.—On the medial aspect of the olecranon.

Remarks.—In *Dipodomys* the insertion includes the caudal surface of the olecranon. In many rodents the deep fibers are continuous with those of M. anconeus. These muscles are treated separately.

M. triceps brachii, caput longus (Figs. 16 and 17A)

Origin.—From the distal one-fifth of the axillary border of the scapula, from the infraglenoid tuberosity, and from the ventral surface of the acromion via a strong flat tendon which runs ventrad over M. infraspinatus.

Insertion.—On the posterior surface of the olecranon.

Remarks.—The tendon at origin forms a sling from the acromion to the proximal infraspinatus. M. triceps longus originates midway along the tendinous sling. In *Dipodomys, Microdipodops, Perognathus,* and *Thomomys* the tendinous sling is incompletely developed and the proximal origin is fibrous (Hill, 1937). In these and many other rodents this tendinous sling attaches to the axillary border of the scapula but not to the surface of the infraspinatus. This condition is also found in dipodoids (Klingener, 1964) and murids (Parsons, 1896; Rinker, 1954). The tendinous sling (also referred to as the aponeurotic envelope by Woods, 1972) is widespread among rodents.

M. anconeus (Fig. 16B)

Origin.—From the posterior surface of the distal half of the humerus along the lateral epicondylar ridge distad to the lateral epicondyle. The most proximal part of the origin is slightly medial on the humerus and deep to M. brachialis.

Insertion.—Onto the lateral groove of the olecranon and the posterodorsal portion of the olecranon.

Remarks.—In *Aplodontia,* sciurids, dipodoids, microtines, geomyoids, and "hystricomorphs" it is difficult to separate the origin of this muscle from M. triceps medialis, but the insertion is distinct (Hill, 1937; Klingener, 1964; Stein, 1986; Woods, 1972).

Extensor Group of the Forearm (Figs. 17, 18)

M. brachioradialis

I found no muscle having an insertion on the radial side of the carpals. This is in agreement with Hill (1937) and Klingener (1964), who stated that this muscle is absent in geomyoids. The loss of the brachioradialis is thought to be a derived state (character 23) since the muscle is retained in many mammal groups, including dipodoids (Klingener, 1964), *Erethizon* (Parsons, 1894), sciurids (Bryant, 1945), and *Aplodontia* (although it is reduced, Woods, 1972).

M. extensor carpi radialis longus (Figs. 17B and 18)

ORIGIN.—From the proximal part of the lateral epicondylar ridge of the humerus.

INSERTION.—On the dorsum of metacarpal two at its midpoint.

REMARKS.—This muscle is the most proximal of the muscles originating on the lateral epicondylar ridge. The tendon passes deep to the much broader tendon of M. abductor pollicis longus. In *Dipodomys* the insertion is on the dorsomedial surface of the second metacarpal. Geomyid rodents do not differ significantly from the condition described above for *Heteromys* (Hill, 1937; pers. obs.).

M. extensor carpi radialis brevis (Figs. 17B and 18)

ORIGIN.—From the anterolateral epicondylar ridge of the humerus, just distal to the origin of M. extensor carpi radialis longus.

INSERTION.—On the medial side of the third metacarpal near its base.

REMARKS.—Howell (1932) was mistaken in reporting the insertion on the second metacarpal in *Dipodomys*.

M. supinator (not figured)

ORIGIN.—From the capitulum of the humerus and the capsule of the humero-radial joint.

INSERTION.—Onto the proximal half of the radius.

REMARKS.—In *Dipodomys* this muscle is more robust and is tendinous at its origin. In *Thomomys,* a well developed sesamoid bone is embedded in this tendon. Stein (1986) found comparable sesamoid bones in all the microtines she dissected. Parsons (1896) observed sesamoid bones in myomorph rodents. No sesamoid bones were found in "hystricomorph" rodents, however (Woods, 1972).

M. extensor pollicis brevis (part of M. extensor metacarpi pollicis of Howell, 1932)

This muscle was not found in the heteromyid rodents I dissected. Woods (1972) discussed in detail the loss of M. extensor pollicis brevis and the presence in some mammals of two slips of M. abductor pollicis longus.

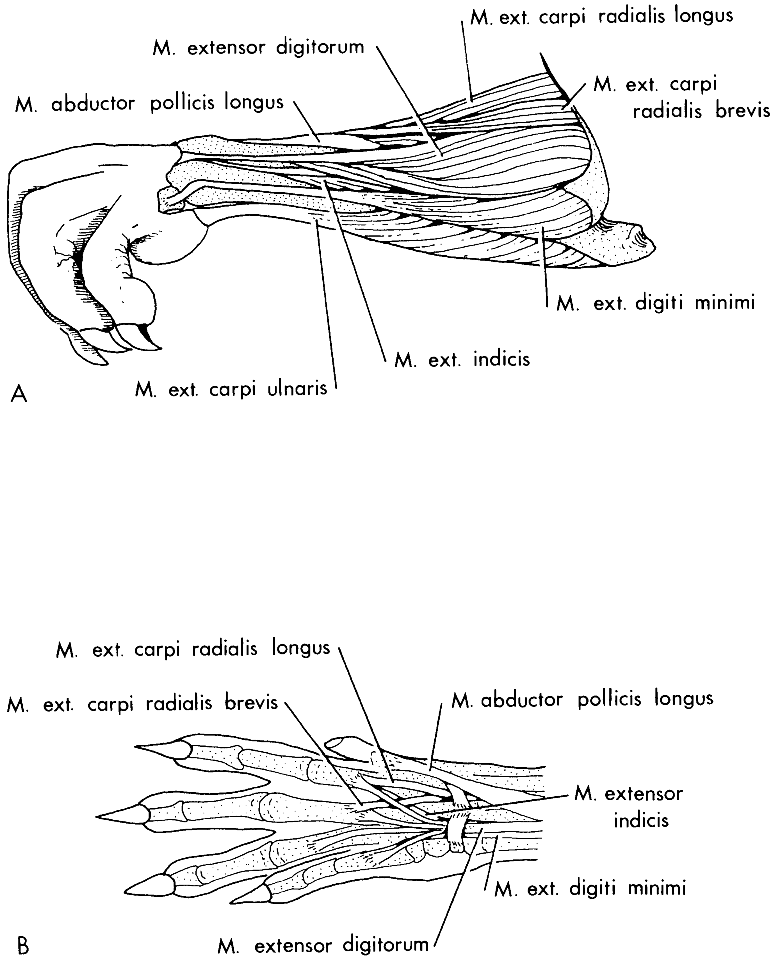

Fig. 18. A) Lateral view of the forearm muscles in *Heteromys,* B) dorsal view of the tendons inserting on the manus in *Heteromys.*

M. abductor pollicis longus (Figs. 17B and 18; M. extensor metacarpi pollicis of Howell, 1932)

Origin.—From the ulna and interosseous membrane in the middle third of the forearm.

Insertion.—Via a tendon onto the first metacarpal.

Remarks.—The muscle lies deep to the extensores carpi radiales at origin and passes a broad tendon to the medial radius through the medialmost osteofibrous canal. Hill (1937) stated "In rodents, as in most mammals, there is no extensor pollicis brevis." However, Klingener (1964) described M. extensor pollicis brevis and M. abductor pollicis longus in dipodoids, as did Rinker (1954) for murids. Woods (1972) described two tendons of this muscle in hystricomorphs, one inserting on the first metacarpal and a second, smaller tendon inserting on the radial side of the falciform bone. Only the former tendon was found in geomyoids. Stein (1986) described three separate insertions of this muscle in microtine rodents (except *Synaptomys*).

M. extensor digitorum (Fig. 18; M. extensor digitorum communis of Howell, 1932; Hill, 1937; Rinker, 1954)

ORIGIN.—From the lateral epicondylar ridge of the humerus distal to M. extensor carpi radialis brevis and proximal to M. extensor digiti minimi.

INSERTION.—Onto the dorsal surfaces of digits two through five.

REMARKS.—This pinnate muscle gives off four distinct tendons. The superficial radial part sends a tendon to the second digit. The medial ulnar head sends a tendon to digit five only, and the superficial ulnar head has two parts going to digits three and four. All tendons pass through a groove on the wrist in common with the tendons of M. extensor indicis and M. extensor digiti tertii proprius. The tendons are bound together over the dorsum of the manus by heavy fascia. In *Dipodomys* the insertion does not include the fifth digit and the bellies are not separable as they are in *Heteromys*. In microtines the tendon diverges on the dorsum of the manus and inserts via three tendons on digits two, four, and five. Digit three receives two separate tendons (Stein, 1986). Woods (1972) reported that considerable variation exists in the number and extent of fusion of these tendons in "hystricomorphs."

M. extensor indicis (Fig. 18)

ORIGIN.—From the middle third of the ulna.

INSERTION.—On the dorsum of digit two.

REMARKS.—The tendon passes through a compartment at the wrist with those of M. extensor digitorum. The belly of this muscle is reduced in *Dipodomys*. A thin branch tendon may pass to the pollex in the muroids *Neotoma* and *Peromyscus* (Rinker, 1954). Likewise, Hill (1937) reported a slip to the pollex in *Thomomys*, as did Woods (1972) for "hystricomorph" rodents. The slip to the pollex (character 24) is considered derived and is lacking in heteromyids, *Aplodontia*, and sciurids (Hill, 1937; pers. obs., but see Woods, 1972, for *Sciurus*).

M. extensor digiti tertii proprius

This muscle is not found in heteromyids. It is also absent in murids (Rinker, 1954) and geomyids (Hill, 1937), but present in sciurids (Bryant, 1945), dipodoids (Klingener, 1964), and the "hystricomorphs" *Thryonomys* and *Coendou* (Woods, 1972). Lack of this muscle is considered the derived condition for rodents (character 25).

M. extensor digiti minimi (Fig. 18; M. extensor digiti quinti of Howell, 1932)

ORIGIN.—From the lateral epicondyle of the humerus between the origins of M. extensor digitorum proximally and M. extensor carpi ulnaris distally.

Insertion.—On the dorsal surfaces of digits four and five.

Remarks.—The tendon crosses the wrist in a groove or compartment slightly lateral to the compartment for tendons of M. extensor digitorum, M. extensor digiti tertii proprius, and M. extensor indicis. Hill (1937) reported that geomyids have a single insertion on digit five. Howell (1932) also described a single insertion on digit five for *Dipodomys*. I found two insertions in my specimens of *Dipodomys*. *Aplodontia* and sciurids have both insertions (Hill, 1937), as do dipodoids (Klingener, 1964), muroids (Rinker, 1954; Stein, 1986), and "hystricomorphs" (Woods, 1972).

M. extensor carpi ulnaris (Fig. 18A)

Origin.—From the lateral epicondyle of the humerus and from the proximal quarter of the lateral ridge of the ulna, distad from the semilunar notch.

Insertion.—On the lateral base of metacarpal five.

Remarks.—The tendon passes through a small groove in the ulna at the wrist.

Pectoral Group (Fig. 10)

M. subclavius (not figured)

Origin.—From the lateral half of the first costal cartilage.

Insertion.—Onto the dorsocaudal surface of the middle third of the clavicle.

Remarks.—The description given here characterizes most rodents. Woods (1972) gave a detailed discussion of the origin of this muscle and its relationship to the "sternoclavicular."

M. pectoralis major (not figured; M. pectoralis superficialis part a of Howell, 1932)

Origin.—From the mid-ventral line of the manubrium and from the sternebrae.

Insertion.—The smaller, anterior part runs laterad, passing deep to M. deltoideus anteriorly to insert on the proximal one-third of the humerus. The fibers of the deeper, posterior part insert with those of the anterior part on the lateral crest of the humerus.

Remarks.—This muscle forms a thin sheet over the chest and is difficult to separate from the deeper pectoralis muscles.

M. pectoralis minor (not figured)

Origin.—From sternebrae two through four and not extending to the xiphisternum.

Insertion.—Via a narrow tendon onto the coracoid and medial head of the humerus.

REMARKS.—This muscle is triangular and narrows sharply at insertion. In geomyids the insertion does not include the humerus (Hill, 1937).

M. pectoralis abdominalis (not figured)

ORIGIN.—From the sternebrae posterior to M. pectoralis minor and from the xiphisternum.

INSERTION.—Onto the proximal lateral crest of the humerus.

REMARKS.—In sciurids the insertion is further distad on the humerus (Hill, 1937). In *Dipodomys* the origin is via fascia superficial to M. obliquus abdominis externus and from the xiphisternum. See the comments below under M. cutaneus maximus. In sciurids (Bryant, 1954) and most "hystricomorphs" (Woods, 1972), the insertion is restricted to the capsule of the humerus and the lesser tuberosity. In *Ctenomys, Aplodontia, Thomomys,* and heteromyids it inserts further distad on the lateral crest of the humerus. This condition may be associated with fossorial or semi-fossorial habits.

M. cutaneus maximus (Fig. 10A; M. panniculus carnosus of Howell, 1932)

ORIGIN.—From the skin over the dorsum, from the area posterior to the scapula caudad to the sacral region.

INSERTION.—The fibers converge anteriorly as they pass medial to the humerus. The ventralmost fibers overlap with M. pectoralis abdominalis and then run deep to those fibers to insert with M. pectoralis abdominalis on the lateral crest of the humerus. The dorsal fibers insert proximally on the humerus.

REMARKS.—In dipodoids and muroids the humeral and ventral parts of this muscle are not separable (Klingener, 1964; Rinker, 1954). Woods and Howland (1977) described this muscle in detail for many "hystricomorph" rodents.

Flexor Group of the Arm (Figs. 16, 17)

M. coracobrachialis (Fig. 17A)

ORIGIN.—Via a narrow tendon from the anteromedial tip of the coracoid.

INSERTION.—On the medial surface of the humerus distal to the insertion of M. teres major and M. latissimus dorsi.

REMARKS.—This muscle shares a common tendon at origin with the short head of M. biceps brachii. In *Dipodomys* the tendon of M. coracobrachialis lies deep to that of M. biceps brachii. Hill (1937) described two parts of this muscle in sciurids and geomyids. His "short part" separates from the remainder near the origin and inserts on the humerus proximal to the insertions of M. teres major and M. latissimus dorsi. This "short part" is also present in *Aplodontia* (Hill, 1937), the cricetine *Cricetus,* the cricetomyine *Cricetomys* (Parsons, 1896), and in *Neotoma* and *Peromyscus* (Rinker, 1954). Howell (1932) described this "short head" in *Dipodomys.* Only a single part was found in *Heteromys.*

M. biceps brachii (Fig. 17A)

Origin.—From the base of the coracoid process by a common tendon with M. coracobrachialis (short head), and via a tendon from the lip of the glenoid fossa of the scapula (long head).

Insertion.—On the medial ridge of the ulna just anterior to the semilunar notch.

Remarks.—An attachment to the tuberosity of the radius was not found. Hill (1937) reported a radial insertion for *Citellus* (= *Spermophilus*), *Sciurus,* and *Aplodontia.* The short head is absent in many rodents (Parsons, 1894), including *Castor,* many dipodoids (Klingener, 1964), and some muroids (Rinker, 1954).

M. brachialis (Fig. 16B)

Origin.—From the posterolateral surface of the proximal third of the humerus, from the anteromedial side of the deltoid crest, and from the distal half of the humerus.

Insertion.—Onto the brachial crest of the ulna.

Remarks.—The insertional tendon splits M. biceps brachii. The two heads at origin are not closely tied, but fibers of the two heads join distal to the deltoid crest and are then difficult to separate. The origin in *Dipodomys* wraps around the medial side of the humerus. The medial head is small in sciurids and *Aplodontia,* but is present in geomyids (Hill, 1937), heteromyids, dipodoids (Klingener, 1964), muroids (Rinker, 1954), and many "hystricomorphs" (Woods, 1972). Only one slip, or two inseparable slips, were found in microtine rodents (Stein, 1986).

Flexor Group of the Forearm (Fig. 17)

M. epitrochleoanconeus (Fig. 17B)

Origin.—From the posterior surface of the medial epicondyle of the humerus.

Insertion.—On the medial olecranon process of the ulna.

Remarks.—Howell (1926) was mistaken in reporting that the innervation is via the radial nerve. This is not the case in heteromyids (or other rodents), in which innervation is via the ulnar nerve (Hill, 1937).

M. flexor carpi ulnaris (Fig. 17B)

Origin.—From the medial olecranon process and fascially from the proximal third of the medial ulna.

Insertion.—On the pisiform bone.

Remarks.—In *Aplodontia,* sciurids, murids, other rodents, and members of other mammalian orders an epicondylar head is present (Leche, 1900; Parsons, 1894; Rinker, 1954; Hill, 1937). No such humeral head was found in dipodoids (Klingener, 1964), geomyids (Hill, 1937), heteromyids, or microtines (Stein, 1986). Hill (1937) believed that the presence of an epicondylar head is primitive for rodents (character 26).

M. palmaris longus (Fig. 17B)

Origin.—From the distal part of the medial epicondyle, superficial to the origin of M. flexor digitorum superficialis.

Insertion.—Via a tendon onto the palmar fascia on the ulnar side of the hand, deep to the palmar pads.

Remarks.—The tendon does not diverge and insert in several places as Rinker (1954) suggested for murids; rather it becomes fan-like prior to its insertion onto the fascia of the ulnar pad. In sciurids this muscle is almost vestigial and inserts into fascia (Hill, 1937). The conditions in geomyids and *Aplodontia* are similar to those found in heteromyids (Hill, 1937). In some murids the tendon of this muscle further diverges into two parts before inserting on the thumb, falciform, and thenar pads on the radial side of the manus (Rinker, 1954). Stein (1986) did not find this dual tendon in microtines, however.

M. flexor carpi radialis (Fig. 17B)

Origin.—From the medial epicondyle distal to the origin of M. pronator teres and proximal to the origin of M. flexor digitorum profundus.

Insertion.—Onto the base of metacarpal two.

Remarks.—The insertional tendon is fascially bound to the radius for part of its length. It then runs deep to the scapholunaris to insert on the palmar surface at the base of the second metacarpal. In *Thomomys* the insertion includes the third metacarpal (Hill, 1937). In "hystricomorphs" the insertion often includes the second metacarpal (Woods, 1972).

M. pronator teres (Fig. 17B)

Origin.—From the medial epicondyle.

Insertion.—On the proximal three-quarters of the dorsomedial radius.

Remarks.—This muscle is more developed in sciurids, *Aplodontia* (Hill, 1937), and in *Erethizon* and *Ctenomys* (Woods, 1972). This may represent either the primitive condition for rodents or else an adaptation to fossorial or arboreal habits.

M. flexor digitorum superficialis (Fig. 17B)

Origin.—From the medial epicondyle deep to the origin of M. palmaris longus.

Insertion.—Via three tendons onto the second phalanges of digits two through four.

Remarks.—The insertional tendons are perforated by the tendons of M. flexor digitorum profundus. In sciurids the medialmost of the three tendons divides again to insert on digits four and five, and in *Aplodontia* there is an additional muscle belly and tendon (Hill, 1937).

M. flexor digitorum profundus (Fig. 17B)

Origin.—Via four heads: 1) from the medial epicondyle distal to the origin of M. flexor carpi radialis, 2) from the medial trochlea of the humerus, 3) from the middle third of the ulna distal to the semilunar notch, and 4) from the proximal third of the radius and adjacent interosseous membrane.

INSERTION.—On the distal phalanges of digits one to five.

REMARKS.—The radial and ulnar heads are separable in heteromyids, and only the trochlear head is reduced in size. In the dipodoids *Zapus* and *Jaculus* the radial and ulnar heads give rise to a common tendon (Klingener, 1964).

M. pronator quadratus (not figured)

ORIGIN.—From the distal fifth of the medial surface of the ulna.

INSERTION.—On the adjacent surface of the radius.

REMARKS.—This muscle is reduced in sciurids (Hill, 1937). It is lacking altogether in dipodoids (Klingener, 1964). Hill (1937) reported that this muscle may represent the vestiges of the interosseous membrane muscle.

PELVIC GIRDLE AND LIMB

Iliacus Group (Figs. 19–21)

M. iliacus (Figs. 19 and 20)

ORIGIN.—From the iliac fossa.

INSERTION.—On the lesser trochanter of the femur distal to the insertion of M. psoas major.

REMARKS.—In *Dipodomys* the insertion is restricted to the anterior surface of the lesser trochanter. In *Thomomys* the origin includes the transverse processes of the last lumbar vertebra (Hill, 1937). The femoral nerve emerges between M. psoas major and M. iliacus. In sciurids and *Aplodontia* the lumbar origin is greatly enlarged (Hill, 1937; Bryant, 1945). The lumbar origin is lost in dipodoids (Klingener, 1964) and heteromyids. In murids the lumbar origin is present (Rinker, 1954), but it is variable in microtines (Stein, 1986).

M. psoas major (Fig. 20)

ORIGIN.—From the bodies and transverse processes of the posterior five lumbar vertebrae.

INSERTION.—On the proximal aspect of the lesser trochanter of the femur.

REMARKS.—In *Microdipodops* the fibers of this muscle also insert on the caudal belly of M. iliacus. The insertional tendons of M. psoas major and M. iliacus are difficult to separate in many specimens. However, the two bellies are separable by the femoral nerve.

M. pectineus (Figs. 20 and 21)

ORIGIN.—From the ventral margin of the pubis anterior to the origin of M. adductor longus.

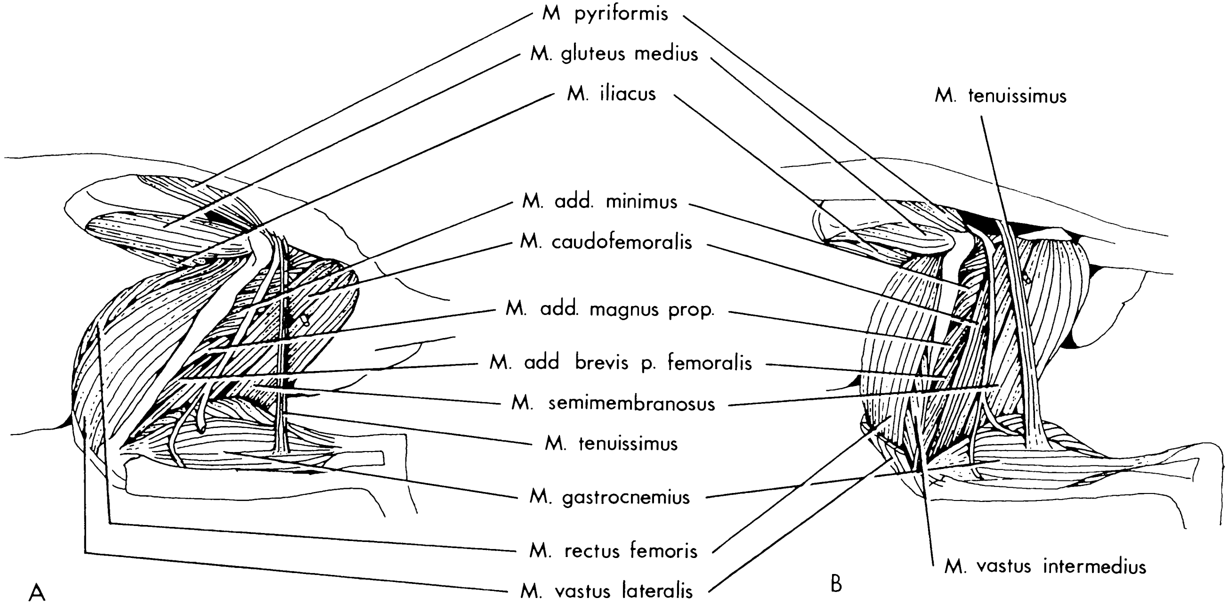

FIG. 19. Lateral views of the deep muscles of the pelvic limb: A) *Heteromys*, B) *Dipodomys*.

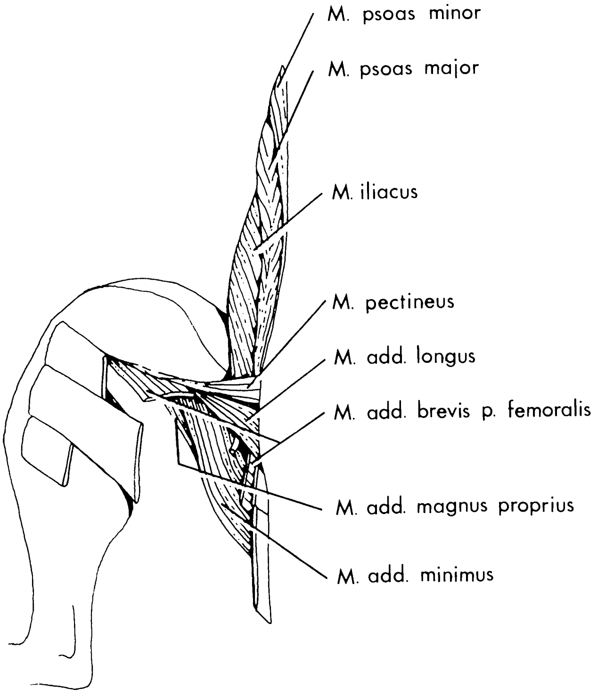

FIG. 20. Medial view of the deep muscles of the thigh in *Heteromys*.

INSERTION.—Via a flat tendon along the posteromedial shaft of the femur, just proximal to the insertion of M. adductor longus.

REMARKS.—In *Perognathus* the origin lies deep to M. adductor longus. In *Dipodomys* the origin is several millimeters anterior to the acetabulum, and the insertion is on the medial aspect of the femur at the level of the lateral crest. In *Microdipodops* the origin is at the level of the actetabulum and the insertion extends medially on the femur, from proximal to the insertion of M. adductor longus to the lesser trochanter. An origin anterior to the actetabulum is considered a synapomorphy for dipodomyines (character 27). Hill (1937) described a complex insertion in *Thomomys,* but not in *Geomys.* In *Sciurus,* M. pectineus is apparently fused to M. adductor longus (Bryant, 1945). Howell (1932) described innervation of this muscle via both the femoral and obturator nerves. He therefore considered it to be of compound origin. I found no innervation via the obturator nerve in the specimens I dissected, and neither did Rinker (1954) for murids nor Klingener (1964) for dipodoids.

Gluteal Group (Figs. 19, 21, 22)

The superior gluteal nerve innervates M. tensor fasciae latae, M. gluteus medius, M. gluteus minimus, and M. pyriformis. M. gluteus maximus and

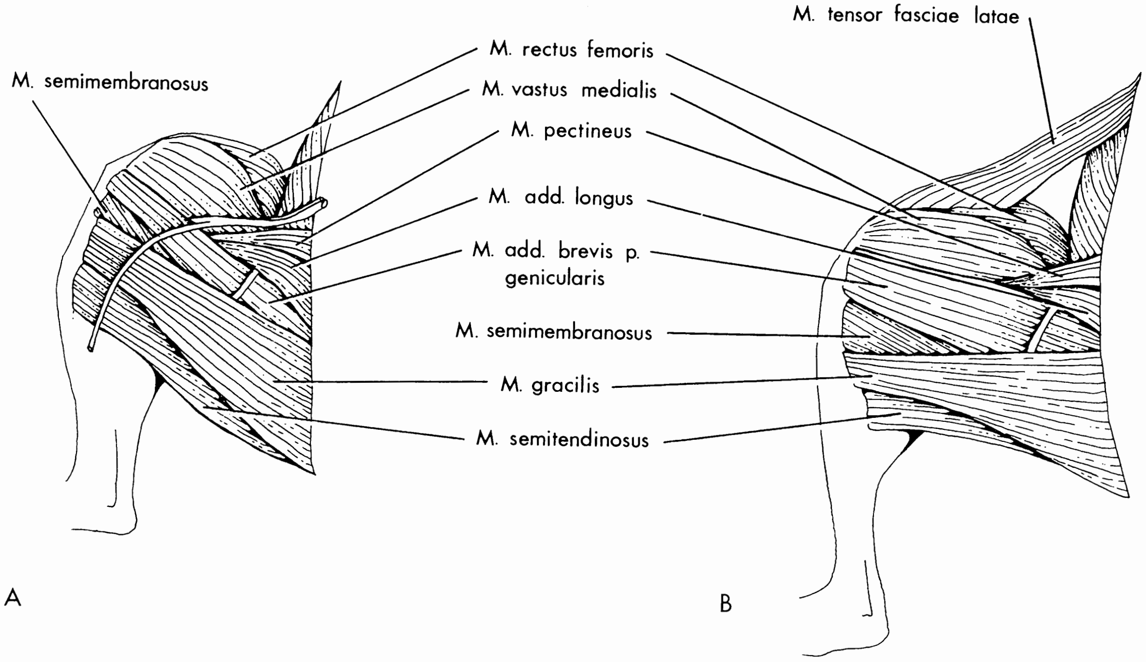

Fig. 21. Medial views of the superficial muscles of the thigh: A) *Heteromys,* B) *Dipodomys.*

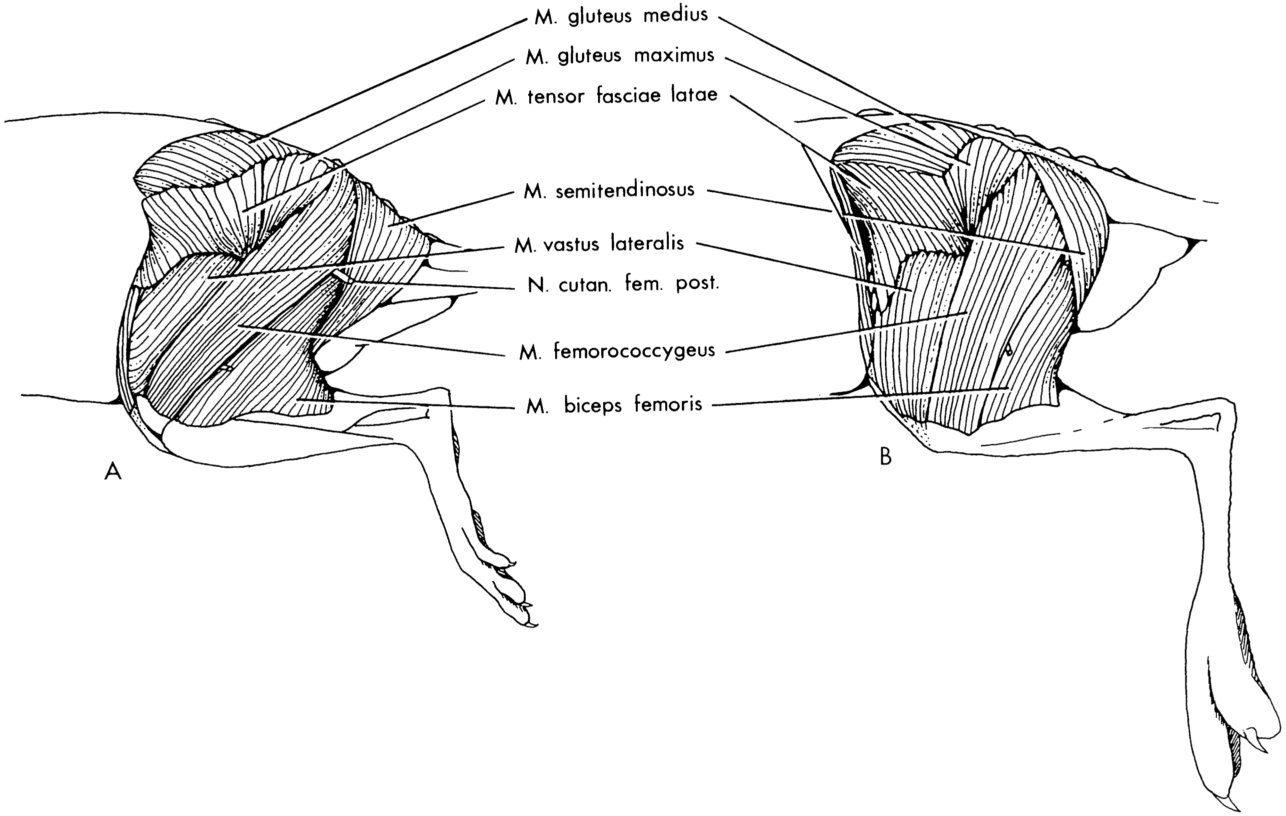

FIG. 22. Lateral views of the pelvic limb: A) *Heteromys*, B) *Dipodomys*.

M. femorococcygeus are supplied by the inferior gluteal nerve, while M. tenuissimus is innervated by a branch of the common peroneal nerve.

M. tensor fasciae latae (Figs. 21B and 22)

ORIGIN.—From the iliac spine superficial to M. gluteus medius, from lumbodorsal fascia over M. gluteus medius, and from the fascia ventral to M. gluteus medius along the margin with M. iliacus.

INSERTION.—Fascially superficial to M. vastus lateralis and proximally onto the lateral crest of the femur.

REMARKS.—This muscle is triangular and robust in heteromyids and has been confused with M. sartorius, which is lacking in heteromyids (character 28). M. tensor fasciae latae thins as it runs from the origin. It covers the cranial surface of the thigh but does not run onto the medial surface. The posterior fibers are difficult to separate from those of M. gluteus maximus. In *Liomys* this muscle is more robust than in *Heteromys.* It extends further distad on the vastus and rectus muscles and extends slightly onto the medial surface of the thigh. The insertion includes the medial surface of the thigh in *Chaetodipus, Perognathus* (except here the muscle is thinner and less robust), and *Dipodomys.* A medial insertion of M. tensor fasciae latae is considered derived (character 29). In *Microdipodops,* there is no medial insertion, but the muscle runs on the cranial surface of the thigh almost to the patella. In *Dipodomys* the medial part originates from the iliac spine and from the anterior iliac ridge between M. iliacus and M. psoas major, and inserts on the medial thigh almost to the knee. It forms a "false sartorius." It is innervated by the superior gluteal nerve. I agree with Howell (1932) that in many rodents M. tensor fasciae latae does not fuse with M. sartorius, but rather the latter is usually absent, resulting in the secondary expansion of the former, which partially assumes the function of the lost sartorius. The medial sheet of M. tensor fasciae latae is also found in the dipodoid *Jaculus* (but not *Sicista* or *Zapus;* Klingener, 1964), microtines (Stein, 1986), and murid rodents (Rinker, 1954). Interestingly, there is no medial part of M. tensor fasciae latae in geomyids (Hill, 1937; pers. obs.). In sciurids there is a "true sartorius" innervated by the saphenous branch of the femoral nerve (Bryant, 1945; pers. obs.), which is considered primitive for rodents (character 28). A true sartorius is also found in the gliroid *Glis* (pers. obs.). The terminology used here differs somewhat from that used by Howell (1932) for *Dipodomys.* His M. gluteus superficialis corresponds to my M. tensor fasciae latae and M. gluteus maximus. Lance Jones (1979) found that M. tensor fasciae latae is derived embryonically from the deep gluteal musculature and does not fuse with M. gluteus maximus until later in development, after it has lost its connection with the deep gluteal.

M. gluteus maximus (Fig. 22)

ORIGIN.—From the fascia over the posterior part of M. gluteus medius and from lumbosacral fascia along the intrinsic back and tail muscles.

Insertion.—Via a broad flat tendon onto the proximal part of the lateral crest of the femur.

Remarks.—This muscle is thin and smaller than M. tensor fasciae latae, and slightly hidden by M. femorococcygeus at both insertion and origin. The anterior fibers are difficult to separate from those of M. tensor fasciae latae. The posterior fibers insert via an aponeurosis onto the gluteal tuberosity. In sciurids and *Aplodontia* this muscle is also difficult to separate from M. femorococcygeus (Hill, 1937). Howell (1926, 1932) considered this muscle to be part of M. gluteus superficialis. He described a muscle called M. gluteus maximus in *Dipodomys,* but this is actually the posterior part of M. gluteus medius. Although difficult to separate from M. tensor fasciae latae, the two muscles are separable based on innervation (see general comments above). Klingener (1964) stated that this muscle is reduced in the bipedal dipodoid *Jaculus.* It is not reduced in the bipedal heteromyid *Dipodomys,* however.

M. femorococcygeus (Fig. 22; M. biceps femoris anticus of Howell, 1932)

Origin.—From the spines of the sacral vertebrae, from the dorsal margin of the ischial spine, and from the area between the ischial spine and the spine of the last sacral vertebra.

Insertion.—On the lateral surface of the patellar tendon and slightly onto the shank of the tibiofibula.

Remarks.—The origin lies deep to M. semitendinosus. The femorococcygeus is difficult to separate from M. biceps femoris, which led Howell (1932) to consider it a part of M. biceps femoris. It is separated from M. biceps femoris by a branch of the posterior femoral cutaneous nerve and is not innervated by the tibial nerve. Lance Jones (1979) showed that M. femorococcygeus is derived from a common muscle anlage with M. gluteus maximus. In *Liomys* the origin includes the spine of the first caudal vertebra, and insertion on the tibiofibula is lacking. In *Perognathus* the insertion includes the lateral epicondyle of the femur. In dipodomyines this muscle is relatively larger and extends further caudad at origin. In sciurids, *Aplodontia,* murids, and dipodoids the origin does not include the ischium (Hill, 1937; Rinker, 1954; Klingener, 1964). Appleton (1928) considered the primitive insertion for mammals to be on the proximal part of the femur. Insertion on the patella is thus considered the derived condition (Hill, 1937) and is common in rodents.

M. tenuissimus (Fig. 19)

Origin.—Via fascia from the intrinsic back and tail muscles in the region of the last few sacral vertebrae, deep to M. femorococcygeus.

Insertion.—Onto the lateral midpoint of the tibiofibula deep to M. biceps femoris.

Remarks.—In one specimen this muscle is only present halfway down the thigh. This muscle forms a very narrow (several millimeters in width) band that lies superficial to tibial and peroneal nerves. In both *Perognathus* and *Chaetodipus,* the origin is via fascia at the level of the acetabulum. In dipodomyines the muscle is larger. This muscle is variably present in *Thomomys* and absent in *Geomys* (Hill, 1937; pers. obs.). It is present is *Aplodontia,* and in sciurids it ranges from vestigial in *Citellus* (= *Spermophilus*) to large in *Sciurus* (Hill, 1937). It is also present in the specimen of the gliroid *Glis glis* I examined. Klingener (1964) found this muscle among dipodoids only in *Sicista,* and Rinker (1954) found it in *Neotoma* and *Peromyscus* but not in *Sigmodon* or *Oryzomys.* It is absent in microtines (Stein, 1986), but I found it in the cricetine *Phodopus.* A vestigial tenuissimus is found in the murid *Mus* (Lance Jones, 1979). It occasionally appears as an atavism in rodents (Raikow *et al.,* 1979). In *Mus* it is innervated by a branch of the peroneal nerve and is never attached to bone. By day 10 of development the muscle has been completely resorbed and is absent in the adult, suggesting that the genetic program is present to form this muscle even though it does not complete development.

M. gluteus medius (Figs. 19 and 22)

ORIGIN.—From the anterodorsal margin of the iliac crest, from the anterior gluteal fossa, and from fibers of the lumbosacral transversospinalis.

INSERTION.—Via a tendon on the lateral and caudal aspects of the greater trochanter, with some dorsal fibers wrapping around the greater trochanter and inserting caudally between the greater trochanter and the lateral crest.

REMARKS.—In *Liomys* the origin reaches the sacral vertebrae, as Hill (1937) described for *Geomys.* In *Dipodomys* there are more fibers wrapping around the greater trochanter. Hill (1937) described two parts of this muscle in *Thomomys.* In *Aplodontia* it is difficult to separate from M. pyriformis (Hill, 1937). Two parts of this muscle are described in dipodoids (Klingener, 1964) and three parts in muroids (Rinker, 1954). Klingener (1964) discussed in detail the relationships of these various parts of M. gluteus medius.

M. gluteus minimus (not figured)

ORIGIN.—From the iliac ridge and entire iliac fossa.

INSERTION.—On the anterolateral surface of the greater trochanter.

REMARKS.—In heteromyines this muscle is relatively more robust than in *Geomys.* In *Dipodomys* and *Microdipodops* this muscle is less extensive and originates from only the posterior three-quarters of the iliac fossa (I use the term iliac fossa to describe that portion of the ilium ventral to the iliac spine). In sciurids the origin is also from the iliac fossa (Bryant, 1945). In dipodoids the origin is primarily from the gluteal fossa (Klingener, 1964).

M. pyriformis (Fig. 19)

ORIGIN.—From the caudal surface of the gluteal fossa and from the transverse processes of the second through fourth sacral vertebrae.

INSERTION.—On the medial surface of the greater trochanter.

Remarks.—This muscle is difficult to separate from M. gluteus medius at its insertion. In *Perognathus* the origin does not include the gluteal fossa. In *Aplodontia* the origin includes a portion from the ventral sacrum (Hill, 1937). M. pyriformis is separable from M. gluteus medius (to which it is sometimes fused) by the superior gluteal nerve.

Quadriceps Femoris Group (Figs. 19, 21, 22)

Heteromyids lack a true sartorius innervated by the femoral nerve. The lack of a sartorius is common among rodents, except in the sciuroids and gliroids where a true sartorius is present (pers. obs.). Lance Jones (1979), however, showed that the embryonic sartorius is present in 13 day *Mus* embryos. It is lost later in development. The remaining muscles in this group are all innervated by the femoral nerve.

M. rectus femoris (Figs. 19 and 21)

Origin.—Via a tendon from the anterior margin of the acetabulum, and via a tendon from the iliac tuberosity anterior to the acetabulum.

Insertion.—On the cranial surface of the patella.

Remarks.—The bulk of this muscle lies medial to M. vastus lateralis. The lateral position of M. rectus femoris is a synapomorphy for geomyids (character 30). In *Perognathus* the tendon at origin is fan-shaped and not Y-shaped as in other heteromyids. The condition in most heteromyids is similar to that pictured for *Sigmodon* by Rinker (1954: fig. 16a). Bryant (1945) described these two tendons of origin as "clearly separable" in *Sciurus, Tamiasciurus,* and *Neotamias*. I disagree with Howell (1932), who described only a single tendon at origin for *Dipodomys*. A single head is present in *Geomys* and a double head in *Thomomys* (Hill, 1937). Likewise, both heads are present in *Zapus* and *Sicista,* but only a single head in *Jaculus* (Klingener, 1964).

M. vastus lateralis (Figs. 19 and 22)

Origin.—From the anterior surface of the greater trochanter and from the anterolateral surface of the femur as far distad as the distalmost part of the lateral crest.

Insertion.—On the lateral surface of the patella and on M. rectus femoris.

Remarks.—In *Chaetodipus* the origin is restricted to the femoral shaft proximal to the lateral crest, and the belly covers the craniomedial quarter of the thigh. In *Perognathus,* however, the origin is restricted to the anterior and lateral surfaces of the greater trochanter. This muscle also covers the craniomedial surface of the thigh in dipodomyines.

M. vastus medialis (Fig. 21)

Origin.—From the proximal half of the anteromedial femur.

Insertion.—On the medial surface of the patella.

Remarks.—This muscle is slightly reduced in size in *Liomys*. M. vastus medialis and M. vastus intermedius are inseparable (Hill, 1937; pers. obs.) in geomyids. This condition is considered a synapomorphy for geomyids (character 31). In sciurids, except *Neotamias* and *Marmota,* these two muscles are distinct (Bryant, 1945).

M. vastus intermedius (Fig. 19B; M. vastus femoris of Howell, 1932)

Origin.—From the distal three-quarters of the cranial surface and distal half of the medial surface of the femur.

Insertion.—On the anterior aspect of the patella deep to the insertion of M. vastus lateralis.

Remarks.—In *Liomys* this muscle is reduced in size relative to *Heteromys*. In *Perognathus* it originates from the distal half of the cranial surface and the distal seven-eighths of the medial surface of the femur. In *Dipodomys* the origin is restricted to the midpoint of the lateral crest, and in *Microdipodops* it originates from the distal five-eighths of the cranial portion of the femur.

Tibial Extensor Group (Figs. 23, 24)

M. extensor digitorum longus (Fig. 23A)

Origin.—From the lateral epicondyle of the femur via a strong thin tendon anterior to the fibular collateral ligament.

Insertion.—On the dorsal surfaces of digits two through five.

Remarks.—The anterior belly of this muscle lies deep to M. tibialis anterior. The tendon divides into four branches between the transcrural retinaculum and the ligamentous trochlea over the calcaneum. In *Chaetodipus* and *Dipodomys* the tendon divides proximal to the transcrural retinaculum. *Perognathus* is similar to *Heteromys* rather than to *Chaetodipus*. In *Thomomys* and dipodoids the tendon also divides proximal to the transcrural ligament (Hill, 1937; Klingener, 1964). Of the dipodoids studied by Klingener (1964), only *Sicista* has an insertion on digit five. In *Jaculus* this muscle is divided into three parts (Klingener, 1964). In murids the condition is much as that described for heteromyids (Rinker, 1954; Stein, 1986).

M. extensor hallucis longus (Fig. 24)

Origin.—From the fascia between M. tibialis anterior and M. extensor digitorum longus, from the peroneus muscles, and from the distal part of the interosseous membrane.

Insertion.—On the terminal phalanx of the hallux.

Remarks.—The tendon runs in common with M. tibialis anterior, diverging from it distal to the ligamentous trochlea. *Thomomys* has a similar condition (Hill, 1937), and Hill suggested that this muscle may have been derived from M. tibialis anterior. In the five-toed species of *Dipodomys* the insertion is on the distal phalanx of digit two. Prior to its insertion it sends off a small thin tendon at the midpoint of the proximal phalanx, which

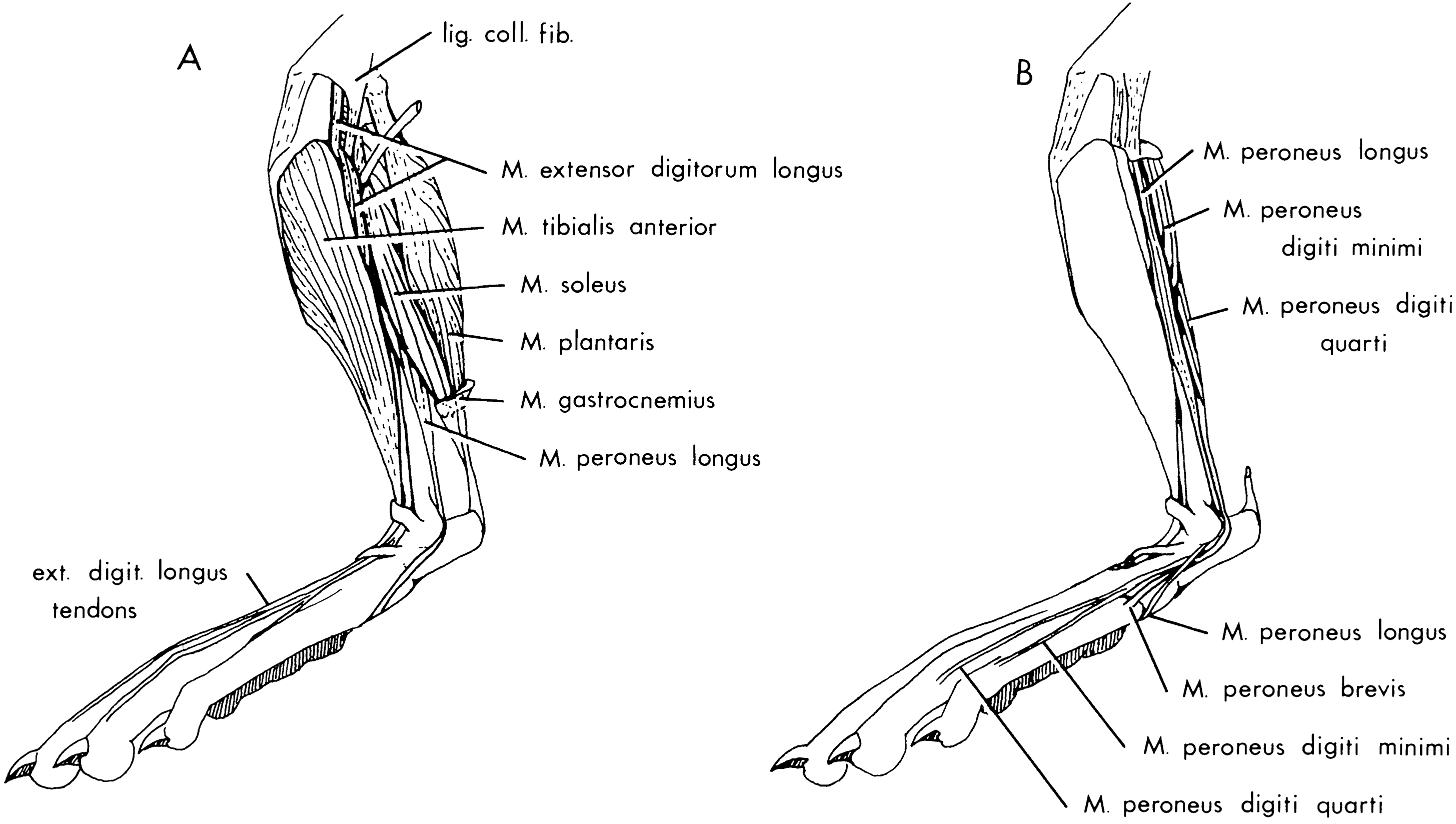

FIG. 23. Lateral views of the muscles of the lower leg in *Heteromys:* A) superficial muscles, B) deeper muscles.

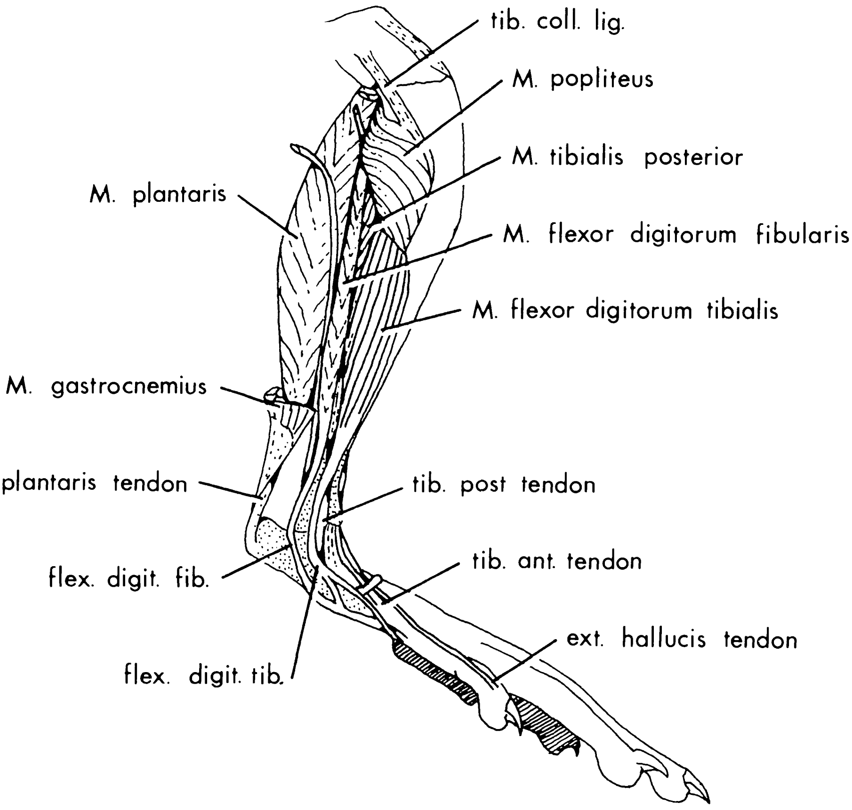

FIG. 24. Medial view of the muscles of the lower leg in *Heteromys*.

inserts on the hallux. In four-toed species of *Dipodomys* the insertion is on the second digit only.

M. tibialis anterior (Figs. 23A and 24)

ORIGIN.—From the proximal part of the lateral fossa of the tibia distal to the tibial head, from the cranial edge of the tibial fossa distal to the midpoint of the tibia, and fascially from the belly of M. extensor digitorum longus.

INSERTION.—Via a tendon passing deep to the transcrural retinaculum, on the proximal surface of the middle cuneiform.

REMARKS.—The tendon passes on the medial side of the foot and runs distad to metacarpal one but does not insert there. In *Chaetodipus* the origin from the cranial part of the tibia continues distad two-thirds of the way down the shank. In *Perognathus* the origin includes the proximal surface of the peroneus muscles. In *Dipodomys* the origin is more medial on the shank. In sciurids (Bryant, 1945), *Thomomys,* and *Aplodontia* (Hill, 1937) it inserts on the first cuneiform and the base of the first metatarsal. No such insertion was found in heteromyids, murids (Rinker, 1954), or microtines (Stein, 1986).

Mm. extensores breves (not figured)

Two small muscles originate from the dorsal surface of the calcaneus. They run deep to the tendons of M. extensor digitorum longus along the lateral margins of digits two and three. The tendons are narrow but do not overlap or fuse with M. extensor digitorum longus. The lack of Mm. extensores breves in *Dipodomys* and *Microdipodops* is considered derived (character 32). Both muscles are present in geomyids (Hill, 1937), but only the muscle to digit three is present in the dipodoid *Zapus* and both are lost in *Jaculus* (Klingener, 1964). Both muscles are present in murids (Rinker, 1954) and microtines (Stein, 1986).

Peroneal Group (Fig. 23)

M. peroneus longus (Fig. 23)

Origin.—From the fibular head ventral to the fibular collateral ligament and from fascia over M. extensor digitorum longus.

Insertion.—On the lateral surface of the first metatarsal.

Remarks.—The tendon curves around the lateral malleolus and passes posteroventral to the base of the fifth metatarsal before crossing to the medial side of the foot. In *Thomomys* the insertion includes the first cuneiform, and some individuals have an additional attachment on the third cuneiform.

M. peroneus brevis (Fig. 23B)

Origin.—From the posterolateral margin of the fibular head and interosseous membrane.

Insertion.—On the base of metatarsal five.

Remarks.—This is the deepest of the peroneal muscles. The tendon of this muscle passes behind the lateral surface of the malleolus and over the trochlear process of the calcaneus. In *Microdipodops* the tendon runs superficial to those of M. peroneus digiti quarti and minimi. This muscle is absent in the dipodoids *Allactaga* (Howell, 1932) and *Jaculus* (Klingener, 1964).

M. peroneus digiti quarti (Fig. 23B)

Origin.—From the middle third of the fibula.

Insertion.—On the dorsum of digit four.

Remarks.—In *Microdipodops* the belly is greatly reduced.

M. peroneus digiti minimi (Fig. 23B; M. peroneus digiti quinti of Howell, 1932)

ORIGIN.—From the proximal third of the free part of the fibula and slightly from the head of the fibula.

INSERTION.—On the dorsum of digit five.

REMARKS.—In *Microdipodops* the belly is greatly reduced. This muscle is absent in the dipodoids *Allactaga* and *Jaculus* (Howell, 1932; Klingener, 1964).

Adductor Group (Figs. 19–21, 25)

These muscles have been confused by many rodent anatomists. The descriptions below are based on the topographic relationship of these muscles to the branches of the obturator nerve that supply the adductor muscles of the thigh.

M. gracilis (Fig. 21; M. gracilis posterior of Howell, 1932)

ORIGIN.—From the ventral ischial ramus and inferior ischial tuberosity.

INSERTION.—On the medial surface of the shank immediately proximal to the insertion of M. semitendinosus.

REMARKS.—The gracilis is single in all geomyoids, and this is the primitive condition for rodents. In *Dipodomys* the origin includes the inferior ischial tuberosity. In *Microdipodops* the gracilis is thicker than in *Dipodomys*. M. gracilis inserts further distad on the medial shank in *Dipodomys* and *Microdipodops*. The gracilis lies superficial (in medial view) to the origin of M. adductor brevis pars genicularis. It is innervated by the obturator nerve, which passes superficial to the M. adductor brevis pars genicularis before running deep to M. gracilis. Hill (1937) reported finding both cranial and caudal parts of M. gracilis in some specimens of *Thomomys*. I found a single M. gracilis in the specimens of *Thomomys* and *Geomys* I dissected and it is possible Hill confused M. adductor brevis with the cranial part. He further stated that the loss of the cranial sheet was probably secondary in pocket gophers. Howell's (1932) description of adductor muscles of *Dipodomys* is problematic; Klingener (1964) provided a table of synonyms for adductor muscles in rodents which clarifies matters considerably. Howell (1932) described both anterior and posterior parts of M. gracilis for *Dipodomys*. In fact, only his M. gracilis posterior is a "true" gracilis; his M. gracilis anterior is actually M. adductor brevis pars genicularis. Hill (1937) was correct in stating that sciurids have a single M. gracilis, as does *Aplodontia* (see also Bryant, 1945). M. gracilis is single in dipodoids (Klingener, 1964), but double in murids (Rinker, 1954) and microtines (Stein, 1986). I found a double M. gracilis in the cricetids *Mesocricetus* and *Phodopus*. In the gliroid *Glis* that I dissected, M. gracilis was single but greatly enlarged. Lance Jones (1979) showed that M. gracilis in *Mus* begins development as a single condensation which splits into two separate muscles at day 13 of development.

M. adductor longus (Figs. 20 and 21)

ORIGIN.—From the ventral margin of the pubis between the M. pectineus cranially and the pubic symphysis caudally.

INSERTION.—Via a tendon on the distal half of the medial surface of the shaft of the femur.

REMARKS.—The nerve to M. gracilis emerges between this muscle and M. adductor brevis. In *Liomys, Perognathus, Chaetodipus, Dipodomys,* and *Microdipodops* the origin does not extend all the way posteriorly to the pubic symphysis. In *Dipodomys* the origin is further anterior on the pelvis, at the level of the acetabulum. Howell (1932) divided M. adductor longus into two parts: longus primus and longus accessorius. His M. adductor longus accessorius is synonymous with M. adductor longus as used here, while his M. adductor longus primus is actually M. adductor brevis pars femoris. The superficial obturator nerve runs over M. adductor brevis to supply M. gracilis. Bryant (1945) stated that M. adductor longus may become fused to M. adductor brevis in some sciurids. I did not find this to be the case in *Eutamias*. The condition of M. adductor longus in *Glis, Mesocricetus,* and *Phodopus* is similar to that described above for heteromyids.

M. adductor brevis pars genicularis (Fig. 21)

ORIGIN.—From the lateral surface of the pubis adjacent to the origin of M. adductor longus and superficial to M. adductor magnus proprius and M. adductor minimus.

INSERTION.—On the medial epicondyle of the femur distal to the insertion of M. caudofemoralis and on the medial surface of the tibiofibula.

REMARKS.—The origin of this muscle lies deep to M. gracilis. It runs more craniad than M. gracilis to its insertion. At the insertion the genicular part of M. adductor brevis lies superficially on the medial surface of the thigh and all but hides the insertion of M. semimembranosus. It also lies superficial to the origin and insertion of M. adductor brevis pars femoris. In *Perognathus* pars genicularis is relatively wider than in *Heteromys*. Hill (1937) confused M. gracilis anterior with M. adductor brevis pars genicularis. He stated that it was variably present in *Thomomys,* but I did not find it in any of the three specimens of *Thomomys* I dissected. M. adductor brevis pars genicularis is lacking is sciurids (pers. obs.; Bryant, 1945), in which only the pars femoris is found. Only a single M. adductor brevis, corresponding to pars femoris, is present in *Glis* (pers. obs.). A double M. adductor brevis is found in *Aplodontia* (Fry, 1961), heteromyids, dipodoids (Klingener, 1964), murids (Rinker, 1954), and cricetines (pers. obs. for *Phodopus*), and is considered derived for rodents (character 33). I also found both parts to be present in the microtine *Microtus;* however, Stein (1986) described only the femoral part for the four genera of microtines she dissected.

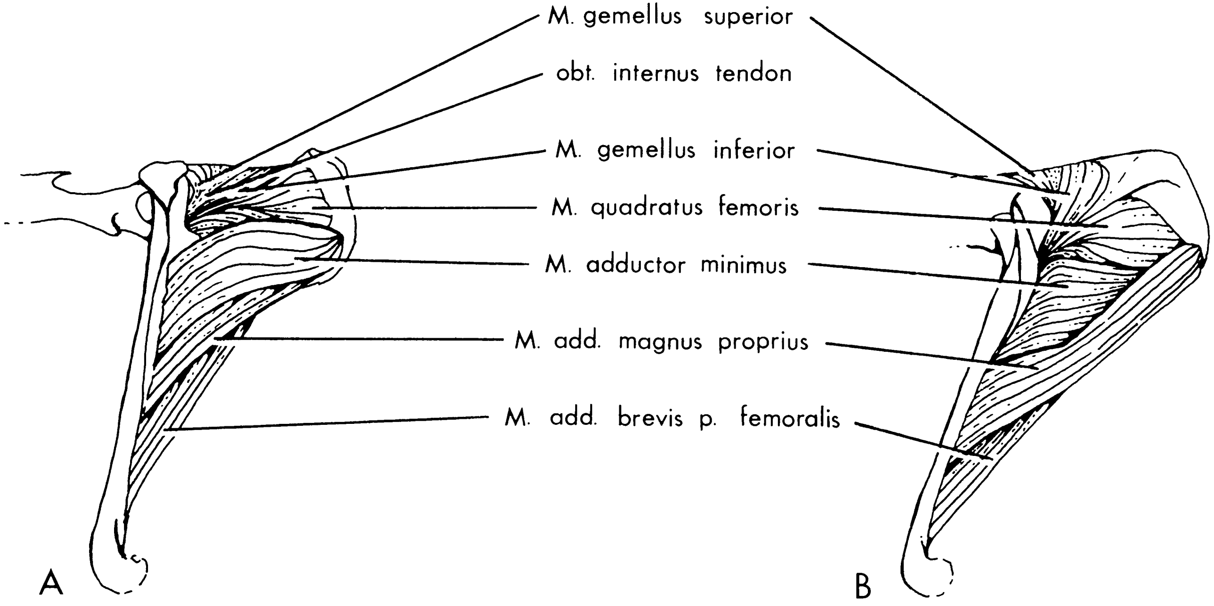

FIG. 25. Lateral views of the adductor muscles of the pelvic limb: A) *Heteromys*, B) *Dipodomys*.

M. adductor brevis pars femoralis (Figs. 19, 20, and 25)

ORIGIN.—From the ventral pubis, ventral to the obturator muscles and anterior to the pubic symphysis.

INSERTION.—On the posteromedial femur along its distal one-third.

REMARKS.—This part of M. adductor brevis lies deep to M. adductor brevis pars genicularis, caudal to M. adductor longus, and ventral to M. adductor magnus. In *Liomys* and *Dipodomys* the insertion is on the distal half of the femur. See the comments above for M. adductor brevis pars genicularis for a discussion of the condition of this muscle in other rodents.

M. adductor magnus proprius (Figs. 19, 20, and 25)

ORIGIN.—From the ventral surface of the pubis posterior to and including the ischial tuberosity.

INSERTION.—On the posteromedial femoral shaft, the distal two-thirds of the lateral crest, and the adjacent shaft.

REMARKS.—The origin is ventral to M. quadratus femoris, deep to M. adductor minimus, and superficial to M. adductor brevis pars femoris (lateral view). The insertion lies deep to M. adductor minimus (medial view). Innervation is via the deep obturator nerve, which passes ventral to M. quadratus femoris, deep to M. adductor minimus, and into M. adductor magnus proprius laterally. In *Perognathus* the origin does not include the ventral ischial tuberosity. In *Dipodomys* and *Microdipodops* the origin is from the posterior part of the inferior ischial tuberosity and the lateral surface of the ischium just anterior to the tuberosity. In dipodomyines the origin of M. adductor magnus proprius lies superficial (lateral view) to M. adductor minimus, not deep to it as in the other heteromyids, and is considered the derived condition (character 34). Thus, in the quadrupedal heteromyids the origin of M. adductor magnus proprius lies deep to that of M. adductor minimus, while in the bipedal heteromyids the reverse is true. The insertion is distal to that of M. adductor minimus on the caudal surface of the femur. In *Microdipodops* the fibers of this muscle are difficult to separate from those of M. adductor minimis. This pattern holds true for the quadrupedal geomyids as well. Fry (1961) further divided M. adductor magnus into deep and superficial parts in *Aplodontia.* In dipodoids, microtines, and murids, M. adductor magnus is not divided into M. adductor magnus proprius and M. adductor minimus (Klingener, 1964; Stein, 1986; Rinker, 1954). Likewise, in the gliroid *Glis* and the cricetines *Phodopus* and *Mesocricetus* that I dissected there was only a single M. adductor magnus. The distribution of taxa with both M. adductor magnus proprius and M. adductor minimus suggests that this is the primitive condition for rodents.

M. adductor minimus (Figs. 19, 20, and 25)

ORIGIN.—Superficial to M. adductor magnus proprius along the ventral part of the posterior ischial ramus, ventrolateral surface of the ischium, and ventral ischial tuberosity.

Insertion.—On the entire posterior surface of the lateral crest of the femur.

Remarks.—This muscle runs superficial to M. adductor magnus proprius and to the ventral part of M. quadratus femoris. In *Chaetodipus* the origin is on the ventral ischial tuberosity and the ventral surface of the ischium anterior to the tuberosity. As stated above, in *Dipodomys* the origin of M. adductor minimis lies deep to M. adductor magnus proprius (lateral view). In both *Dipodomys* and *Microdipodops* innervation is via a branch of the deep obturator nerve that emerges from the obturator foramen and passes between M. quadratus femoris and M. adductor minimus.

M. obturator externus (not figured)

Origin.—From the borders of the obturator foramen and obturator membrane.

Insertion.—On the intertrochanteric fossa.

Ischiotrochanteric Group (Fig. 25)

M. obturator internus (Fig. 25A)

Origin.—From the pelvic surface of the ischium and ventral border of the obturator foramen.

Insertion.—Via a tendon over the sciatic notch and on the intertrochanteric fossa.

Remarks.—In *Dipodomys* the origin is from the ventral border of the obturator foramen and the lateral surface of the pubis and ischium. In *Microdipodops* the origin is from the anteroventral border of the obturator foramen and not the caudal portion. In *Aplodontia* this muscle is enlarged and its origin covers most of the pelvic surface of the hip (Hill, 1937). This muscle is absent in the dipodoid *Jaculus* but present in other dipodoids (Klingener, 1964).

M. gemellus superior (Fig. 25)

Origin.—From the dorsal surface of the ischial ridge at the level of the anterior acetabulum, posterior to the point where the obturator tendon crosses.

Insertion.—On the obturator tendon and intertrochanteric fossa.

Remarks.—This muscle is not equivalent to the muscle of the same name used by Howell (1932), who mistook this muscle for M. gluteus medius or minimus. The gemelli muscles and the obturator internus arise from a single muscle condensation during early development (Lance Jones, 1979). Later the obturator internus migrates to the obturator membrane.

M. gemellus inferior (Fig. 25)

Origin.—From the dorsal ischial margin anterior to the dorsal ischial tuberosity and cranially as far as the tendon of M. obturator internus.

INSERTION.—On the tendon of M. obturator internus and into the intertrochanteric fossa.

REMARKS.—In *Dipodomys* the origin is shifted further anterior on the ischium. A few fibers may also insert on the intertrochanteric fossa. In the dipodoid *Jaculus* the gemelli are a single muscle (Klingener, 1964).

M. quadratus femoris (Fig. 25)

ORIGIN.—From the lateral surfaces of both the superior ischial tuberosity and inferior ischial ramus.

INSERTION.—On the lesser trochanter of the femur.

REMARKS.—In *Liomys* the origin does not include the superior ischial tuberosity, and some anterior fibers lie deep to M. gemellus inferior. The perognathine M. quadratus femoris is relatively more robust than in heteromyines. In *Dipodomys* the origin does not extend to the superior ischial tuberosity nor to the ischial ramus, and anteriorly it lies ventral to the ischial spine and deep to the posterior part of M. gemellus inferior. In *Dipodomys* this muscle is separable into dorsal and ventral components, with the ventral part inserting on the ventromedial surface of the lesser trochanter. This muscle is large in geomyids (Hill, 1937), but not in sciurids. The tendency toward division of this muscle into dorsal and ventral parts is seen in murids (Rinker, 1954), but not in dipodoids (Klingener, 1964). This muscle and M. adductor magnus form a single condensation in early development (Lance Jones, 1979).

Hamstring Group (Figs. 19, 21, 22)

M. caudofemoralis (Fig. 19; M. semimembranosus, anterior part of Howell, 1932)

ORIGIN.—From the dorsal ischial tuberosity anterior to the origin of M. semimembranosus.

INSERTION.—On the anteromedial surface of the shank and on the medial epicondyles of the femur.

REMARKS.—At origin this muscle lies anterior to M. semimembranosus, deep to M. biceps femoris and M. femorococcygeus, and superficial to the nerves of the hamstrings. Distally, M. semimembranosus becomes partially medial to M. caudofemoralis. In perognathines the insertion is on both epicondyles of the femur. In *Dipodomys* the origin is anterior to the superior ischial tuberosity along the dorsal margin of the ischium and deep to both M. femorococcygeus and M. semitendinosus. In *Microdipodops* the insertion is on the medial epicondyle.

There has been considerable confusion over the identities of M. caudofemoralis and M. presemimembranosus. Rinker (1954) discussed these muscles in detail. To summarize, M. caudofemoralis originates from either the caudal vertebrae or the ischium and lies superficial to the nerve to the hamstrings, while M. presemimembranosus originates from the ischium and lies deep to the hamstring nerves. The insertion of M.

caudofemoralis was considered by Rinker (1954) to be on the femur proximal to the lateral epicondyles, while that of M. presemimembranosus is on the medial epicondyle. Based on innervation and position, the muscle in geomyids (Hill, 1937) is M. caudofemoralis. In *Dipodomys* Howell (1932) found some fibers deep to the hamstring nerve. This condition was also seen by Klingener (1964) for *Dipodomys merriami.* I found no such split in the specimens I dissected. Rather, all heteromyids I dissected show a true M. caudofemoralis. In *Aplodontia* and some sciurids there is instead a M. presemimembranosus (Hill, 1937). Murids and dipodoids have the M. caudofemoralis. Hill (1934) believed that the two muscles are homologous and relationship to the hamstring nerve varies. In contrast, Rinker (1954) hypothesized that the two muscles are not homologous and stated that they tend to fuse in some taxa and not others. Lance Jones (1979) studied the ontogeny of the hind-limb muscles in *Mus* and showed that early in development M. caudofemoralis, M. semitendinosus, and M. semimembranosus all form from a single mid-thigh condensation. At day 13 a condensation of muscle mesenchyme joins M. caudofemoralis and M. semimembranosus in the proximal thigh. This slip lies deep to the tibial nerve and fuses with M. semimembranosus distally. This may represent the anlage of M. presemimembranosus (Lance Jones, 1979). It never receives innervation and is lost after day 15 of development.

M. semitendinosus (Figs. 21 and 22)

ORIGIN.—From fascia along the spines of the third sacral vertebra and first two caudal vertebrae.

INSERTION.—On the medial surface of the shank distal to the insertion of M. gracilis.

REMARKS.—In *Liomys* the origin is from the spines and transverse processes of the first three caudal vertebrae. In *Perognathus* the origin also includes fascia over the caudal area, and the insertion is further distad on the shank. In *Dipodomys* the fibers are difficult to separate from those of M. semimembranosus. Hill (1937) described a separate head originating from the dorsal ischial tuberosity in *Thomomys.* The two heads (spinal and ischial) are even more distinct in sciurids and *Aplodontia* (Hill, 1937; Bryant, 1945). In the gliroid *Glis* that I dissected both heads were present. Klingener (1964) reported that both heads are present in the dipodoid *Jaculus* but not in *Sicista* or *Zapus.* Both heads are also present in murids (Rinker, 1954), microtines (Stein, 1986), and cricetines (pers. obs.). The single head of M. semitendinosus is a synapomorphy for heteromyids (character 35).

M. semimembranosus (Figs. 19 and 21B)

ORIGIN.—From the posterior margin of the superior ischial tuberosity and from the caudal border of the ischium.

INSERTION.—On the medial surface of the lower shank proximal to the insertion of M. gracilis.

REMARKS.—The origin from the superior ischial tuberosity is reduced in *Liomys*. In heteromyids this muscle becomes very difficult to separate from M. gracilis near its insertion. In the perognathines the insertion lies partially deep to M. adductor brevis pars genicularis. In *Dipodomys* the origin is further anterior, and this muscle is larger than the adjacent M. caudofemoralis.

M. biceps femoris (Fig. 22)

ORIGIN.—From the dorsolateral surface of the superior ischial tuberosity.

INSERTION.—Fascially on the lateral surface of the proximal half of the shank.

REMARKS.—In *Liomys* the origin is from the posterolateral surface of the superior ischial tuberosity. In perognathines and dipodomyines the insertion does not extend as far craniad on the shank, and in *Perognathus* the origin includes the dorsal third of the ischial ramus. As described by Hill (1937), the lateral sural nerve separates M. biceps femoris from M. femorococcygeus. M. biceps femoris fuses with M. femorococcygeus during the last few prenatal days (Lance Jones, 1979, for *Mus*).

Flexor Group of the Leg (Figs. 19, 23, 24)

M. gastrocnemius (Figs. 19, 23A, and 24)

ORIGIN.—From the lateral, medial, and caudal surfaces of the lateral and medial epicondyles of the femur. Some fibers take origin from the belly of the proximal M. plantaris.

INSERTION.—On the calcaneus.

REMARKS.—Two sesamoid bones are enclosed in the tendons at origin, and the two heads fuse distally to form a single belly. In *Chaetodipus* the two bellies are not heavily fused, yet in *Perognathus* the two bellies fuse at the proximal third of the shank. In *Dipodomys* the two bellies fuse at the level of the distal third of the shank, but the tendon begins midway along the shank. In heteromyids, as in many other rodents, the two heads enclose the M. plantaris muscle.

M. plantaris (Figs. 23A and 24)

ORIGIN.—From the lateral sesamoid bone and lateral head of M. gastrocnemius, which surround it at origin.

INSERTION.—Via a tendon that passes medial to M. gastrocnemius before continuing on the foot as M. flexor digitorum brevis.

REMARKS.—At its origin, the tendon lies deep to that of M. gastrocnemius. However, distally the M. plantaris tendon crosses onto the medial side of the M. gastrocnemius tendon and wraps around it to lie posterior to the tendon of M. gastrocnemius at the level of the calcaneus.

M. soleus (Fig. 23A)

ORIGIN.—Via a narrow tendon from the caudolateral surface of the fibular head.

INSERTION.—On the anterior portion of the gastrocnemius tendon.

REMARKS.—In *Chaetodipus* the origin is via a Y-shaped tendon from the caudolateral surface of the head of the fibula. However, in *Perognathus* the origin is via a single tendon as in *Heteromys*. In the dipodomyines the tendon begins further proximally.

M. popliteus (Fig. 24)

ORIGIN.—From the lateral epicondyle of the femur anterior to the fibular collateral ligament.

INSERTION.—On the proximal third of the medial surface of the tibia and on the belly of M. flexor digitorum fibularis.

REMARKS.—This muscle is tendinous at origin and runs deep to the fibular collateral ligament, ventral to the lateral epicondyle, and dorsal to the fibular head before turning mediad and becoming muscular. The insertion is on the proximal half of the medial part of the tibia in *Chaetodipus,* on the medial fourth in *Microdipodops,* and on the proximal fifth in *Dipodomys*.

M. flexor digitorum tibialis (Fig. 24)

ORIGIN.—From the medial ridge of the tibia distal to the insertion of M. popliteus and from the fascia over M. tibialis posterior.

INSERTION.—Via two tendons. The single tendon branches distal to the astragalus, sending one tendon to the sole of the foot to join the tendon of M. flexor digitorum fibularis. The other tendon inserts on the plantar fascia of the proximomedial sesamoid bone.

REMARKS.—There has been much discussion concerning the insertion of this muscle since Dobson's (1883) paper. He divided the insertion of this muscle into two basic categories; "hystricomorphine-type" and "myomorphous and sciuromorphous type." In the former, the tendon of M. flexor digitorum tibialis joins that of M. flexor digitorum fibularis on the plantar surface of the foot. In the latter category, the tendon of M. flexor digitorum tibialis does not join that of M. flexor digitorum fibularis, but instead inserts on the first digit. Unfortunately, there are intermediate conditions that invalidate the approach taken by Dobson (1883). For example, although Howell (1932) described an "hystricomorphine-type" in *Dipodomys,* heteromyids have a variation of the "myomorphous and sciuromorphous type." Hill (1937) correctly described the condition for geomyids and I found the same condition (described above) in heteromyids. Further, Klingener (1964) also found the same "geomyoid type" (my quotes) in the dipodoids he dissected.

Hildebrand (1978) discussed and illustrated the considerable variation attributable to this muscle in rodents. To summarize his findings, there are five possible insertions in rodents: 1) On the medial sesamoid bone. This condition is found in sciurids, castorids, pedetids, anomalurids, and in the bathyergids. 2) On both the medial sesamoid and plantar pad (pads). This condition is found in aplodontids, sciurids, anomalurids, glirids, and bathyergids. 3) On the medial sesamoid bone and on the tendon of M. flexor digitorum fibularis. Geomyoids and zapodids exhibit this derived condition (character 36). 4) On the tendon of M. flexor digitorum fibularis only. This condition is widespread in "hystricomorphs" and the "myomorph" families Spalacidae, Rhizomyidae, and Dipodidae (excluding the zapodids). 5) Insertion is solely on the plantar pads or skin. Hildebrand (1978) found this last condition in cricetids and murids.

Hildebrand (1978) believed the type 1 insertion on the medial sesamoid to be primitive for rodents. He described two evolutionary transition series. In one series the primitive insertion went through a stage where the insertion included the plantar pad. The primitive insertion on the medial sesamoid was lost leaving the insertion on the plantar pads. The other transition series included the insertion of M. flexor digitorum fibularis and subsequently lost the primitive insertion on the medial sesamoid, leaving only the insertion of the fibularis tendon.

M. tibialis posterior (Fig. 24)

ORIGIN.—From the caudal surface of the lateral and medial crests of the tibia just distal to the head, and from fascia over M. flexor digitorum fibularis.

INSERTION.—Via a tendon on the posterior border of the medial tarsal bone.

REMARKS.—Fibers of this muscle run deep to M. popliteus and become tendinous at the midpoint of the tibia. This tendon continues deep to the tendon of M. flexor digitorum tibialis and a small ligament before reaching its insertion. In all the genera Hildebrand (1978) dissected, the insertion is always on the medial tarsal with minor variation in position. The medial tarsal bone, as used here, is thought to be either a sesamoid bone or a remnant of the prehallux, and is not to be confused with the cuneiform (Hill, 1937). In *Pedetes* there is no medial tarsal, and M. tibialis posterior is correspondingly lost. In anomalurids, which also lack the medial tarsal, the M. tibialis posterior is present and inserts on the first cuneiform. Hildebrand (1978) believed that the medial tarsal in these genera may have fused with the cuneiform, bringing M. tibialis posterior with it.

M. flexor digitorum fibularis (Fig. 24)

ORIGIN.—From the caudal tibial and fibular heads, from the interosseous membrane, and from the caudal surfaces of the tibia and fibula on either side of that membrane.

INSERTION.—Via a tendon on the terminal phalanges of all five digits.

REMARKS.—The tendon runs caudad to the malleolus and onto the plantar surface, where it joins the tendon of M. flexor digitorum tibialis. In *Chaetodipus* the origin includes the ventral epicondyles of the femur.

Flexor Group of the Pes (not figured)

Reduction in pedal flexor muscles is a derived condition in rodents (character 37).

M. flexor digitorum brevis

ORIGIN.—As a continuation of the M. plantaris tendon.

INSERTION.—On the bases of digits two through four.

REMARKS.—Very small bellies attach to these tendons at mid-foot, but these muscles are mainly tendinous. In *Perognathus* the insertion includes digit five, suggesting that the insertion may vary. In *Thomomys* one slip inserts on digit two while the remaining slips fuse with M. plantaris (Hill, 1937).

Mm. flexores breves accessorii

These small muscles were not found in heteromyids. They are also lacking in dipodoids (Klingener, 1964), but have been described for murids (Rinker, 1954) and other rodents.

M. abductor hallucis brevis

ORIGIN.—From the plantar surface of the navicular.

INSERTION.—On the metatarsal-phalangeal joint of the hallux.

REMARKS.—This muscle is lacking in four-toed species of *Dipodomys,* such as *D. microps*. It is present in *Microdipodops* but is considerably more tendinous.

M. abductor ossis metatarsi quinti

ORIGIN.—From the ventromedial aspect of the proximal calcaneus.

INSERTION.—On the base of metatarsal five.

REMARKS.—This muscle is tendinous throughout most of its length. In sciurids, *Aplodontia,* and *Neotoma* it is muscular for much of its length (Hill, 1937).

M. abductor digiti minimi

ORIGIN.—From the distal end of the calcaneus.

INSERTION.—On the metatarsal-phalangeal joint of digit five.

REMARKS.—In all heteromyids except *Microdipodops* the entire length is tendinous.

M. flexor hallucis brevis

This muscle was not found in any of the heteromyids dissected, nor was it found in dipodoids (Klingener, 1964). In *Thomomys* it originates from the plantar surface of the third cuneiform and inserts "on sesamoid bones at metatarsophalangeal joints" (Hill, 1937).

M. flexor digiti minimi brevis

This muscle was not found in heteromyids, but Klingener (1964) described it for dipodoids.

M. abductor hallucis

Origin.—From the medial and proximal margin of the Mm. interossei.

Insertion.—On the lateral sesamoid of the metatarsal-phalangeal joint of the hallux.

Remarks.—This muscle is lacking in four-toed species of *Dipodomys*. Loss or reduction in this muscle is considered a synapomorphy for dipodomyines (character 38).

M. adductor digiti secundi and *M. adductor digiti quinti*

In general, neither of these muscles was found in heteromyids. However, a small tendon which may represent M. adductor digiti secundi was found in one specimen of *Perognathus parvus*.

Mm. lumbricales

Origin.—From the angles formed by diverging tendons of M. flexor digitorum fibularis.

Insertion.—On the lateral surfaces of digits two through five.

Remarks.—Reduction of these muscles in dipodomyines is considered derived (character 39).

Mm. interossei

This muscle has three main divisions, each of which runs to one of the middle three digits to insert on the lateral and medial surfaces of those digits. The origin appears to be from the bases of the first metatarsal, navicular, and cuboid. Howell (1932) confused Mm. flexores breves in *Dipodomys* with Mm. interossei.

DISCUSSION

Systematists and evolutionary biologists are faced with the difficult task of separating systematically useful shared derived characters from primitive characters. A natural taxon is diagnosed by shared derived characters, while nonnatural (paraphyletic) groups lack uniquely shared homologies. Muscle characters have proven useful in establishing higher-level relationships of rodents (Klingener, 1964; Rinker, 1954; Stein, 1986; Woods, 1972). Myological characters tend to be variable among mammalian genera, due to differences in functional or environmental constraints. However, muscle homology can be determined reliably based on ontogeny and innervation pattern (Lance Jones, 1979; Rowe, 1986). The embryonic derivation and ontogeny of many muscles has been described for mammals, providing an important criterion for establishing homology (Lance Jones, 1979; Cheng, 1955). For example, we know that a single embryonic muscle condensation will ultimately give rise to several adult muscles, each of which has a unique origin and insertion. The positions of insertion and origin generally do not change after they have made contact with bone. As the bone grows the muscles retain the same relative position and are "dragged" along with the growing bone (Hurov, 1986).

Muscular Variation Within the Heteromyidae

A discussion of character variability for many muscles can be found under the remarks section in the descriptive portion of this paper. However, a brief description of muscular variation within the family Heteromyidae is necessary to understand the polarity of several of these characters.

Cranial muscles of heteromyids are variable. The rostral origin of M. masseter superficialis is further anterior in heteromyines relative to the other heteromyids. In addition, in perognathines and dipodomyines the insertion on the mandible is further posterior and slightly more dorsal. Functionally, these changes in orientation provide a more horizontal component of force for gnawing. M. masseter lateralis profundus pars anterior does not originate as far rostrad in *Dipodomys*. In *Dipodomys,* and to a lesser extent in *Microdipodops,* the origin of M. masseter lateralis profundus pars posterior includes the dorsal surface of the posterior zygoma. The functional consequences of this condition are not known. Of all the masticatory muscles, M. temporalis is the most variable. It is well developed in *Heteromys* and *Liomys,* intermediate in the perognathines, somewhat more reduced in *Microdipodops,* and drastically reduced in *Dipodomys* (even relative to *Microdipodops*). In geomyids and other rodents this muscle is generally quite large, suggesting the reduction is secondary. The temporalis is also greatly reduced in the bipedal dipodoid *Jaculus* (Klingener, 1964). This reduction is considered to be in response to a shift toward a grinding dentition in *Jaculus* (Klingener, 1964). A similar temporalis, lacking the anterodorsal component, is found in *Dipodomys,* which also possesses a grinding dentition (Brylski, 1985). However, it should be noted that geomyids possess a robust temporalis and dentition similar to *Dipodomys* (Hill, 1937). Yet it seems likely that the reduction of the anterodorsal component of the temporalis in *Jaculus* and *Dipodomys* evolved convergently in response to inflation of the auditory bullae and a shift to a grinding dentition. The auditory bullae of *Dipodomys,* and certain jerboas, are so enlarged that the total bullar volume is larger than the cranial cavity (Webster and Webster, 1975; Howell, 1932). The inflation of the bulla has drastically reduced the size of the sites for muscle attachment on the temporal region of the skull.

The superficial facial musculature is well developed in the heteromyines and perognathines but is reduced in dipodomyines. In *Dipodomys* and *Microdipodops* the auricular slip of the platysma myoides sheet is absent.

Additionally, the remainder of M. platysma myoides is reduced, although not nearly as reduced as in the dipodoid *Jaculus*. The pouch retractor muscle is also reduced in width in dipodomyines. Both *Perognathus* and *Dipodomys* lack M. cervico-auricularis posterior profundus. Except in relative sizes, heteromyids show little variation in M. sphincter colli profundus partes intermedia ventralis and intermedia dorsalis. This muscle sheet is somewhat reduced in dipodomyines, but again, not to the extent found in *Jaculus*.

The musculature associated with the mystacial pad and rhinarium are well developed in heteromyids. A similar condition is found in the bipedal dipodoids (Klingener, 1964). Elaborate vibrissal musculature in *Jaculus* is associated with the ventral orientation of the elongate vibrissae during bipedal locomotion (Klingener, 1964). In heteromyids the vibrissal musculature is only slightly more developed in dipodomyines than in quadrupedal heteromyids.

In the family Heteromyidae, M. nasolabialis profundus pars maxillaris superficialis et pars maxillaris profunda show greater variability than any other muscle. In the Geomyidae both muscles originate from the lateral masseter and zygomatic plate (Fig. 8C). In heteromyids there are two distinct conditions. In *Heteromys, Liomys, Microdipodops,* and *Dipodomys* both muscles take origin from inside the lateral wall of the infraorbital foramen. They emerge in common with a large bundle of rostral nerves and continue as thin tendons rostrad to the lateral rhinarium (Fig. 8A). The origin from the infraorbital foramen is in accord with "a large perforation in the wall of the rostrum anterior to the infraorbital foramen," which Wahlert (1985) described as a synapomorphy for the Heteromyidae. Surprisingly, the perognathines exhibit an intermediate character state between that found in geomyids and the heteromyines and dipodomyines. In both *Chaetodipus* and *Perognathus,* M. nasolabialis profundus pars maxillaris originates from the lateral masseter. Only M. nasolabialis profundus pars maxillaris profunda originates from inside the infraorbital foramen. The two bellies fuse halfway to the rhinarium and become tendinous (Fig. 8B).

Of the remaining superficial facial muscles, only M. bucco-naso-labialis shows intrafamilial variation. In dipodomyines its origin includes the leading edge of the incisor root anteriorly. In perognathines and heteromyines, the origin is restricted to the ventral border of the incisor root.

The inflation of the auditory bullae in dipodomyines may have caused the origin of the posterior digastric to shift to the exoccipital process. The digastric originates from the jugular process in the remaining heteromyids. M. cleidomastoideus is present in all heteromyids except dipodomyines. Dipodomyines also have a relatively poorly developed M. splenius, likely associated with the inflated auditory bullae and the sharply flexed neck.

Heteromyid rodents exploit a wide range of locomotory patterns for such a small group. Heteromyines and perognathines are strictly quadrupedal, while dipodomyines are largely bipedal. Variations in epaxial muscles reflect the adaptations to a specific locomotory mode. In the bipedal dipodomyines, M. iliocostalis lumborum, M. iliocostalis dorsi, and M. iliocostalis cervicis are reduced, while M. longissimus dorsi is enlarged. Likewise M. transversospinalis is expanded in the lumbosacral region in bipeds. In the quadrupedal heteromyines and perognathines, M. transversospinalis is expanded slightly laterad in the pelvic region relative to other quadrupedal rodents. In contrast, bipedal dipodomyines (especially *Dipodomys*) have M. transversospinalis expanded laterally almost to the iliac and ischial spines. The expansion of the musculature in the lumbosacral region in bipeds compensates for the lost support of the pectoral limbs during locomotion. The lumbosacral transversospinalis is not as laterally expanded in *Microdipodops* as it is in *Dipodomys*.

Another correlate of bipedal locomotion is a shortened, highly flexed neck with fused cervical vertebrae (Hatt, 1932). As a result, several of the muscles in the cervical region are reduced in dipodomyines. The pectoral girdle and limbs have also become reduced during the shift to bipedal locomotion. M. serratus posterior superior is reduced in dipodomyines. In *Dipodomys* and *Perognathus,* but not *Microdipodops,* the posterior insertion of M. serratus anterior and M. rhomboideus continues past the posterior scapula as a small tendon. M. latissimus dorsi inserts, via a common tendon, with M. teres major on the medial aspect of the humerus. In dipodomyines the tendon of the latissimus dorsi inserts directly onto the tendon of M. teres major and does not continue to the humerus. M. subscapularis is also reduced in dipodomyines, probably as a consequence of the reduced locomotory function of the forelimbs. Only *Heteromys* and *Liomys* have a well developed tendinous sling at the origin of M. triceps brachii caput longus. Except for minor differences in relative size and slight shifts in origin and insertion, the remaining forearm muscles show little variation in heteromyids.

Differences in hind-limb musculature reflect the diversity in locomotory mode. In bipedal dipodomyines M. pectineus and M. adductor longus originate further anteriad on the pubis. M. tensor fasciae latae is relatively small in heteromyines. In perognathines this muscle is more robust and its insertion runs onto the medial thigh. A medial insertion is also found in *Liomys* and dipodomyines. In the bipedal *Dipodomys* the origin of M. tensor fasciae latae includes the iliac spine and anterior iliac ridge. In *Dipodomys* this muscle runs along the anteromedial thigh almost to the knee, forming a "false sartorius." This condition is apparently an adaptation for bipedal locomotion, as it is also found in the bipedal dipodoid *Jaculus* but not in quadrupedal heteromyids or dipodoids. Likewise, bipedal dipodomyines have a reduced M. gluteus minimus.

In the hamstring group, M. biceps femoris has a broader insertion on the lateral shank in quadrupedal heteromyids. In bipedal dipodomyines the origin of M. adductor magnus proprius has shifted onto the lateral ischium superficial to M. adductor minimus (Fig. 25). This condition is not found in bipedal dipodoids.

In *Perognathus* the tendon at the origin of M. rectus femoris is fan-shaped rather than Y-shaped as it is in *Chaetodipus* and the other heteromyids. In this case the two perognathines differ more than the two genera of heteromyines. Likewise, in *Chaetodipus* the origin of M. vastus lateralis is restricted to the femoral shaft proximal to the lateral crest, while the origin of this muscle in *Perognathus* is restricted to the anterolateral surface of the greater trochanter. The two heads of the gastrocnemius muscle in *Chaetodipus* fuse much further distad along the shank (as in *Dipodomys*) than in *Perognathus*. In addition, of all heteromyids only *Chaetodipus* has a Y-shaped tendon at the origin of M. soleus. In another case, the tendons of M. extensor digitorum longus divide proximal to the transcrural retinaculum in *Chaetodipus* and *Dipodomys*. *Perognathus* is similar to heteromyines, and its tendons divide after passing distad to the transcrural retinaculum. Differences between *Perognathus* and *Chaetodipus* are often greater than differences between *Heteromys* and *Liomys*. However, only one species from each genus, *Perognathus parvus* and *Chaetodipus hispidus,* were dissected in this study.

Bipedal heteromyids have greatly elongate hind feet, and there is a tendency to reduce the bellies of the limb muscles and to elongate their distal tendons. The result is a decrease in the weight of the distal limb. In four-toed *Dipodomys* the muscles of the foot are necessarily reduced. M. extensor hallucis longus ordinarily inserts on the hallux, but in four-toed kangaroo rats the insertion is transferred to the second digit. Likewise, four-toed kangaroo rats lack M. abductor hallucis brevis and M. abductor hallucis. In both *Microdipodops* and *Dipodomys,* Mm. extensores breves are absent due to the reduction of the distal musculature, and Mm. lumbricales are heavily reduced.

The Relationships of Heteromyids to Other Rodents

Historically, the classification of rodents has been based on Brandt's (1855) designation of three rodent suborders: Sciuromorphi, Myomorphi, and Hystricomorphi. These suborders are based primarily on the condition of the masseter muscle and its relationship to the infraorbital foramen. Geomyoid rodents have a sciuromorphous masseter, but even Brandt (1855) grouped geomyoids with myomorph rodents based on shared characters in the postcranial skeleton and in the reproductive tract, ignoring the zygomasseteric morphology. Later authors (e.g. Simpson, 1945) allied geomyoids with sciuromorph rodents, based solely on the shared sciuromorphous masseter condition.

Rodent systematists have recognized that Brandt's subordinal classification, while it may be convenient, does not accurately reflect the phylogenetic history of rodents (e.g. Wilson, 1949). The three arrangements of the masseters probably evolved in response to a shift toward increased reliance on gnawing in rodents. Gnawing requires increased power to the lower incisors during occlusion, which in turn required the rearrangement of the masseter muscles to shift the mandible forward and bring the lower incisors into position with the upper incisors. This was accomplished evolutionarily by moving parts of the masseter complex further out onto the rostrum. This rostral migration of the masseter provides a horizontal component force that shifts the mandible forward during gnawing.

It is currently thought that gnawing evolved more than once in rodent evolutionary history. Indeed there is some support for the theory that the myomorphous masseter condition evolved independently several times. As a result, many rodent systematists suspect that the zygomasseteric complex has been subject to considerable parallel evolution and search for evidence of relationship in other morphological systems.

Despite the lack of agreement on the subordinal affinities of geomyoids, there is little question that this group is monophyletic. The following fourteen characters are synapomorphies for the Geomyoidea: 1) presence of both M. nasolabialis profundus pars maxillaris muscles, 2) presence of pars auriculosaccularis, 3) M. buccinatorius pars intermaxillaris anterior on the palate, 4) presence of M. buccinatorius pars orbicularis sacculi, 5) a weakly hystricomorphine digastric, 6) reduction or absence of the stylohyal cartilage and muscles, 7) presence of external fur-lined cheek pouches, 8) a cheek pouch retractor muscle innervated by facial and accessory nerves, 9) M. acromiotrapezius including the clavicle at insertion, 10) absence of the brachioradialis, 11) absence of M. extensor digiti tertii proprius, 12) lack of the epicondylar head of M. flexor carpi ulnaris, 13) absence of the sartorius, and 14) insertion of the tendon of M. flexor digitorum tibialis on the tendon of M. flexor digitorum fibularis.

The first character is also shared with dipodoids, gliroids and murids, but has not yet been found in any other rodents. This character may eventually be shown to be a synapomorphy for larger group including geomyoids, dipodoids, gliroids, and murids. The second, third, fourth, seventh, and eighth characters are not shared by any group of rodents outside the Geomyoidea. The fifth character has probably evolved convergently in "hystricomorph" rodents. Character six, the reduction or absence of the stylohyal cartilage and muscles, is also found is some murids. Characters 10 and 11, absence of the brachioradialis and extensor digiti tertii proprius, are found in some murid rodents but not in dipodoids, suggesting that the absence in those murids is secondary. The sartorius is found in sciurids and glirids and its presence is considered primitive for rodents. The last character, insertion of the tendon of M. flexor digitorum tibialis on the tendon of M. flexor digitorum fibularis, was considered by Hildebrand (1978) to be intermediate between the condition found in sciurids, aplodontids, anomalurids, glirids, and castorids, and the condition found in dipodoids and muroids.

Myological evidence thus suggests that geomyoids are monophyletic. However, there is little evidence concerning the relationships of geomyoids with respect to dipodoids and muroids, and not enough is known about the myology of the glirids, anomalurids, and various other rodent groups to make any statements about their higher-level relationships.

PHYLOGENY OF THE HETEROMYIDAE

Phylogenetic systematics of the Geomyoidea has been the subject of several recent analyses, including Wahlert's (1985) cladistic analysis of cranial foramina, Brylski's (1985) discussion of skeletal, dental, and soft anatomy, and a review of morphological and biochemical data by Hafner and Hafner (1983). These data sets are not fully concordant.

Two basic questions remain disputed. 1) Is the Heteromyidae monophyletic? 2) Is the subfamily Dipodomyinae monophyletic? Put another way, have *Microdipodops* and *Dipodomys* evolved bipedalism independently?

A summary of PAUP analyses (ALLTREES) of myological characters and interpretations of polarity is presented in Tables 2 and 3. The most parsimonious phylogenetic tree found (Fig. 26) has a length of 45 and a consistency index of 0.956 (if characters 2 and 10 are run unordered the length is 44 with a consistency index of 0.977). In addition to the 14 synapomorphies for the Geomyoidea, there are seven shared derived characters that support the monophyly of the Heteromyidae (characters 6, 8, 10″, 12, 33, 35, 37). Three characters (24, 30, 31) distinguish the Geomyidae as the monophyletic sister group of the Heteromyidae (Fig. 26 and Table 3). Yet the Heteromyidae was considered paraphyletic by Brylski (1985), Lindsay (1972), Rensberger (1971), and Shotwell (1967). All but Brylski (1985) based their phylogenetic conclusions on dental similarity. While all four authors interpret the Heteromyidae as a paraphyletic group, Shotwell (1967) united geomyines and dipodomyines in a clade based solely on similarities in dentition. The remaining authors supported a clade containing geomyines and heteromyines. Based on virtually the same data Wilson (1949) and Wood (1931,1935) concluded that the Heteromyidae is monophyletic (Fig. 1).

The reason for the wide difference of opinion, given the same data, is that the dental characters are based on similarity with no consideration of polarity. Brylski (1985) listed the following characters as supporting a geomyine-heteromyine clade: 1) stapes reduced, 2) stapedial artery absent, 3) P^4 protoloph with three cusps, 4) P^4 anteroconid present, 5) P_4 anterior cingulum with three cusps, and 6) P_4 metalophid and hypolophid with three cusps. Characters three through six are in some cases probably functionally correlated (i.e., upper and lower P4 having three cusps) and in all cases are polarized based on fossil geomyoids (functionally an ingroup), not by outgroup analysis. The loss of the stapedial artery in geomyines and heteromyines was also noticed by Wahlert (1985), but he considered it the result of parallelism. Bugge (1971) considered the presence of the stapedial artery to be primitive for rodents. The stapedial artery is present in *Marmota* but absent in *Aplodontia* (Wahlert, 1974). Even if a reduced stapes and the loss of the stapedial artery supported a geomyine-heteromyine clade, there are four myological characters (data presented herein) and seven cranial characters (Wahlert, 1985) that support heteromyid monophyly.

The question of relationships within the Heteromyidae is more compli-

TABLE 2
DATA MATRIX FOR PAUP ANALYSIS*

Character	Sciurids	Geomyids	Het	Lio	Per	Cha	Mic	Dip
1	0	0	0	0	0	0	0	1
2	0	0	0	0	1	1	1	2
3	0	1	1	1	1	1	1	1
4	0	0	0	0	0	0	1	1
5	0	0	0	0	0	0	1	1
6	0	0	1	1	1	1	1	1
7	0	1	1	1	1	1	1	1
8	0	0	1	1	1	1	1	1
9	0	1	1	1	1	1	1	1
10	0	1	3	3	2	2	3	3
11	0	0	0	0	0	0	1	1
12	0	9	1	1	1	1	1	1
13	0	1	1	1	1	1	1	1
14	0	0	0	0	0	0	1	1
15	0	1	1	1	1	1	1	1
16	0	0	0	0	0	0	1	1
17	0	1	1	1	1	1	1	1
18	0	0	0	0	0	0	1	1
19	0	0	0	0	0	0	1	1
20	0	1	1	1	1	1	1	1
21	0	0	0	0	0	0	1	1
22	0	0	0	0	0	0	1	1
23	0	1	1	1	1	1	1	1
24	0	1	0	0	0	0	0	0
25	0	1	1	1	1	1	1	1
26	0	1	1	1	1	1	1	1
27	0	0	0	0	0	0	1	1
28	0	1	1	1	1	1	1	1
29	0	0	0	1	1	1	0	1
30	0	1	0	0	0	0	0	0
31	0	1	0	0	0	0	0	0
32	9	0	0	0	0	0	1	1
33	0	0	1	1	1	1	1	1
34	0	0	0	0	0	0	1	1
35	0	0	1	1	1	1	1	1
36	0	1	1	1	1	1	1	1
37	0	0	1	1	1	1	1	1
38	0	0	0	0	0	0	1	1
39	0	0	0	0	0	0	1	1
40	0	1	1	1	1	1	1	1

*Het = *Heteromys*, Lio = *Liomys*, Per = *Perognathus*, Cha = *Chaetodipus*, Mic = *Microdipodops*, Dip = *Dipodomys*.

Character states: 0 = primitive; 1,2,3 = derived ordered states; 9 = missing data.

TABLE 3

MYOLOGICAL CHARACTERS USED IN PAUP ANALYSIS*

1. M. masseter lateralis profundus pars posterior origin; 1 = dorsal zygoma
2. M. temporalis; 1 = reduced; 2 = very reduced
3. M. digastric; 0 = sciuromorphine, 1 = weakly hystricomorphine
4. Superficial facial muscles; 1 = reduced
5. M. platysma myoides pars auricularis; 1 = absent
6. M. platysma cervicale; 1 = inserts into pouch retractor muscle at 'fusion zone'
7. Cheek pouch retractor muscle; 1 = dual innervation, facial and accessory
8. M. cervico-auricularis; 1 = divided into three slips
9. M. sphincter colli profundus pars auriculosaccularis; 1 = present
10. M. nasolabialis profundus pars maxillaris muscles; 0 = absent, 1 = origin from lateral zygoma, 2 = dual origin, 3 = origin from IOF
11. M. bucco-naso-labialis; 1 = anterior origin from dorsal margin of the bulge created by the incisor root
12. M. buccinatorius pars intermaxillaris; 1 = anterior on palate
13. M. buccinatorius pars orbicularis sacculi; 1 = present
14. Posterior digastric origin; 0 = paraoccipital, 1 = exoccipital
15. Stylohyal cartilage and muscles; 1 = reduced or absent
16. M. cleidomastoideus; 1 = absent
17. M. acromiotrapezius insertion; 1 = includes clavicle
18. Iliocostal group; 1 = reduced
19. Lumbosacral transversospinalis; 1 = laterally expanded
20. M. rectus abdominus; 1 = lateral part present
21. M. latissimus dorsi insertion; 1 = on teres major tendon
22. M. subscapularis; 1 = reduced
23. M. brachioradialis; 1 = absent
24. M. extensor indicis; 1 = slip to pollex
25. M. extensor digiti terti proprius; 1 = absent
26. M. flexor carpi ulnaris; 1 = lacks epicondylar head
27. M. pectineus; 1 = origin anterior to acetabulum
28. M. sartorius; 1 = absent
29. M. tensor fasciae latae insertion; 1 = includes medial thigh
30. M. rectus femoris; 1 = lateral thigh
31. M. vastus medius; 1 = fused to intermedius
32. Mm. extensores breves; 1 = absent
33. M. adductor brevis; 1 = double
34. M. adductor minimus; 1 = superficial at origin
35. M. semitendinosus; 1 = single head
36. M. flexor digitorum tibialis insertion; 0 = medial sesamoid and plantar pads, 1 = medial sesamoid and flexor digitorum fibularis tendon
37. Pedal flexors; 1 = reduced
38. M. abductor hallucis; 1 = absent
39. Mm. lumbricales; 1 = reduced or absent
40. External fur-lined cheek pouches; 1 = present

*1,2,3 = derived ordered states.

cated. The placement of *Microdipodops* in the Dipodomyinae is problematic. Wood (1935) contrasted the morphology of *Microdipodops* relative to both *Dipodomys* and *Perognathus* and he discussed the many morphological similarities between *Microdipodops* and *Perognathus* at length. Although Wood

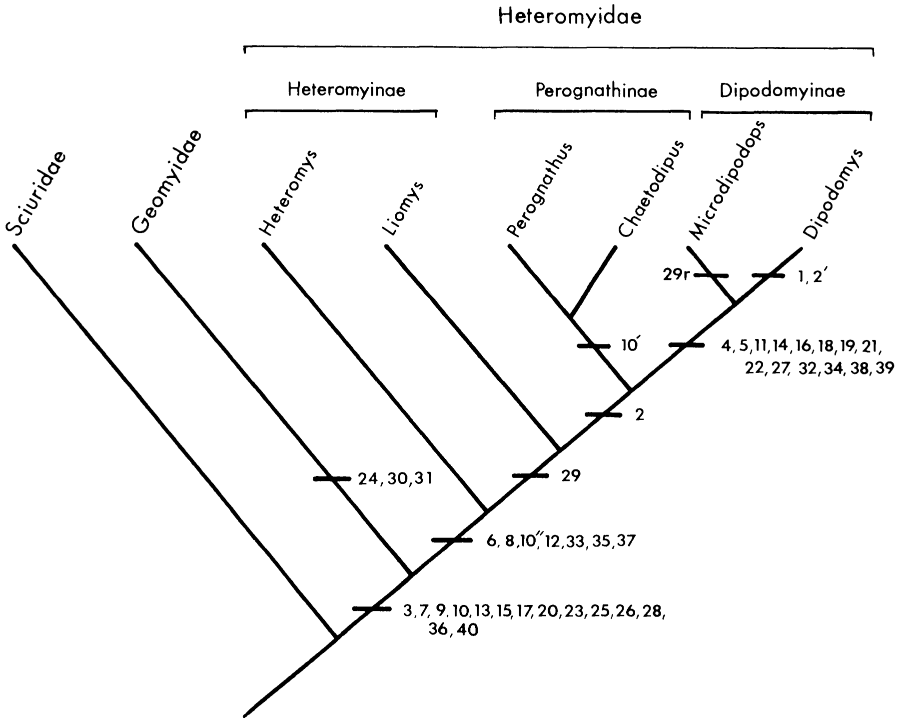

FIG. 26. Phylogenetic relationships of the Geomyoidea based on a PAUP analysis (ALLTREES) of 40 myological characters. Characters with more than two states are denoted by prime (′) symbols. Perognathines are united on the basis of a unique state for character ten. No change in the phylogeny was observed when characters 18, 19, 22, 27, 32, 34, 38, and 39, which are related to bipedal locomotion, were dropped from a similar PAUP analysis. A list of the 40 characters and their polarities are found in Tables 2 and 3. The symbol r denotes a reversal.

(1935) remained equivocal regarding the assignment of *Microdipodops* to the perognathine clade, such an hypothesis was supported by Hafner (1976, 1978). Both Wood (1935) and Hafner (1976, 1978) provided some data to lend credence to the idea that inflated auditory bullae and bipedal locomotion evolved independently in *Dipodomys* and *Microdipodops*.

The PAUP analyses (ALLTREES) of the 40 myological characters from Tables 2 and 3 provides 14 synapomorphies for the clade containing *Microdipodops* and *Dipodomys* (Dipodomyinae). A similar PAUP analysis (length = 37.0; consistency = 0.946) was run excluding the eight characters thought to be associated with bipedal locomotion (characters = 18, 19, 22, 27, 32, 34, 38, 39). These characters would be considered parallelisms by Hafner (1976, 1978). The results still provide six characters supporting the inclusion of *Microdipodops* in the Dipodomyinae (Fig. 26).

The most parsimonious phylogenetic tree based on myological characters is presented in Figure 26. Here *Heteromys* is considered the primitive sister group of the clade containing *Liomys* and the perognathines and dipodomyines. *Heteromys* is separated from its traditional placement with *Liomys* (subfamily = Heteromyinae) by character 29 (the inclusion of part of the medial thigh in the insertion of M. tensor fasciae latae). It is worth noting that this character shows some variability in certain genera and that only two specimens of *Liomys* were available for analysis. Therefore, this is not strong evidence for excluding *Liomys* from the Heteromyinae. *Heteromys* and *Liomys* have many primitive characters relative to other heteromyids and finding synapomorphies for this clade (Heteromyinae) has always been problematic. However, Kelly (1969) and Genoways (1973) provided three synapomorphies for the Heteromyinae based on analysis of the glans penis. Given their data, the medial insertion of M. tensor fasciae latae in *Liomys* and perognathines can be considered a parallelism.

Characters 10 and 29 are the sources of the homoplasy on the tree in Figure 26. Character 29 reverses in *Microdipodops*. When multistate characters were run unordered, character 10, origin of the two M. nasolabialis profundus pars maxillaris muscles, shows no homoplasy. When run ordered, however, character 10 changes to 10′ and 10″ on the heteromyid branch and reverses to 10′ in perognathines, adding one extra step to the tree.

Are the conclusions based on myology concordant with other data sets? Wahlert (1985) presented a phylogeny of the Geomyoidea based on cranial characters. He provided seven synapomorphies for the Heteromyidae, three synapomorphies for the Heteromyinae, two for the Perognathinae, and seven for the Dipodomyinae. Hafner and Hafner (1983) reanalyzed Wood's 1935 data, using heteromyines as an outgroup for perognathines and dipodomyines. They found six synapomorphies that unite *Perognathus* with *Microdipodops,* nine uniting *Perognathus* with *Dipodomys,* and 12 synapomorphies for *Microdipodops* and *Dipodomys.* Likewise, Hafner and Hafner (1983) reanalyzed Hafner's 1978 phenetic data. They were able to establish polarity for 17 of the original 40 characters. The results also support uniting *Dipodomys* and *Microdipodops* in a clade independent of perognathines.

In summary, cladistic analyses of 40 myological characters presented herein and data from various other sources (Hafner and Hafner, 1983; Kelly, 1969; Genoways, 1973; Wahlert, 1985) support the following interpretation of geomyoid relationships: 1) The Geomyoidea is a monophyletic group containing two separate clades recognized as the families Heteromyidae and Geomyidae. 2) There are six myological characters that support heteromyid monophyly. 3) Based on the anatomy of the male reproductive tract (Kelly, 1969; Genoways, 1973) and cranial foramina (Wahlert, 1985), *Heteromys* and *Liomys* form a monophyletic group; myological evidence on this point is equivocal. 4) Based on 15 myological characters *Microdipodops* is united with *Dipodomys* in the dipodomyine clade and did not evolve bipedalism independently. 5) The morphological differences between *Perognathus* and *Chaetodipus* are at least as great as those between *Heteromys* and *Liomys.*

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LITERATURE CITED

Adams, L.A. 1919. A memoir on the phylogeny of the jaw muscles in Recent and fossil vertebrates. Annals New York Acad. Sci., 28:51–166.

Alston, E.R. 1876. On the classification of the order Glires. Proc. Zool. Soc. London, 1876:61–98.

Appleton, A.B. 1928. The muscles and nerves of the post-axial region of the tetrapod thigh. J. Anat., 62:364–438.

Becht, G. 1953. Comparative biologic-anatomical researches on mastication in some mammals. I and II. Kon. Nederland. Akad. Wetensch. Proc., 65(C):508–527.

Bereke, A. 1983. The comparative functional morphology of some head muscles of the rodents *Tachyoryctes splendens* and *Rattus rattus*. I. Mammalia, 47:395–419.

Bock, W. and C. Shear. 1972. A staining method for the gross dissection of vertebrate muscles. Anat. Anz., 130:222–227.

Brandt, J.F. 1855. Beitrage zur nahern Kenntniss der Saugetiere Russlands. Mem. Acad. Imp. Sci. St. Petersbourg, ser. 6, 9:1–375.

Bryant, M.D. 1945. Phylogeny of Nearctic Sciuridae. Amer. Midland Natur., 33:257–390.

Brylski, P.V. 1985. Morphological evolution and comparative development of geomyoid rodents. Unpublished Ph.D. dissertation. Univ. California, Berkeley, 196 pp.

Bugge, J. 1971. The cephalic arterial system in sciuromorphs with special reference to the systematic classification of rodents. Acta Anat., 80:336–361.

Carus, J.V. 1868. Handbuch der Zoologie. Saugetiere. 1:39–191.

Cheng, C. 1955. The development of the shoulder region of the opossum, *Didelphys virginiana*, with special reference to the musculature. J. Morph., 92:415–471.

Cooper, G. and A.L. Schiller. 1975. Anatomy of the Guinea Pig. Harvard Univ. Press., Cambridge, Massachusetts. 417 pp.

Coues, E. 1877. Saccomyidae. Monographs of North American Rodentia. Rept. U.S. Geol. Surv. Terr. 9:481–542.

——— and J.A. Allen. 1877. Monographs of North American Rodentia. Government Printing Office, Washington, D.C., 1091 pp.

Dobson, G.E. 1883. On the homologies of the long flexor muscles of the feet of Mammalia, with remarks on the value of their leading modification in classification. J. Anat. and Physiol., 17:142–179.

Dunlap, S.S., R.W. Thorington, Jr., and M.A. Aziz. 1985. Forelimb anatomy of New World monkeys: myology and the interpretation of primitive anthropoid models. Amer. J. Phys. Anthro., 68:499–517.

Eastman, C.B. 1982. Hystricomorphy as the primitive condition of the rodent masticatory apparatus. Evol. Theory, 6:163–165.

Edgeworth, F.H. 1916. On the development and morphology of the pharyngeal, laryngeal, and hypobranchial muscles of mammals. Quart. J. Microscopic Sci. London., 61:383–432.

______. 1935. The Cranial Muscles of Vertebrates. Cambridge Univ. Press, London, 493 pp.

Eldredge, N. and J. Cracraft. 1980. Phylogenetic Patterns and the Evolutionary Process. Columbia Univ. Press, New York, 349 pp.

Fink, W.L. 1986. Microcomputers and phylogenetic analysis. Science, 234:1135–1139.

Fahlbusch, V. 1985. Origin and evolutionary relationships among geomyoids. *In* W.P. Luckett and J.L. Hartenberger (eds.), Evolutionary Relationships Among Rodents: A Multidisciplinary Analysis: 617–629. Plenum Press, New York.

Fry, J.F. 1961. Musculature and innervation of the pelvis and hind limb of the mountain beaver. J. Morph., 109:173–198.

Genoways, H.H. 1973. Systematics and evolutionary relationships of spiny pocket mice, genus *Liomys*. Spec. Publ. Mus. Texas Tech. Univ., 5:1–368.

Gray, J.E. 1868. Synopsis of the species of Saccomyidae or pouched mice in the collection of the British Museum. Proc. Zool. Soc. London, 1868:199–206.

Greene, E.C. 1935. Anatomy of the Rat. Trans. Amer. Phil. Soc., N. S., 27:1–370.

Hafner, J.C. 1976. Specific and evolutionary relationships of the kangaroo mice, genus *Microdipodops*. Unpublished Masters thesis. Texas Tech. Univ., Lubbock. 139 pp.

______. 1978. Evolutionary relationships of kangaroo mice, genus *Microdipodops*. J. Mammal., 59:354–366.

______ and M.S. Hafner. 1983. Evolutionary relationships of heteromyid rodents. Great Basin Natur. Mem., 7:3–29.

Hafner, M.S. 1982. A biochemical investigation of geomyoid systematics (Mammalia: Rodentia). Zeit. Zool. Syst. Evolut.-forsch., 20:118–130.

Hatt, R.T. 1932. The vertebral columns of ricochetal rodents. Bull. Amer. Mus. Natur. Hist., 63:599–738.

Hennig, W. 1966. Phylogenetic Systematics. Univ. Illinois Press, Urbana, 263 pp.

Hildebrand, M. 1978. Insertions and functions of certain flexor muscles in the hind leg of rodents. J. Morph., 155:111–122.

Hill, J.E. 1935. The retractor muscles of the pouch in the Geomyidae. Science, 81:160.

______. 1937. Morphology of the pocket gopher mammalian genus *Thomomys*. Univ. California Publ. Zool., 42:81–172.

Howell, A.B. 1926. Anatomy of the Woodrat. Williams and Wilkens Co., Baltimore, 225 pp.

______. 1932. The saltatorial rodent *Dipodomys*: the functional and comparative anatomy of its muscular and osseous systems. Proc. Amer. Acad. Arts Sci., 67:377–536.

Huber, E. 1930. Evolution of facial musculature and cutaneous field of trigeminus. Quart. Rev. Biol., 5:133–188, 389–437.

______. 1931. Evolution of facial musculature and facial expression. John Hopkins Univ. Press, Baltimore, 184 pp.

Hurov, J.R. 1986. Soft-tissue bone interface: How do attachments of muscles, tendons, and ligaments change during growth? A light microscopic study. J. Morph., 189:313–325.

Kelly, T.S. 1969. The comparative morphology of the male phallus in the genus *Dipodomys*. Unpublished Masters thesis. San Fernando Valley State College, Los Angeles, California, 133 pp.

Kesner, M.H. 1980. Functional morphology of the masticatory musculature of the rodent subfamily Microtinae. J. Morph., 165:205–222.

______. 1986. The myology of the manus of microtine rodents. J. Zool., London, 210:1–22.

Klingener, D.J. 1964. The comparative myology of four dipodoid rodents (Genera *Zapus, Napeozapus, Sicista,* and *Jaculus*). Misc. Publ. Mus. Zool. Univ. Michigan., 124:1–100.

______. 1970. Superficial facial musculature in Aplodontia. J. Mammal., 51:35–41.

Lance Jones, C. 1979. The morphogenesis of the thigh of the mouse with special reference to tetrapod muscle homologies. J. Morph., 162:275–310.

Leche, W. 1900. Muskulatur, Saugetiere: Mammalia. *In* Bronn's Klassen und Ordnungen das ThierReichs, 1:649–919.

Lewis, T.H. 1949. The morphology of the pectoral girdle and anterior limb in *Aplodontia.* J. Morph., 85:533–558.

Li, C.-k. 1974. A probable geomyoid rodent from middle Miocene of Linchu, Shantung. Vertebrata PalAsiatica, 12:43–53. (Chinese with English summary).

Lindsay, E.H. 1972. Small mammal fossils from the Barstow Formation, California. Univ. California Publ. Geol. Sci., 93:1–104.

Luckett, W. P. 1985. Superordinal and intraordinal affinities of rodents: developmental evidence from the dentition and placentation. *In* W.P. Luckett and J.L. Hartenberger (eds.), Evolutionary Relationships Among Rodents: A Multidisciplinary Analysis: 617–629, Plenum Press, New York.

Maddison, W.P., M.J. Donoghue, and D.P. Maddison. 1984. Outgroup analysis and parsimony. Syst. Zool., 33:83–103.

Matthew, W.D. 1910. On the osteology and relationships of *Paramys,* and the affinities of the Ischyromyidae. Bull. Amer. Mus. Natur. Hist., 28:43–72.

McLaughlin, C.A. 1984. Protrogomorph, sciuromorph, castoromorph, myomorph (geomyoid, anomaluroid, pedetoid, and ctendactyloid) rodents. *In* S. Anderson and J.K. Jones Jr. (eds.), Orders and Families of Recent Mammals of the World: 267–288. Wiley, New York.

Meinertz, T. 1932. Die Hautmuskulatur der Saugetiere. Untersuchungen uber die Hautmuskulatur der Saugetiere mit besonderer Rucksicht auf das oberflachliche Facialisgebiet I. *Cavia cobaya.* Morph. Jahrb., 69:110–220.

______. 1935a. Die Hautmuskulatur der Saugetiere. Untersuchungen uber die Hautmuskulatur der Saugetiere mit besonderer Rucksicht auf das superfizielle Fazialisgebiet II. Das Kaninchen 1. Cutaneus maximus, Sphincter colli superficialis saunt Platysma und seine Derivate beim Kaninchen. Morph. Jahrb., 75:51–61.

______. 1935b. Die Hautmuskulatur der Saugetiere. Untersuchungen uber die Hautmuskulatur der Saugetiere mit besonderer Rucksicht auf das superfizielle Facialisgebiet II. Das Kaninchen 2. Sphincter colli profundus und Derivate beim Kaninchen. Morph. Jahrb., 75:1–51.

______. 1941. The skin musculature of the Greenland lemming *Dicrostonyx groenlandicus* (Traill.). Medd. om Gronland, 131:119–270.

______. 1943a. Das superfizielle Facialisgebiet der Nager VI. Die Sciuriden. 1. *Sciurus vulgaris* L. Zeit. fur Anat. und Entwicklungsgeschichte, 112:105–135.

______. 1943b. Das superfizielle Facialisgebiet der Nager. VI. Die Sciuriden. 2. *Marmota marmota* (L.). Ziet. fur Anat. und Entwicklungsgeschichte, 112:350–381.

______. 1944. Das superfizielle Facialisgebiet der Nager. VII. Die hystricomorphen Nager. Zeit. fur Anat. und Entwicklungegeschichte, 113:1–38.

______. 1951. Das Facialisgebiet der Nager. VIII. Bathyergini Winge, sowie einige Bemerkungen uber *Pedetes caffer* (Pall.). Morph. Jahrb., 90:105–147.

Merriam, C.H. 1895. Monographic revision of the pocket gophers, family Geomyidae (exclusive of the species of *Thomomys*). North Amer. Fauna, 8:1–258.

Miller, G.S. and J.W. Gidley. 1918. Synopsis of the supergeneric groups of rodents. J. Washington Acad. Sci., 8:441–448.

Nelson, G. and N. Platnick. 1981. Systematics and Biogeography: Cladistics and Vicariance. Columbia Univ. Press, New York, 567 pp.

Novacek, M.J. 1986. The skull of leptictid insectivorans and the higher-level classification of eutherian mammals. Bull. Amer. Mus. Natur. Hist., 183:1–111.

Parsons, F.G. 1894. On the myology of the sciuromorphine and hystricomorphine rodents. Proc. Zool. Soc. London, 1894:251-296.

——. 1896. Myology of rodents. II. An account of the myology of the myomorpha, together with a comparison of muscles of the various suborders of the rodents. Proc. Zool. Soc. London, 1896:159–192.

Priddy, R.B. and A.F. Brodie. 1948. Facial musculature, nerves, and blood vessels of the hamster in relation to the cheek pouch. J. Morph., 83:149–180.

Raikow, R.J., S.R. Borecky, and S. Berman. 1979. The evolutionary re-establishment of a lost ancestral muscle in the bowerbird assemblage. Condor, 81:203–206.

Reeder, W.G. 1956. A review of Tertiary rodents of the family Heteromyidae. Unpublished Ph.D. dissertation, Univ. of Michigan, Ann Arbor, 618 pp.

Rensberger, J.M. 1971. Entoptychine pocket gophers (Mammalia, Geomyoidea) of the early Miocene John Day Formation, Oregon. Univ. California Publ. Geol. Sci., 90:1–209.

——. 1973. Pleurolicine rodents (Geomyoidea) of the John Day Formation, Oregon. Univ. California Publ. Geol. Sci., 102:1–95.

Rinker, G.C. 1954. The comparative myology of the mammalian genera *Sigmodon*, *Oryzomys*, *Neotoma*, and *Peromyscus* (Cricetinae) with remarks on their intergeneric relationships. Misc. Publ. Mus. Zool. Univ. Michigan, 83:1–124.

——. 1963. A comparative myological study of three subgenera of *Peromyscus*. Occ. Pap. Mus. Zool. Univ. Michigan, 632:1–18.

Romer, A.S. 1966. Vertebrate Paleontology, 3rd Ed. Chicago Univ. Press, Chicago, 468 pp.

Rowe, T. 1986. Homology and evolution of the deep dorsal thigh musculature in birds and other Reptilia. J. Morph., 189:327–346.

Ryan, J.M. 1986. Comparative morphology and evolution of cheek pouches in rodents. J. Morph., 190:27–41.

Schrieber, H. 1929. Untersuchung uber die Facialismuskulatur einiger Nager. Morph. Jahrb., 62:243–318.

Schumacher, G.H. and H. Rehmer. 1962. Ueber einige Unterschiede am Kauapparat bei Lagomorphen und Rodentia. Anat. Anz., 111:102–122.

Shotwell, J.A. 1967. Late Tertiary geomyoid rodents of Oregon. Univ. Oregon Mus. Natur. Hist. Bull., 9:1–51.

Simpson, G.G. 1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Natur. Hist., 85:1–350.

Slijper, E.J. 1946. Comparative biologic-anatomical investigations on the vertebral column and spinal musculature of mammals. Verhandl. Koninkl. Nederl. Akad. Wetensch., 5:1–128.

Stein, B. 1986. Comparative limb myology of four arvicolid rodent genera (Mammalia, Rodentia). J. Morph., 187:321–342.

Thaler, L. 1966. Les rongeurs fossiles du Bas-Languedoc dans leurs rapports avec l'histoire des faunes et la stratigraphie du Tertiaire d'Europe. Mem. Mus. Natl. Hist. Natur., 17(C):1–29.

Tullberg, T. 1899. Uber das System der Nagethiere: Eine phylogenetische Studie. Nova Acta Reg. Soc. Sci. Uppsala, 18:1–514.

Wahlert, J.H. 1974. The cranial foramina of protrogomorphous rodents; an anatomical and phylogenetic study. Bull. Mus. Comp. Zool., 146:363–410.

——. 1978. Cranial foramina and relationships of the Eomyoidea (Rodentia: Geomorpha), skull and upper teeth of *Kansasimys*. Amer. Mus. Novitates, 2645:1–16.

——. 1983. Relationships of the Florentiamyidae (Rodentia: Geomyoidea) based on cranial and dental morphology. Amer. Mus. Novitates, 2769:1–23.

——. 1985. Skull morphology and relationships of geomyoid rodents. Amer. Mus. Novitates, 2812:1–20.

Webster, D.B. and M. Webster. 1975. Auditory systems of Heteromyidae: functional morphology and evolution of the middle ear. J. Morph., 146:343–376.

Wiley, E.O. 1981. Phylogenetics: The Theory and Practice of Phylogenetic Systematics. Wiley, New York, 439 pp.

Wilson, R.W. 1949. Early Tertiary rodents of North America. Carnegie Inst. Washington Publ., Contrib. to Paleontol., 584:67–164.

———. 1986. Vertebrates, phylogeny, and philosophy. *In* R.M. Flanagan and J.A. Lillegraven (eds.), Univ. Wyoming Contrib. Geology, 3:165–175.

Wineski, L.E. 1985. Facial morphology and vibrissal movement in the golden hamster. J. Morph., 183:199–217.

Wood, A.E. 1931. Phylogeny of the heteromyid rodents. Amer. Mus. Novitates, 501:1–19.

———. 1935. Evolution and relationships of the heteromyid rodents with new forms from the Tertiary of Western North America. Ann. Carnegie Mus., 24:73–262.

———. 1936. A new subfamily of heteromyid rodents from the Miocene of western United States. Amer. J. Sci., 31:41–49.

———. 1965. Grades and clades among rodents. Evolution, 9:115–130.

Woods, C.A. 1972. Comparative myology of jaw, hyoid, and pectoral appendicular regions of New World and Old World hystricomorph rodents. Bull. Amer. Mus. Natur. Hist., 147:119–198.

——— and J.W. Hermanson. 1985. Myology of hystricognath rodents, an analysis of form, function, and phylogeny. *In* W.P. Luckett and J.L. Hartenberger (eds.), Evolutionary Relationships Among Rodents: 515–548. Plenum Press, New York.

——— and E.B. Howland. 1977. Adaptive radiation of capromyid rodents: anatomy of the masticatory apparatus. J. Mammal., 60:95–116.

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