

Comparative Myology of the Forelimb of Squirrels (Sciuridae)

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ABSTRACT The musculature of the shoulder, arm, and forearm was studied in 19 genera of squirrels, representing the Pteromyinae (flying squirrels) and all 7 tribes of the Sciurinae (tree and ground squirrels). The objective was to locate derived anatomical features of functional or phylogenetic significance and to determine how much morphological variation underlies the diverse locomotor behavior of squirrels, which includes terrestrial and arboreal bounding, climbing, digging, and gliding. The fossil evidence suggests that arboreality is primitive for squirrels, and in fact tree squirrels appear to represent the primitive sciurid morphology. Ground squirrels are less uniform and exhibit a few derived features, including a clavobrachialis muscle not seen in other squirrels. Pygmy tree squirrels, which have evolved independently in three tribes, exhibit convergence of forelimb anatomy, including the loss or reduction of several muscles in the shoulder and forearm. The forelimb anatomy of flying squirrels is the most derived and differs from that of tree squirrels in details of shoulder, arm, and forearm musculature. Some of these muscular differences among squirrels have phylogenetic significance, being shared by closely related genera, but none has significance above the tribal level. Many of the differences suggest a variety of changes in function that are amenable to further study. *J. Morphol.* 234:155–182, 1997. © 1997 Wiley-Liss, Inc.*

Herein we present a study of the forelimb musculature of squirrels, which plays a key role in gliding, climbing, digging, and quadrupedal locomotion. There are three purposes for this study. First, we are looking for derived features that reflect functional changes in the use of the forelimb, especially any that have evolved independently in different taxa and that may be interpreted as adaptations to particular ways of life. Second, we are seeking myological characters that will be useful in formulating phylogenetic hypotheses about the genera of squirrels. Although we do not anticipate finding enough forelimb characters to enable us to conduct a phylogenetic analysis, we hope that a series of studies of squirrel anatomy (Ball and Roth, '95; Thorington et al., '96; Thorington and Darrow, '96; Thorington et al., in press) will provide adequate data for such an analysis in the future. Third, we wish to compile morphological data that can be used to test phylogenetic hypotheses derived from the increasing amount of molecular data on squirrels—immunological, electrophoretic, sequencing, etc.—which is being

collected (Hight et al., '74; Ellis and Maxson, '80; Hafner, '84; Hafner et al., '94; Oshida et al., '96). The muscular anatomy of squirrels is well known for only 11 genera and 23 species (Hoffmann and Weyenbergh, 1870; Parsons, 1894; Alezais, 1900; Brizzee, '41; Peterka, '36; Bryant, '45), with a strong bias toward the two tribes of Holarctic taxa, and no representation among three tribes of Asian and African squirrels. We have studied the musculature of the forelimb in 19 genera and 25 species, including 6 genera of flying squirrels and representatives of all 7 recognized tribes of the Sciurinae.

Modern squirrels occur in a diversity of niches and present a number of cases of convergent evolution. Pygmy tree squirrels have evolved independently in South America, Africa, and Southeast Asia, and are members of three different tribes. Ground squirrels (terrestrial squirrels that often live

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in subterranean burrows) occur in two tribes, the Holarctic Marmotini, including the chipmunks, marmots, prairie dogs, and ground squirrels, and the Xerini, which includes two African genera and one Asian genus. Cursorial terrestrial squirrels (which do not live in burrows) have evolved independently on Borneo (*Rheithrosciurus*, of uncertain tribal allocation) and in Africa (*Epixerus*, of the tribe Protoxerini). Another terrestrial squirrel, *Rhinosciurus*, of the Callosciurini, specializes in eating ants and termites (Askins, '77). Tree squirrels occur in five tribes. Because arboreality is primitive for squirrels (Emry and Thorington, '82), it is probable that it evolved only once. It is also probable that gliding has evolved only once in squirrels (Thorington, '84), but the phylogenetic relationships of the genera of flying squirrels are unclear (McKenna, '62). They occur in North America and Eurasia, with the greatest diversity (12 genera) in Southern Asia.

A trustworthy phylogenetic hypothesis of the family Sciuridae does not exist. Modern squirrels comprise approximately 50 genera and 273 species (Hoffmann et al., '93). They are usually aligned in 2 subfamilies, the flying squirrels, in the Pteromyinae [14 genera, 43 species (Hoffmann et al., '93), but see Thorington et al., '96, for justification that 15 genera should be recognized], and all other squirrels in the Sciurinae, which is in turn divided into 7 tribes. Moore ('59) divided the Sciurinae into eight tribes, but the number has since been reduced to seven by Black ('63), Hight et al. ('74), Hafner et al. ('94). The tribe Sciurini includes the tree squirrels of South America, North America, and northern Eurasia. The Marmotini include the Holarctic chipmunks, marmots, and ground squirrels. Three tribes occur principally in Africa: ground squirrels of the tribe Xerini, and tree squirrels of the tribes Protoxerini and Funambulini. Two other tribes occur in southern Asia: Ratufini, the giant tree squirrels, and Callosciurini, which includes a radiation of 13 genera of arboreal and terrestrial squirrels.

Some genera are probably inappropriately allocated to these tribes. Among these are *Rheithrosciurus*, a terrestrial squirrel of Borneo, which is traditionally placed in the Holarctic and South American Sciurini, and *Sciurillus*, the South American pygmy squirrel, which is also placed in the Sciurini in spite

of its divergent morphological and genetic characteristics (Anthony and Tate, '35; Moore, '59; Hafner et al., '94). The placement of the Indian *Funambulus* in the same tribe with the African genera *Paraxerus*, *Funisciurus*, and *Myosciurus* is also questionable (Hight et al., '74; Thorington and Darrow, '96). The largest systematic problem, however, is the relationship among the tribes. It is unclear how the flying squirrels and the seven tribes of tree and ground squirrels are related one to another. The flying squirrels have long been recognized as a separate subfamily based on their distinctive morphology. Until recently, there was no evidence relevant to when they diverged from other squirrels. Paleontological evidence has been used to argue for an early date of divergence (Mein, '70; DeBrujin and Unay, '89), leading to the suggestion that flying squirrels should be considered a separate family from other squirrels (Corbet and Hill, '92). However, Emry and Korth ('96) conclude that the fossil evidence, based just on teeth, is inadequate to determine whether they are a distinct family. The immunodiffusion evidence of Hight et al. ('74) suggests that the flying squirrels are more closely related to the Sciurini than to other tribes of tree squirrels, but the analysis of Ellis and Maxson ('80) suggests that they are divergent from other tribes of the Sciurinae. Various hypotheses have been suggested about the relationships between tribes of the Sciurinae, such as Moore's ('59) suggestion that the Protoxerini were derived from the Xerini, and Hight et al.'s ('74) dendrogram that suggests the sequential divergence of the Marmotini, Callosciurini, Ratufini, and Sciurini, but none of these hypotheses is well supported by morphological data, and some seem contradicted by it (Thorington and Darrow, '96).

Squirrels are first known from the fossil record of the North American Eocene, 35 mybp (Emry and Thorington, '82). Emry and Korth ('96) allocate the genus *Douglassia* to the tribe Sciurini. *Paleosciurus* occurred in Europe in the early Oligocene, approximately 30 mybp (Vianey-Liaud, '74). By the late Oligocene, the Marmotini appear in the fossil record of North America (*Miospermophilus*) and the Xerini appear in the fossil record of Europe (*Heteroxerus*) (Black, '72). Squirrels of undetermined tribal affinity are first recorded from Africa in the Miocene (Lavocat, '73). On the basis of this evidence,

Black ('63) suggested that the tribes of squirrels diverged in the late Oligocene. However, the paleontological record provides little information useful for showing how the tribes are related one to another.

MATERIALS AND METHODS

Animals dissected are listed in systematic order in the Appendix. Dissectable museum specimens of most of these taxa are rare. During dissection, muscles were bisected between origin and insertion, so that origins and insertions could be examined carefully. We recorded our observations on camera lucida drawings made of the appropriate bones in the collections of the National Museum of Natural History. Innervation of the muscles was verified, especially in cases in which there was a question about homology. Innervations are reported only where they differed with the observations of Hill ('37) and Bryant ('45), or where they are of particular interest.

Anatomical nomenclature remains a problem. The *Nomina Anatomica* ('66) for humans is inappropriate. The *Illustrated Veterinary Anatomical Nomenclature* (Schaller, '92) does not include rodents. Some terms normally used in comparative anatomy differ from both. Except where noted, we follow the terminology for muscles used by Hill ('37) to facilitate comparison.

In the remarks sections, we first make comments on the comparative anatomy of squirrels based on Hoffmann and Weyenbergh (1870) for *Sciurus vulgaris*; Parsons (1894) for *Callosciurus prevostii*, *Pteromys volans*, *Xerus getulus*, *Spermophilus mexicana*, and *Marmota marmota*; Alezais (1900) for *Sciurus vulgaris* and *Marmota marmota*; Peterka ('36) for *Sciurus niger*, *Glaucomys volans*, and *Cynomys ludovicianus*; Hill ('37) for *Sciurus griseus* and *Spermophilus richardsonii*; Brizzee ('41) for *Spermophilus armatus*; Bryant ('45) for *Spermophilus* (seven species), *Ammospermophilus* (two species), *Tamias speciosa*, *Marmota flaviventer*, *Cynomys gunnisoni*, *Sciurus griseus*, *Sciurus niger*, *Tamiasciurus douglasii*, *Glaucomys volans*, and *Glaucomys sabrinus*.

This is followed by comments on the comparative anatomy of other rodents based on Parsons (1894, 1896) for diverse "hystricomorph" and "myomorph" rodents, Alezais (1900) for *Cavia*, *Mus*, and *Dipus*, Howell ('26) for *Neotoma*, Hill ('37) for geomyids, Lewis ('49) for *Aplodontia*, Rinker ('54, '63) for cricetines, Klingener ('64) for dipodoids,

Woods ('72) for "hystricomorphs," McEvoy ('82) for *Erethizon* and *Coendou*, Stein ('86, '90) for arvicolids and dipodoids, and Ryan ('89) for heteromyids.

RESULTS

Trapezius group

M. sternomastoideus

Origin: Arises from the cranial surface of the manubrium.

Insertion (Fig. 1): Inserts on the mastoid process of the skull. The insertion is restricted to a small area of the mastoid in the African genera. It extends from the mastoid slightly onto the nuchal line in other genera, most extensively in *Ratufa* and *Sciurus*.

Remarks: In squirrels, variation in the origins and insertions of this muscle is slight (Parsons, 1894; Brizzee, '41; Bryant, '45). In other rodents, variation is also slight. This muscle originates slightly on the clavicle in some cricetines (Rinker, '54). It inserts on the posterior edge of the auditory meatus in cricetines (Rinker, '54), on the bulla in *Dipodomys* (Ryan, '89), and on the paraoccipital process in the hystricomorph rodent *Myocastor* (Woods, '72). Woods ('72) suggests that the more extensive insertion on the nuchal line may simply reflect that the muscle is relatively stronger in some species.

M. cleidomastoideus

Origin (Fig. 2): Arises from the ventral surface of the clavicle adjacent to the origin of the sternomastoid and deep to the origin of cleido-occipitalis.

Insertion (Fig. 1): Inserts on the mastoid process of the skull just caudal to the insertion of sternomastoid. In *Spermophilus*, the insertion is dorsal to that of the sternomastoid, on the superior nuchal line.

Remarks: Like sternomastoid, the origin and insertion of this muscle are quite conservative in squirrels. Among other rodents, the insertion changes with the insertion of sternomastoid (Rinker, '54). This muscle is missing in *Jaculus* (Howell, '32; Klingener, '64).

M. cleido-occipitalis accessorius

Origin: Arises from the ventral surface of the clavicle immediately adjacent to the cleidomastoid.

Insertion: Inserts on the nuchal ridge for 2 mm adjacent to the mastoid process.

Remarks: Not recorded in other squirrels, this muscle was found in only one specimen

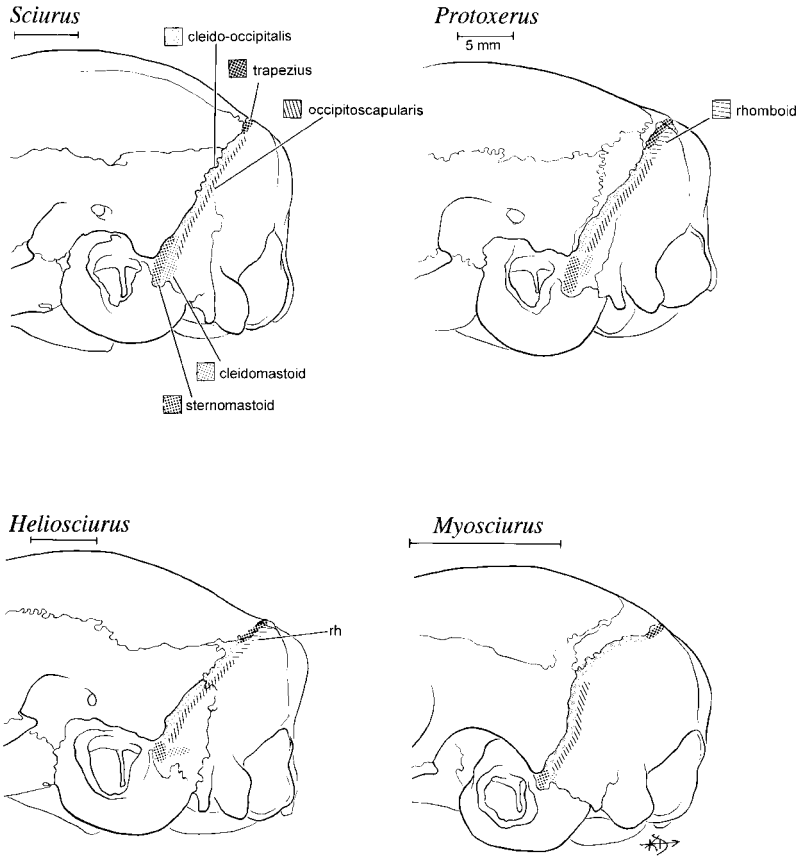


Fig. 1. Posterior surface of the skull showing variations in the extent of the origins of trapezius, occipitoscapularis, and rhomboid, and the insertions of cleido-occipitalis, cleidomastoid, and sternomastoid in eight squirrel genera. Scale bar = 5 mm.

of *Atlantoxerus*. It is probably derived from the immediately adjacent cleidomastoid, but is completely separable from it.

M. cleido-occipitalis

Origin (Fig. 2): Arises from the caudal edge of the clavicle. In most genera, the origin completely covers cleidomastoid. However, in *Nannosciurus*, *Myosciurus*, *Xerus*, *Funambulus*, *Callosciurus*, and *Spermophilus variegatus*, the origin was more lateral and only partly overlapped the origin of cleidomastoid.

Insertion (Fig. 1): Inserts on the nuchal line on the cranium, usually between the sternomastoid and the trapezius (in *Spermophilus*, between the cleidomastoid and the trapezius). Only in *Funisciurus* are the insertions of sternomastoid and cleido-occi-

tal is separated by several millimeters. In genera with extensive cranial origins of trapezius (*Xerus* and *Heliosciurus*), the insertion is restricted to the lateral portion of the nuchal line. In flying squirrels, which lack a cranial origin of trapezius, the insertion is much more extensive: in *Belomys*, *Hylopetes*, and *Pteromys*, it extends from the insertion of sternomastoid nearly to the midline; in *Eoglaucmys*, it extends to the midline; in *Glaucmys* and *Petaurista*, it extends to the midline and for a short distance on the nuchal ligament of the neck. In *Atlantoxerus*, *Sciurus*, and *Spermophilus*, the dorsal edge of cleido-occipitalis is fused with the ventral edge of trapezius.

Remarks: In squirrels, this muscle is completely separable at its origin from the cleidomastoid. The degree of fusion of its insertion

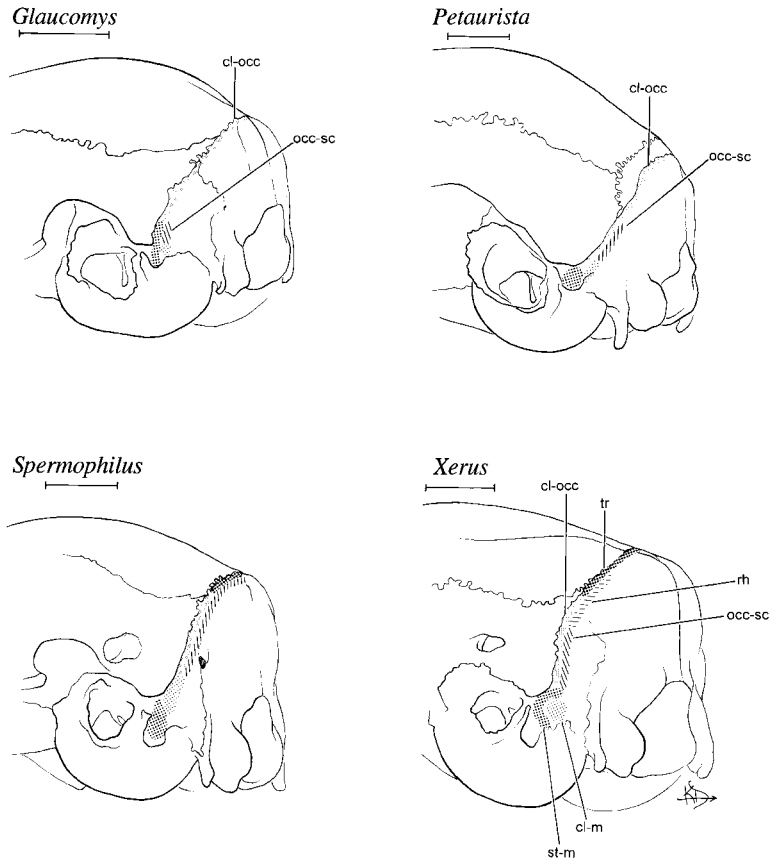


Fig. 1. (Continued)

with the ventral edge of the trapezius varies in the Marmotini, being completely separated in *Marmota* and *Cynomys* (Bryant, '45). Among other rodents, Woods ('72) notes that this muscle in hystricomorphs is not separable from the cleidomastoid at their origins.

M. trapezius

Origin (Fig. 1): In most squirrels, trapezius arises from the nuchal line of the cranium and the midline of the neck and back. The origin extends for half the length of the nuchal line in *Xerus* and *Heliosciurus* and less than half in other tree and ground squirrels. In the flying squirrels (*Belomys*, *Eoglaucomys*, *Glaucomyys*, *Hylopetes*, *Petaurista*, and *Pteromys*), it arises from the neck and back, not from the nuchal line of the skull. In all squirrels, the origin extends caudally to the vicinity of T8 to T10. The muscle is not

separable into distinct parts, although the origin from the midline is aponeurotic opposite the scapular spine in some genera (*Protoxerus*, *Heliosciurus*, *Paraxerus*, *Funisciurus*, *Spermophilus*, *Atlantoxerus*, and *Ratufa*).

Insertion (Fig. 3): Inserts on the scapular spine from the metacromion almost to the vertebral border. Anterior fibers insert on the cranial border of the scapular spine; the most posterior fibers insert on the caudal border of the scapular spine. In *Myosciurus*, few fibers insert on the caudal border of the spine. In *Xerus*, the most caudal fibers form an "auricular slip," passing over the metacromion and joining fibers of the *M. sphincter colli superficialis*.

Remarks: Among squirrels, Bryant ('45) described the insertion of trapezius extending onto the base of the acromion in the Marmotini. We did not observe this in any of our dissections and therefore we do not use

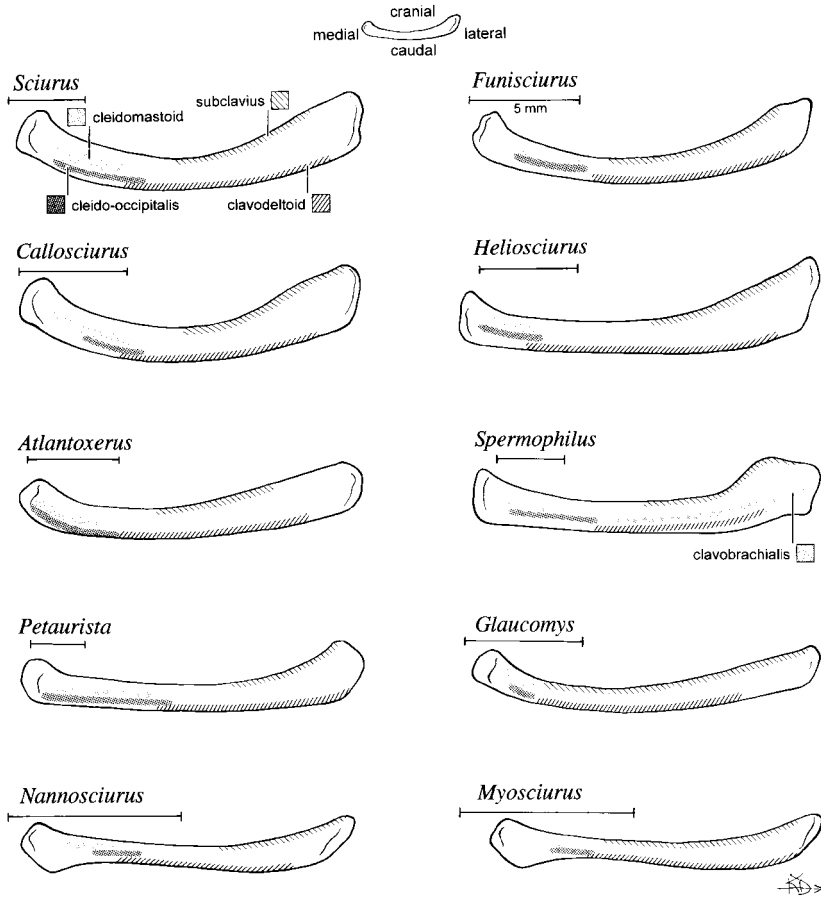


Fig. 2. Ventral surface of the clavicle of ten squirrel genera showing the origin of subclavius and the insertions of cleidomastoid, cleido-occipitalis, clavodeltoid, and, in *Spermophilus*, clavobrachialis. Scale bar = 5 mm.

the name acromiotrapezius for the anterior portion of this muscle. It does not insert on the acromion and it is not separable from the posterior portion (spinotrapezius) which inserts on the caudal border of the scapular spine. In some rodents, the insertion extends onto the clavicle: slightly in dipodoids and heteromyids, extensively in geomyids (Hill, '37; Klingener, '64; Ryan, '89). An auricular slip of the trapezius is widely found among rodents. Among the sciurids, it was noted in *Marmota* (Bryant, '45) and in *Tamiasciurus* (Rinker, '54). It also occurs in *Aplodontia* (Lewis, '49; Klingener, '64), in hystricomorphs (Woods, '72), and among bathyergids, microtines, cricetines, and dipodoids (Klingener, '64, '70), but not geomyoids (Hill, '37; Ryan, '89).

Extensor system

Costo-spino-scapular group

M. levator scapulae et *M. serratus ventralis*

Origin: Arises by slips from the ribs and cervical vertebrae, converging to a single sheet. An origin from the atlas is absent in most genera. In *Heliosciurus rufobrachium* (three of four specimens), there is a slip originating from the ventral surface of the atlas which passes superficial to the scale-nus (Fig. 4).

Insertion: Inserts on the vertebral edge of the scapula and the adjacent costal surface. The insertion extends to the superficial surface of the scapula between rhomboid and teres major in *Sciurus*, *Callosciurus*, *Heliosciurus*, *Paraxerus*, and *Funisciurus*.

Remarks: Contrary to our observations, Bryant ('45) reported an origin from atlas as the common condition for squirrels. Parsons (1894) reported the atlantic origin present in *Callosciurus*, *Pteromys*, and *Marmota*, but absent in *Xerus*. It is present in a wide variety of other rodents as well (Parsons, 1894; Ryan, '89). The occurrence of an atlantic slip of levator scapulae, in addition to the atlantoscaphularis dorsalis, was cited by Woods ('72) as a reason for doubting that the latter muscle was derived from the former (see remarks for atlantoscaphularis dorsalis).

M. rhomboideus

Origin (Figs. 1, 5): Arises from the superior nuchal line, the cervical vertebrae, and the first few thoracic vertebrae. Rhomboid originates on the nuchal line in *Atlantoxerus*, *Xerus*, *Paraxerus*, *Protoxerus*, and *Heliosciurus*. In the other genera, there is no cranial origin. In *Xerus*, the cranial origin is separate from the vertebral origin and forms a distinct rhomboideus capitis. In *Funambulus* and *Heliosciurus gambianus*, the vertebral origin is divided into anterior and posterior portions.

Insertion (Figs. 3, 5): Inserts on the vertebral edge of the scapula from the scapular spine nearly to the caudal angle. Rhomboid inserts on the costal side of the scapula in all genera except for *Sciurus*. In *Funambulus* and *Heliosciurus gambianus*, the posterior portion inserts superficial to the anterior portion and the fibers have a medial-lateral orientation. The fibers of the anterior portion have a more cranial-caudal orientation. The insertion does not extend to the caudal angle of the scapula in *Protoxerus*, *Ratufa*, and *Spermophilus variegatus*.

Remarks: The part of the rhomboid originating on the nuchal line, as described above, should not be confused with the occipitoscaphularis (Fig. 5). The rhomboid and the occipitoscaphularis seem to us always to be distinguishable in squirrels, contrary to the report of Bryant ('45). As reported by Parsons (1894), and noted by us, they are least separable in *Spermophilus*, Bryant's principal subject. They may not be separable at the origin, but it is possible to allocate fibers to their respective muscles on the basis of their separation more distally. Woods ('72) describes them as forming a single sheet in most hystricomorphs. The two muscles are obviously closely related. A distinct posterior portion of the rhomboid, seen by us in *Funambulus* and *Heliosciurus*, was not noted

by Parsons (1894) or Bryant ('45). It is found in some other rodents, e.g., cricetines (Rinker, '54) and arviculids (Stein, '86).

M. occipitoscaphularis

Origin (Figs. 1, 5): Arises from the superior nuchal line of the skull deep to the cleido-occipitalis and medial to the insertion of cleidomastoid. In the pygmy squirrels and in the flying squirrels, the origin is short and is restricted to the lateral half or less of the nuchal line. The origin extends medially to the cranial origin of the rhomboid in *Atlantoxerus*, *Xerus*, *Protoxerus*, *Paraxerus*, and *Heliosciurus*, and almost to the midline in the other genera. The origin is most extensive in *Funisciurus* and *Spermophilus*.

Insertion (Figs. 3, 5): Inserts on the dorsal end of the scapular spine and on the vertebral border of the scapula anterior to the spine. It also inserts on the costal surface of the scapula in the flying squirrels, and in the tree squirrels *Callosciurus*, *Protoxerus*, *Funisciurus*, and *Paraxerus ochraceus*. In *Eoglaucomys*, it also inserts on the surface of the rhomboid. In *Belomys*, *Petaurista*, and *Pteromys*, the insertion is restricted to the cranial portion of the vertebral border of the scapula. In *Protoxerus*, occipitoscaphularis inserts on the surface of the supraspinatus. In *Spermophilus variegatus*, *Ratufa*, *Paraxerus*, *Funisciurus*, and *Heliosciurus*, the insertions of occipitoscaphularis and atlantoscaphularis dorsalis are inseparable.

Remarks: The variation of this muscle in squirrels was not well documented heretofore. A similar amount of variation occurs in other rodents (Hill, '37; Rinker, '54; Klingener, '64). The close association of occipitoscaphularis and atlantoscaphularis dorsalis at their insertion was noted by Woods ('72). In addition, he reported that the origins are contiguous in *Thryonomys* and argued that atlantoscaphularis dorsalis was derived from the occipitoscaphularis.

M. atlantoscaphularis ventralis (omocervicalis)

Origin (Fig. 4): Arises from the ventral arch of the atlas, medial to the attachment of scalenus.

Insertion (Fig. 3): Inserts on the metacromion of the scapula adjacent or partially deep to the trapezius muscle. The trapezius significantly overlaps the atlantoscaphularis ventralis in *Petaurista*, *Protoxerus*, and *Ratufa*. In the other genera, the muscles

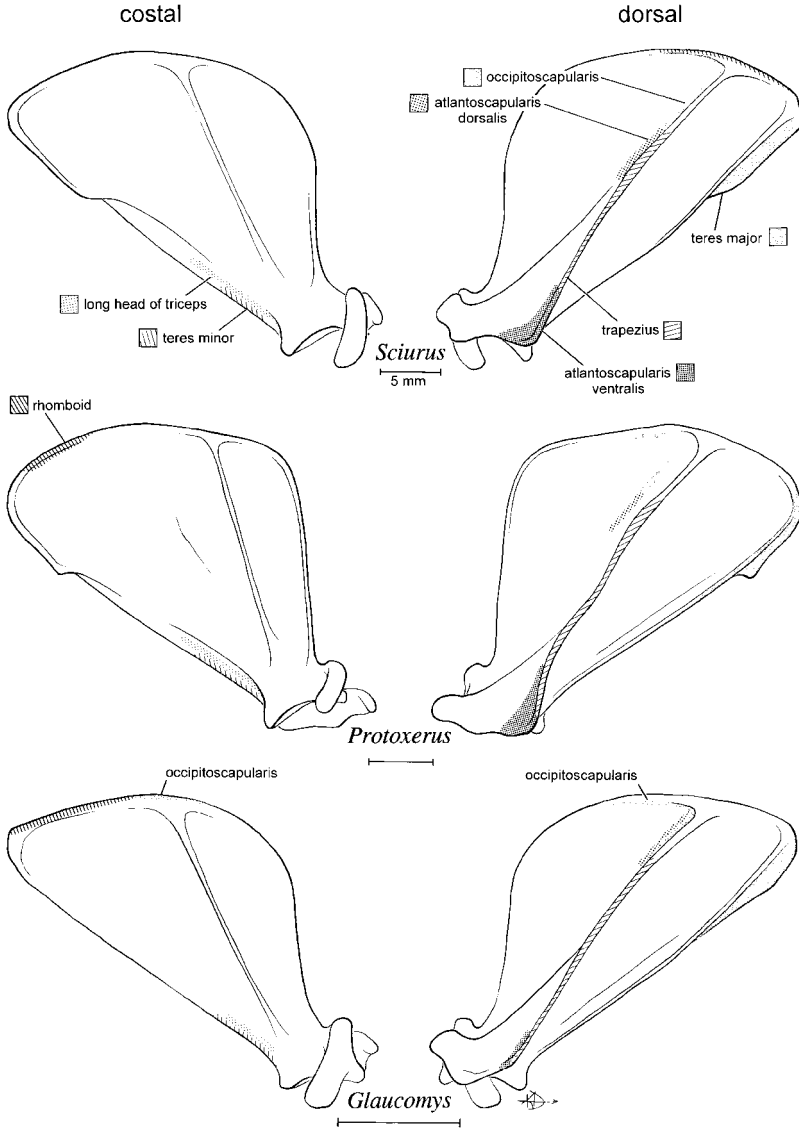


Fig. 3. Costal and dorsal surfaces of the scapula of six squirrel genera showing the origins of teres major, teres minor, and the long head of triceps, and the inser-

tions of occipitoscapularis, rhomboid, atlantoscapularis ventralis, atlantoscapularis dorsalis, and trapezius. Scale bar = 5 mm.

may be adjacent or trapezius may slightly overlap the insertion of atlantoscapularis ventralis. Only in one specimen of *Spermophilus richardsonii* did some fibers of trapezius lie deep to fibers of atlantoscapularis ventralis. The separability of the two muscles at their insertion is variable.

Remarks: Among squirrels, this muscle exhibits very little variation in origin or

insertion. Hill ('37) reports its origin on the basioccipital in *Spermophilus*, but that is not reported for *Spermophilus* in other studies (Brizzee, '41; Bryant, '45). The primitive morphology of the origin for rodents is subject to debate. Parsons (1894) suggests that the primitive origin is on the basioccipital, as seen in diverse rodents, and that the origin from the atlas is derived. In many

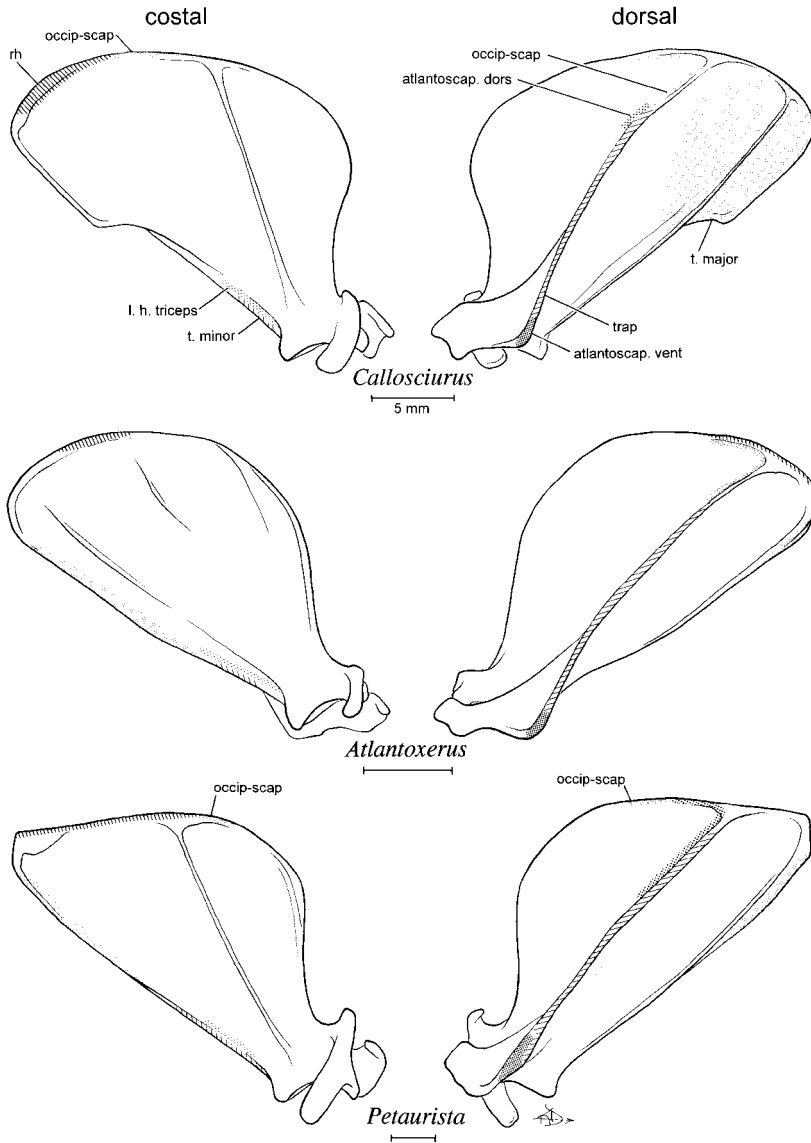


Fig. 3. (Continued.)

other mammals, e.g., *Didelphis* (Stein, '81), and primates (Howell and Straus, '33), the origin is on the transverse process of the atlas. If we use these as out-groups, the basioccipital origin in some rodents would appear to be the most derived, not the primitive condition as suggested by Parsons (1894).

Hill ('37) suggests that the primitive origin is the transverse process of the atlas,

and that this primitive condition is retained in *Heteromys* and *Neotoma*. However, the origin is on the ventral arch, not the transverse process of the atlas, in *Heteromys* (Ryan, '89) and *Neotoma* (Howell, '26; Rinker, '54), thus destroying Hill's ('37) hypothesis. Woods ('72) argues that the origin from the ventral arch of the atlas is the primitive morphology for rodents, as seen in hystricomorphs and sciurids.

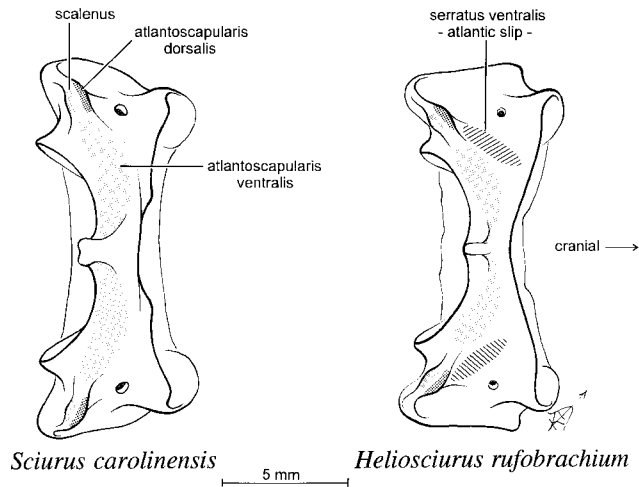


Fig. 4. Ventral surface of the atlas of *Sciurus carolinensis* and *Heliosciurus rufobrachium* illustrating the origin of an atlantic slip of serratus ventralis in *Heliosciurus*.

In *S. carolinensis*, as in most squirrel genera, serratus ventralis does not have an origin on the atlas. Scale bar = 5 mm.

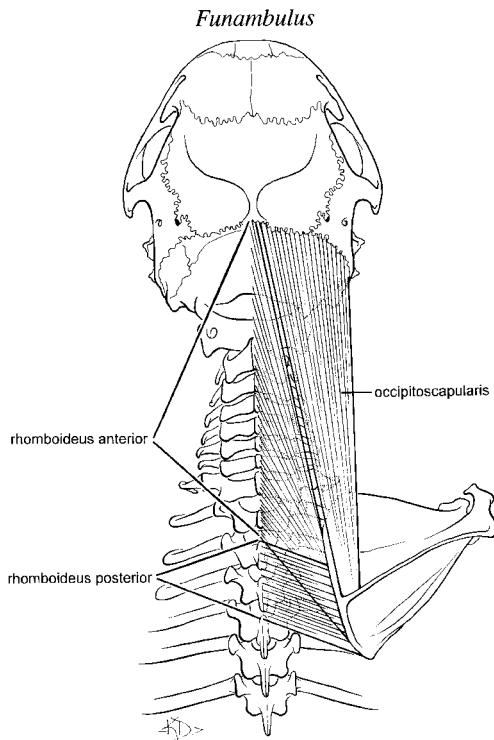


Fig. 5. Dorsal view of occipitoscapularis and rhomboid musculature of *Funambulus*, showing the two parts of rhomboid with rhomboideus posterior overlapping rhomboideus anterior.

This muscle inserts on the metacromion of all squirrels, most muroids, and most hystricomorphs. In the dipodoid rodents, it inserts mostly on the acromion (Klingener, '64). In the geomyids and *Ctenomys*, the burrowing hystricomorph, the insertion is on the clavicle (Hill, '37). There is a similar disagreement about which insertion is primitive for rodents. Hill ('37) argues that it is the acromion and Woods ('72) argues that it is the metacromion.

M. atlantoscapularis dorsalis

Origin (Fig. 4): Arises from the ventral arch of the atlas, lateral to atlantoscapularis ventralis. Atlantoscapularis dorsalis is absent in *Xerus*, *Atlantoxerus*, and *Myosciurus*, and is very thin and narrow in *Nannosciurus*.

Insertion (Fig. 3): Inserts on the scapular spine adjacent to the insertion of occipitoscapularis. The insertion is overlapped partially by the insertion of occipitoscapularis in *Glaucmys*, *Funambulus*, and *Spermophilus columbianus*. In some flying squirrels (*Belomys*, *Eoglaucmys*, *Petaurista*, and *Pteromys*), where the insertion of occipitoscapularis is restricted to the vertebral border of the scapula, the insertion of atlantoscapularis dorsalis extends from the scapular spine onto the vertebral border. The insertions of atlantoscapularis dorsalis and occipitoscapularis are inseparable in *Spermophi-*

lus variegatus, *Ratufa*, *Paraxerus*, *Funisciurus*, and *Heliosciurus*.

Remarks: This muscle is reported absent in *Aplodontia* (Hill, '37; Lewis, '49), four subgenera of *Spermophilus* (Bryant, '45), the dipodoids (Klingener, '64), the muroids (Rinker, '54), and four genera of hystricomorphs (Woods, '72). Bryant reported the muscle absent in the subgenus *Spermophilus* based on his examination of *S. beldingi*. We found it present in two other species of this subgenus, *S. columbianus* and *S. richardsonii*. There appears to be a tendency for it to be lost in burrowing rodents as well as in pygmy squirrels.

There are two hypotheses about the derivation of this muscle. Howell ('37) suggested that it was derived from the serratus sheet, because of its origin on the atlas. Woods ('72) argued that it was derived from the rhomboid sheet via the occipitoscapularis because the two are closely associated at their insertions and because in *Thryonomys* their origins are also adjacent. He submitted that Howell's hypothesis was falsified by the co-occurrence of atlantic slips of both the serratus sheet and the atlantoscapularis dorsalis in the same animal, such as we observed in *Heliosciurus*. However, this is not fatal to Howell's argument if one accepts the possibility of a doubling of the atlantic slip of the serratus sheet. Atlantoscapularis dorsalis occurs in marsupials (Stein, '81), primates (Howell and Straus, '33), insectivores (Campbell, '39; Reed, '51), and other orders of mammals. Therefore, the condition in *Thryonomys* is probably derived and irrelevant to the origin of this muscle in the Mammalia.

Latissimus-subscapular group

M. latissimus dorsi

Origin: This somewhat variable muscle commonly has a fleshy origin from the spinous process of the posterior six thoracic vertebrae, a fascial origin from the first one or two lumbar vertebrae, and again a fleshy origin from the last four ribs.

Insertion (Fig. 6): Inserts with teres major on the medial surface of the humerus, medial to the deltoid ridge. In *Eoglaucmys* and *Funambulus*, latissimus dorsi has an achselbogen that inserts deep to pectoralis major on the deltoid ridge.

Remarks: Bryant ('45) stated that the insertions of latissimus dorsi and teres major were separate in *Glaucmys*. We did not find this in *Glaucmys* or any other squirrels. In other rodents, the two muscles insert sepa-

rately in *Neotoma* and *Peromyscus* (Rinker, '54), and *Phodopus* (Stein, '90). An achselbogen is less common in squirrels than in hystricomorphs, in which it has been carefully described and discussed (Woods, '72).

M. teres major

Origin (Fig. 3): Arises from the axillary edge of the scapula, ventral to the caudal angle, and sometimes from the caudal surface of the axillary border and the adjoining surface of subscapularis. Its origin extends one- to two-thirds of the length of the axillary edge. In tree squirrels, there is a distinct teres fossa on the axillary border of scapula for the origin of this muscle. In *Callosciurus* and *Funambulus*, teres major originates partially from infraspinatus as well.

Insertion (Fig. 6): Inserts with latissimus dorsi on the medial surface of humerus, medial to the deltoid ridge.

Remarks: In the Sciuridae, a prominent teres major fossa is characteristic of tree squirrels and is absent from the marmotine and xerine ground squirrels. In contrast, Lehmann ('63) noted a prominent teres major fossa in the burrowing rodents *Geomys* and *Ctenomys* which was lacking in the non-fossorial rodents she studied.

M. subscapularis

Origin: Arises from the subscapular fossa, except for its vertebral edge.

Insertion: Inserts on the lesser tuberosity of the humerus.

Remarks: The internal structure and subdivision of this muscle (Lehmann, '63) were not studied.

Deltoid group

M. deltoideus

Divisible into three parts: the clavodeltoid, the acromiodeltoid, and the spinodeltoid.

Origin (Fig. 2.): Clavodeltoid takes origin from the caudoventral surface of the clavicle over the lateral two-thirds of its length. It extends further medially in *Heliosciurus*, *Eoglaucmys*, and *Glaucmys*. It is always separable from acromiodeltoid, although their origins closely approximate one another in most genera. The origins are most separated in *Atlantoxerus* and *Glaucmys*. In *Spermophilus*, the most superficial fibers form a separate M. clavobrachialis, which arises from the clavicle, superficial to the clavodeltoid.

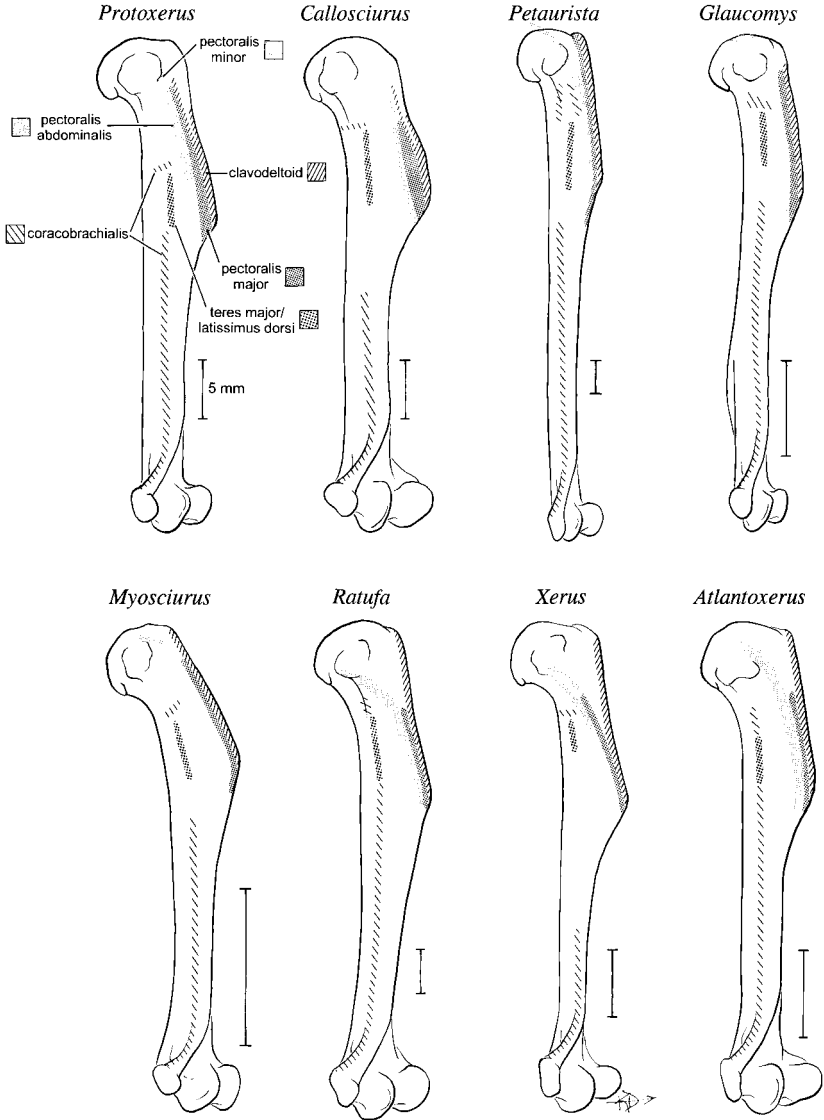


Fig. 6. Medial surface of the humerus for eight squirrel genera, showing insertions of seven muscles. Scale bar = 5 mm.

The acromiodeltoid arises from the acromion, lateral to the insertion of atlantoscapularis ventralis.

Spinodeltoid takes origin from the ventral half of the scapular spine to the vicinity of the metacromion. In *Atlantoxerus*, *Xerus*, *Callosciurus*, *Funambulus*, *Myosciurus*, *Eoglaucomys*, and *Glaucomys*, it also originates slightly from the surface of the infraspinatus. In *Myosciurus* and *Nannosciurus*,

the origin extends nearly to the vertebral border of the scapula.

Insertion (Figs. 6, 7): Clavodeltoid inserts along the distal three-fourths of the medial side of the deltoid ridge of the humerus. In *Petaurista*, *Atlantoxerus*, *Myosciurus*, *Ratufa*, and *Funambulus*, the insertion of clavodeltoid extends to the proximal end of the humerus. In all genera except *Atlantoxerus*, spinodeltoid fuses with acromiodel-

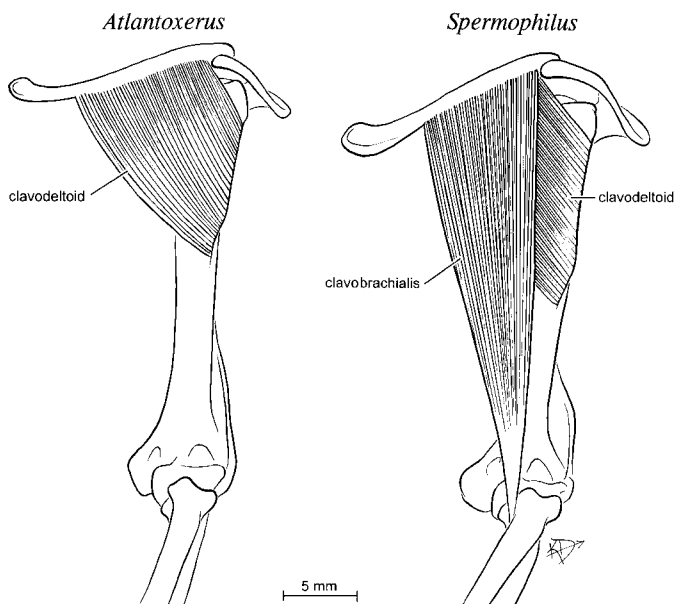


Fig. 7. Deltoid musculature of *Atlantoxerus* and *Spermophilus*, showing the special clavobrachialis, found in the marmotine ground squirrels *Spermophilus*, *Cynomys*, and *Marmota*, but not in the African xerine ground squirrels *Atlantoxerus* and *Xerus*. Scale bar = 5 mm.

toid, which then inserts on the lateral side of the deltoid ridge. In *Atlantoxerus*, the spinodeltoid inserts tendinously, separate from the acromiodeltoid. In *Myosciurus*, *Petaurista*, and *Funambulus*, this insertion extends to the top of the humerus. In most genera, the insertion of acromiodeltoid is relatively thin, but in *Atlantoxerus*, *Petaurista*, *Eoglaucmys*, *Glaucmys*, and *Ratufa*, the insertion is thick. In *Spermophilus*, the clavobrachialis inserts with brachialis on the proximal end of the ulna.

Remarks: In squirrels, a clavobrachialis, innervated by the axillary nerve, occurs in *Spermophilus*, *Cynomys*, and *Marmota*, but is absent in other members of this tribe: *Ammospermophilus*, *Tamias*, and *Sciurotamias* (Parsons, 1894; Brizzee, '41; Bryant, '45). In the hystricomorphs *Cavia* and *Dasyprocta*, the clavodeltoid inserts distally on the humerus, but this is very different from the clavobrachialis of *Spermophilus*, which crosses the elbow joint and inserts on the ulna.

M. teres minor

Origin (Fig. 3): Arises from the axillary surface of the scapula adjacent to the glenoid process, superficial to the origin of the long head of triceps. In most genera, the

origin of the long head of triceps extends further from the glenoid than does the origin of the teres minor. The opposite is true in *Spermophilus columbianus*, in the flying squirrels *Glaucmys* and *Belomys*, and especially in *Petaurista*.

Insertion: Inserts on the distal surface of greater tuberosity of the humerus, distal to the insertion of the infraspinatus muscle. In *Ratufa*, and to a greater degree in *Petaurista*, the insertion is elongated, rather than circular.

Remarks: In many squirrels this muscle is minuscule and therefore is not easily differentiated from the infraspinatus.

Suprascapular group

M. infraspinatus

Origin: Arises from the infraspinous fossa of the scapula.

Insertion: Inserts on the greater tuberosity of the humerus, between the insertions of supraspinatus and teres minor.

Remarks: Differences in the relative sizes of the infraspinatus and supraspinatus muscles and their fossae vary among genera, but this variation is better studied in a series of scapulae than in dissections (e.g., Swidersky, '93).

M. supraspinatus

Origin: Arises from the supraspinous fossa of the scapula.

Insertion: Inserts on the greater tuberosity of the humerus, proximal to the insertion of infraspinatus.

*Triceps group***M. triceps brachii**

Origin (Fig. 3): The long head arises from the axillary border of the scapula adjacent to the glenoid fossa, deep to the origin of teres minor. In *Funambulus*, the origin of the long head has shifted away from the glenoid.

In most squirrels, the lateral head arises aponeurotically distal to the insertion of teres minor, along the lateral surface of the deltoid ridge, adjacent to the insertion of deltoid. It extends distally to the crest of the deltoid ridge in *Myosciurus*, *Protoxerus*, *Heliosciurus*, and *Funambulus*, while in *Funisciurus* and *Ratufa*, the origin barely extends to the deltoid ridge. The condition in the other genera is intermediate. In some flying squirrels (*Belomys*, *Eoglaucomys*, and *Pteromys*), the lateral head has a fleshy origin distal to the insertion of teres minor. This contrasts with the strictly tendinous origin in *Glaucomys* and *Hylopetes*. In *Petaurista*, the fleshy origin covers a larger area on the lateral surface of the humerus and extends onto the proximal third of the posterior surface of the humerus.

In most squirrels, the medial head of triceps arises extensively from the posterior surface of the humerus, from a point between the head and the lesser tuberosity to a point only slightly proximal to the medial epicondyle. In *Petaurista*, the origin of the medial head is restricted to the distal two-thirds of the humerus. In *Funambulus*, the medial head is divided into superficial and deep parts by the radial nerve.

Insertion (Figs. 8, 9): The long head and the medial head insert on the distal tip of the olecranon. The lateral head inserts on the olecranon with the long head, and along the lateral surface of the ulna to a point slightly distal to the semilunar notch. In *Petaurista*, the insertion of the lateral head is restricted to the distal end of the olecranon process.

Remarks: The separation of the medial head into superficial and deep parts is rare in squirrels, but is seen in nine genera of hystricomorph rodents (Woods, '72). A tendi-

nous or aponeurotic origin of the lateral head, common in squirrels, is found in most other rodents, also.

M. anconeus

Origin: Arises from the posterior surface of the lateral epicondylar ridge of the humerus.

Insertion (Fig. 9): Inserts on the lateral surface of the olecranon process of the ulna and extends distal to the semilunar notch.

Remarks: The most distal fibers pass on the flexor side of the elbow joint when the arm is flexed. Only when the elbow is partly extended could they act to further extend the arm.

M. dorsoepitrochlearis

Origin: Arises from both teres major and latissimus dorsi near their common insertion on the humerus.

Insertion (Fig. 10): Inserts on the medial side of the proximal end of the ulna. In *Atlantoxerus* and *Xerus*, the dorsoepitrochlearis inserts on the dense connective tissue on the medial side of the elbow, overlying flexor carpi ulnaris. In *Protoxerus*, there is an additional insertion on the superficial surface of anconeus.

Remarks: The usual origin of this muscle in squirrels is from both teres major and latissimus dorsi. Bryant ('45) reports an origin, in some species of *Spermophilus*, from the teres major and the scapula, but not from latissimus dorsi. In contrast, the muscle takes origin almost exclusively from the latissimus dorsi in hystricomorphs (Woods, '72). Howell ('37) and Cheng ('55) consider this muscle to be derived from the latissimus dorsi, in spite of its innervation by the radial nerve. Therefore, Woods ('72) suggests that the origin from the latissimus dorsi is primitive. Origin from the teres major is commonly found in other rodents as well as squirrels.

*Extensor group of the forearm***M. brachioradialis**

Origin: Arises from the anterior surface of the lateral epicondylar ridge of the humerus, proximal to extensor carpi radialis longus.

Insertion (Fig. 9): Inserts tendinously on the distal end of the radius. In *Petaurista*, the tendinous insertion is elongated over the distal one-third of the radius. In *Ratufa in-*

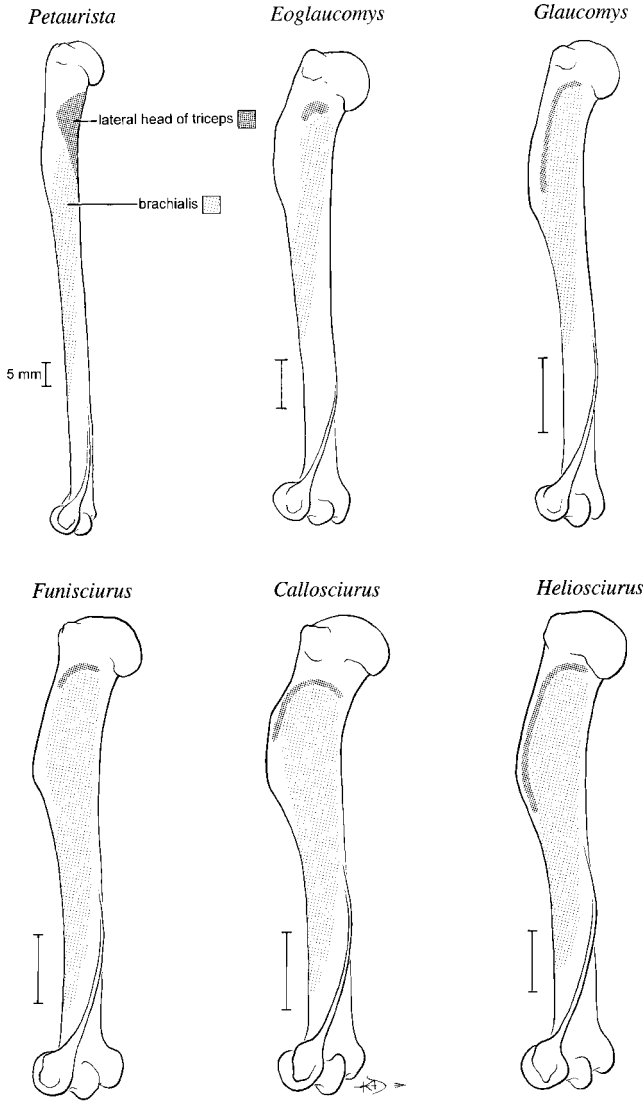


Fig. 8. Lateral view of the humerus for six genera of squirrels, demonstrating the variation in the origin of the lateral head of triceps. Scale bar = 5 mm.

dica, but not in other species of *Ratufa*, the insertion is fleshy, rather than tendinous, and extends over the distal one-fourth of the radius.

Remarks: Although universally present in squirrels, this muscle is commonly lost in other rodents. It is absent in *Aplodontia* (Hill, '37; Lewis, '49), all hystricomorphs except *Erethizon* and *Coendou* (Woods, '72;

McEvoy, '82), *Castor* (Parsons, 1894), geomyids (Hill, '37), and some muroids (Rinker, '54).

M. extensor carpi radialis longus

Origin (Fig. 9): Arises from the anterior surface of the lateral epicondylar ridge of the humerus, between brachioradialis and extensor carpi radialis brevis.

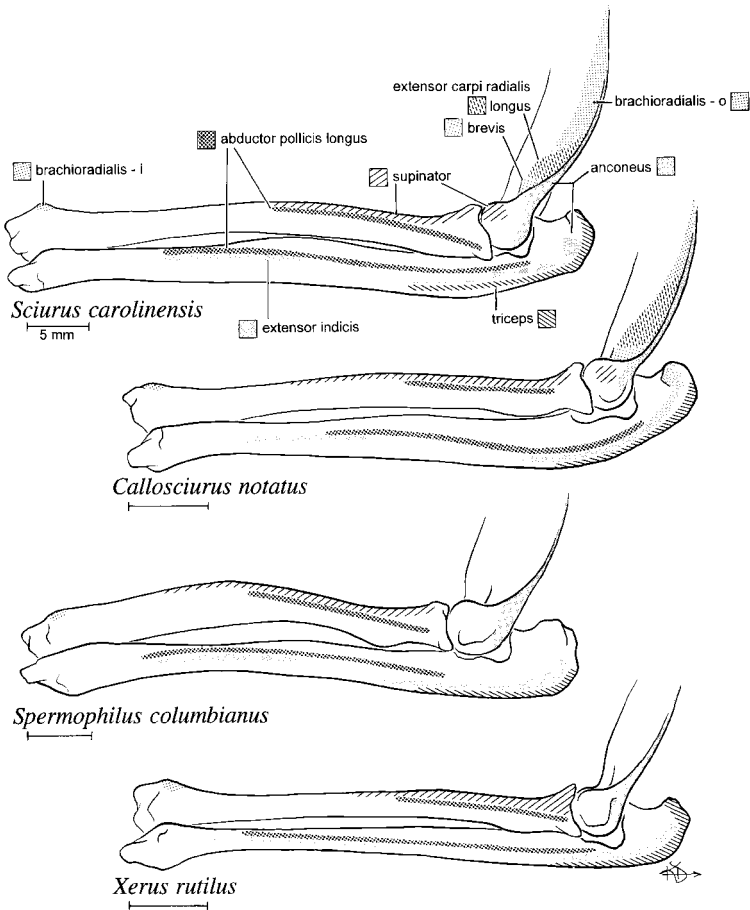


Fig. 9. Extensor surface of the forearm (radius, ulna, and distal end of humerus) of ten genera of squirrels, showing the origins of seven muscles and the insertions of brachioradialis, supinator, anconeus, and triceps. Scale bar = 5 mm.

Insertion: Inserts on the proximal end of the second metacarpal.

Remarks: In sciurids, this is always larger than extensor carpi radialis brevis. In the hystricomorphs *Myocastor* and *Thryonomys*, geomyids, and others, the reverse is true (Hill, '37; Woods, '72).

M. extensor carpi radialis brevis

Origin (Fig. 9): Arises from the anterior surface of the lateral epicondylar ridge of the humerus, distal to extensor carpi radialis longus.

Insertion: Inserts on the proximal end of the third metacarpal.

M. supinator

Origin (Fig. 9): Arises from the anterior portion of the lateral epicondyle of the humerus.

Insertion (Fig. 9): Inserts on the lateral surface of the proximal half of the radius. At its proximal end, the insertion also wraps around to the medial surface of the radius. In *Callosciurus* and *Spermophilus*, supinator inserts on more than half the length of the radial shaft.

Remarks: In squirrels, a sesamoid bone does not occur in the tendon of origin of the supinator. Such a sesamoid is found in other rodents: geomyids (Hill, '37), cricetines

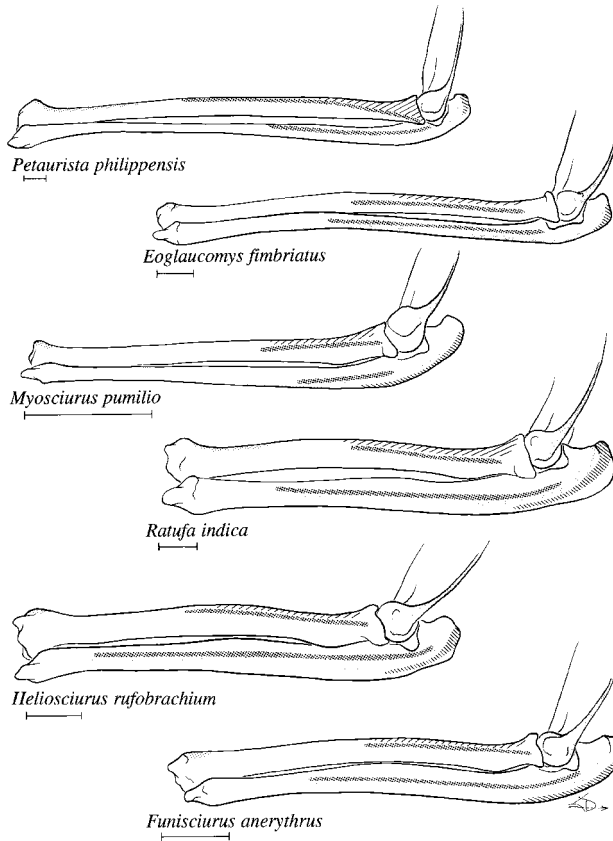


Fig. 9. (Continued.)

(Rinker, '54), and microtines (Stein, '86), but not in dipodoids (Stein, '90).

M. abductor pollicis longus

Origin (Fig. 9): Arises linearly from the lateral surface of the ulna, from the lateral surface of the radius, and from the interosseous membrane. The ulnar origin begins near the elbow joint and continues distally two-thirds of the way down the shaft. The radial origin begins at the radial head and extends distally halfway down the shaft. In all genera except for *Myosciurus*, *Petaurista*, *Glaucomys*, and *Atlantoxerus*, the ulnar origin is much longer than the radial origin.

Insertion: Inserts via a bifurcated tendon on the radial side of the first metacarpal and on the falciform. In *Ratufa* and *Funambulus*, there is only one broad tendon, which inserts across the two bones.

Remarks: In sciurids, the tendon varies from a single broad insertion on both the first metacarpal and the falciform to a distinctly bifurcated tendon. Bryant ('45) reported the absence of the insertion on the falciform in *Sciurus*, *Tamiasciurus*, and *Glaucomys*. We observed a falciform insertion in all specimens we dissected. In flying squirrels, the falciform is connected by a ligament to the styloform cartilage by means of which the abductor has the important function of extending the wingtip (Thorington et al., in press). Therefore, reports of the absence of a falciform insertion in flying squirrels should be viewed as dubious.

In seven genera of hystricomorphs, the muscle is described as having two distinct tendons. In dipodoids and some muroids, Rinker ('54) and Klingener ('64) considered it to be two separate muscles, using the

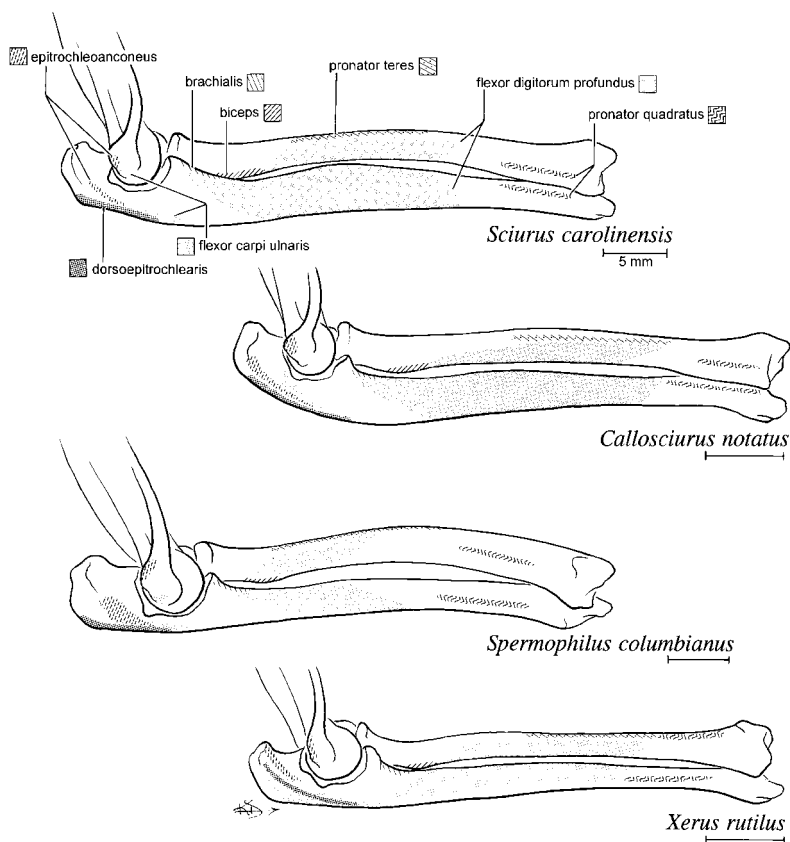


Fig. 10. Flexor surface of the forearm (radius, ulna, and distal end of humerus) of ten genera of squirrels, showing the origins of epitrochleo-anconeus, flexor carpi ulnaris, flexor digitorum profundus, and pronator quadra-

tus, and the insertions of epitrochleo-anconeus, dorsoepitrochlearis, brachialis, biceps, pronator teres, and pronator quadratus. Scale bar = 5 mm.

name *M. extensor pollicis brevis* for the part that inserted on the falciform. Woods ('72) argued that it was not the extensor, but rather a subdivided abductor. The difference between the two hypotheses is moot, because the extensor pollicis brevis is a derived feature in primates, found in *Homo* and *Gorilla* (Howell and Straus, '33). Therefore, the subdivision of the abductor pollicis in rodents, no matter what it is called, is independent of the evolution of the extensor pollicis brevis in primates.

M. extensor digitorum communis

Origin: Arises from the proximal surface of the lateral epicondyle of the humerus.

Insertion: Inserts on digits 2-5. In *Xerus*, *Atlantoxerus*, *Ratufa*, *Sciurus*, *Callosciurus*, *Funisciurus*, and *Spermophilus*, there are

two tendons to digit 3. In *Eoglaucmys*, the tendon to digit 2 arises from a separate head of the muscle.

M. extensor indicis

Origin (Fig. 9): Arises from the lateral surface of the ulna toward the distal end of the bone. The origin is distal to the origin of abductor pollicis longus in all genera except *Atlantoxerus*, *Sciurus*, and *Spermophilus columbianus*.

Insertion: Inserts on digit 2. In *Ratufa*, *Protoxerus*, *Heliosciurus*, *Callosciurus*, *Paraxerus*, *Funisciurus*, and *Spermophilus columbianus*, there was an additional insertion on digit 1.

Remarks: The insertion on the pollex was not observed by Hill ('37) or Bryant ('45) in nearctic sciurids, but it was present in speci-

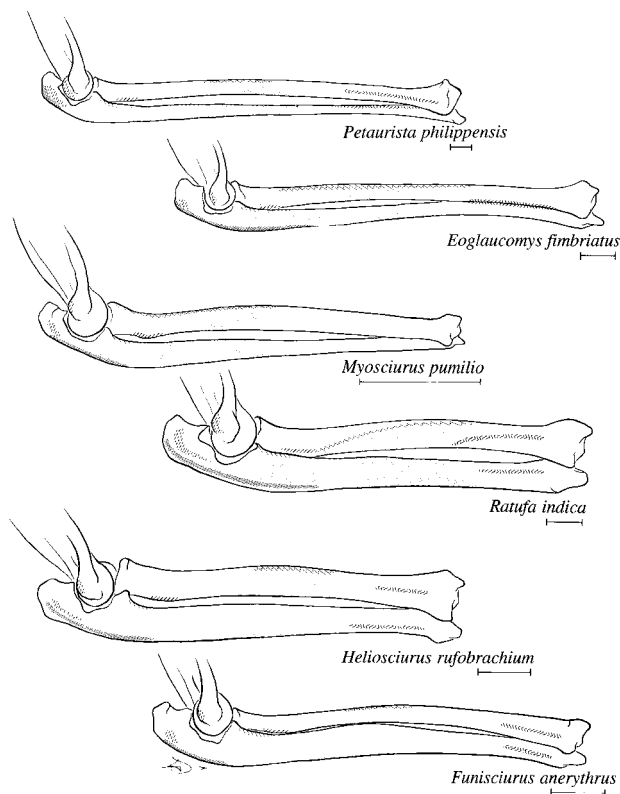


Fig. 10. (Continued)

mens of *Sciurus carolinensis* dissected by Woods ('72). Our dissections demonstrate that it is common in sciurids as a bifurcation of the tendon to the index finger. Woods ('72) found it in ten genera of hystricomorphs, and in one of these, *Mesomys*, there was a completely separate tendon to the pollex. Hill ('37) suggested that the extensor pollicis brevis has been incorporated into the extensor indicis, but this interpretation assumes that the extensor pollicis brevis of humans is primitive for rodents, which it surely is not.

M. extensor digiti quinti proprius

Origin: Arises from the lateral epicondyle of the humerus and is inseparable from the origin of the extensor digitorum communis, except in *Spermophilus columbianus*.

Insertion: Inserts on digits 3-5. In *Xerus*, *Atlantoxerus*, *Ratufa*, *Sciurus*, *Callosciurus*, *Heliosciurus*, and *Spermophilus*, the insertion is restricted to digits 4 and 5. In *Ratufa* and *Eoglaucmys*, the muscle belly that in-

serts on digits 3 and 4 is completely separate from the belly that inserts on digit 5.

Remarks: The frequent insertion of this muscle into digit 3 suggests that the extensor digiti tertii has been incorporated into the extensor digiti quinti, as suggested by Klingener ('64).

M. extensor carpi ulnaris

Origin: Arises from the distal end of the lateral epicondyle of the humerus.

Insertion: Inserts on the proximal end of the fifth metacarpal.

Flexor system

Pectoral group

M. pectoralis major (ectopectoralis of Hill, '37)

Origin: Arises from the sternebrae, from the manubrium to the xiphisternum in all genera.

Insertion (Fig. 6): Inserts on the deltoid ridge of the humerus, deep to the insertion of clavodeltoid, usually along the distal three-

fourths of the ridge. In *Petaurista* and *Funambulus*, the insertion of pectoralis major extends to the proximal end of the humerus.

Remarks: The origin of a few fibers from the clavicle was reported in *Tamias* and *Glaucmys* (Bryant, '45) and in *Aplodontia* (Lewis, '49).

M. pectoralis minor

Origin: Takes origin deep to the pectoralis major, commonly from sternebrae 2–5 and the sternal ends of costal cartilages 2–4, and sometimes 5. There is some variation in the extent of the origin. It has shifted slightly caudally in *Heliosciurus*, *Protoxerus*, and *Spermophilus*, in which it did not take origin from sternebra 2 or costal cartilage 2. In *Atlantoxerus*, the origin extended from sternebra 2 to the xiphisternum.

Insertion (Fig. 6): Inserts on the deltoid ridge of the humerus, deep to the insertion of pectoralis major. It extends to the distal end of the pectoralis major insertion in one flying squirrel (*Petaurista*), but not the others; in three tree squirrels (*Ratufa*, *Paraxerus*, and *Callosciurus*), but not the other tree squirrels; and in one ground squirrel (*Atlantoxerus*), but not the others (*Xerus* and *Spermophilus*). The proximal end of the insertion extends to the proximal end of the humerus, distal to the insertion of supraspinatus, in all genera except *Protoxerus*. The insertion continues onto the coracoid process of the scapula in the large flying squirrels, *Petaurista* and *Eoglaucmys*. In *Myosciurus* and *Glaucmys*, the insertion is restricted to the proximal end of the humerus, near the insertion of supraspinatus. The insertion is short and is proximal to and aligned with the insertion of pectoralis major in *Xerus*. In *Callosciurus*, pectoralis minor splits into two slips, the dorsal slip inserting just distal to supraspinatus insertion and the ventral slip inserting further distally on the deltoid ridge.

Remarks: In other rodents, insertion on the coracoid process is common (Parsons, 1896; Rinker, '54). An insertion onto the clavicle, as seen in many hystricomorphs (Woods, '72), was not found in any sciurids.

M. pectoralis abdominalis

Origin: Arises from abdominal fascia, caudal to the xiphisternum. It is most extensive in *Funambulus*. It has a very narrow origin in *Petaurista*.

Insertion (Fig. 6): Inserts on the proximal end of the medial side of the deltoid ridge.

The proximal end of the insertion is most extensive in *Funambulus*, *Petaurista*, and *Eoglaucmys*, where both insert on the proximal end of the humerus; in *Petaurista* and *Eoglaucmys*, the insertion continues onto the coracoid process of the scapula. The insertion does not extend onto the deltoid ridge in *Callosciurus*, *Paraxerus*, *Myosciurus*, and *Funisciurus*. The insertion of pectoralis abdominalis extends onto the deltoid ridge in *Sciurus*, *Protoxerus*, and *Heliosciurus*, and is most extensive in *Atlantoxerus* and *Funambulus*. In *Glaucmys*, the insertion is restricted to the proximal end of the humerus, just distal to the insertion of supraspinatus.

Remarks: We found the insertion to extend further distally on the humerus in some genera than was reported by Bryant ('45) for nearctic sciurids. If the insertion on the shoulder capsule is the primitive condition for rodents (Woods, '72), then the more distal insertion in *Atlantoxerus* and *Funambulus* is derived.

M. entopectoralis profundus

Origin: Arises as a thin membranous sheet from 2 to 4 costal cartilages (between cartilages 2 and 5) and adjoining sternebrae.

Insertion: Inserts on the first rib, lateral to the origin of the subclavius.

M. cutaneus maximus

Origin: Arises from the skin over the thoracic and lumbar regions.

Insertion: Inserts on the shoulder joint (anterior fibers) and further down on the humerus deep to pectoralis major, usually with pectoralis minor, pectoralis abdominalis, and latissimus dorsi. In *Myosciurus*, it inserts independently on the humeral head. In *Petaurista*, cutaneus maximus inserts independently as well, but its insertion extends onto the coracoid of the scapula. In *Eoglaucmys*, cutaneus maximus inserts only on the coracoid process.

Remarks: The derived condition of this muscle in the gliding membrane of flying squirrels was not examined. See Johnson-Murray ('77).

M. subclavius

Origin: Arises from the proximal end of the first costal cartilage.

Insertion (Figs. 2, 11): Inserts on the dorsal surface of the distal half of the clavicle. The insertion of subclavius extends to the

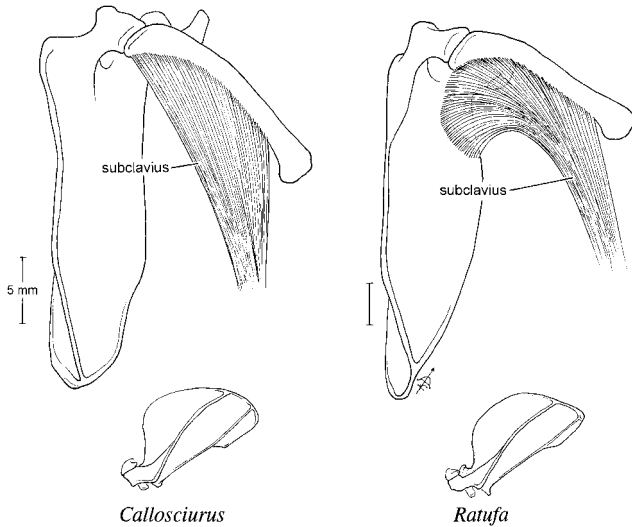


Fig. 11. Cranial view of clavicle and scapula, showing the insertion of subclavius in *Callosciurus*, as it is in most squirrels, and the insertion extending onto the suprascapular muscle of the scapula in *Ratufa*. Scale bar = 5 mm.

distal end of clavicle in most genera. It does not extend quite to the distal end in *Sciurus*, *Heliosciurus*, *Funisciurus*, *Myosciurus*, *Spermophilus*, and *Atlantoxerus*. In *Ratufa*, the insertion extends onto the surface of the suprascapular muscle of the scapula.

Remarks: In hystricomorphs (Woods, '72), bathyergids (Parsons, 1896), and other mammals, there is a scapuloclavicularis muscle which originates on the clavicle and inserts on the scapular spine or vertebral border. This is superficially similar to the scapular insertion of subclavius in *Ratufa*, but the origins and insertions are different. Thus, the morphology in *Ratufa* is probably independently derived from the scapuloclavicularis of other rodents.

Flexor group of the arm

M. coracobrachialis

Origin: Arises from the coracoid process.

Insertion (Fig. 6): Short head inserts on the medial surface of the humerus slightly distal to the greater tuberosity. The linear insertion is perpendicular to the insertion of teres major. *Atlantoxerus*, *Glaucomyss*, and *Ratufa* have a more dot-like insertion. In *Petaurista*, the short head has two points of insertion, adjacent to each other. The long head inserts on the distal half of the medial surface of the humerus and on the medial epicondylar ridge. The insertion of coracobra-

chialis begins near the peak of deltoid ridge in *Sciurus*, *Protoxerus*, *Heliosciurus*, *Atlantoxerus*, *Ratufa*, *Petaurista*, *Eoglaucomyss*, *Glaucomyss*, *Spermophilus columbianus*, and *Paraxerus*. In *Myosciurus*, *Callosciurus*, *Xerus*, *Spermophilus variegatus*, *Funambulus*, and *Funisciurus*, the insertion begins distal to the deltoid ridge.

Remarks: The short head has been found in all genera of squirrels studied, in *Aplodontia* and in the geomyids (Hill, '37), heteromyids (Howell, '32), dipodoids (Klingener, '64), and some muroids (Rinker, '54). The distal insertion in sciurids, *Aplodontia* (Hill, '37; Lewis, '49), and most myomorphs (Parsons, 1896) reputedly includes the middle and long heads described by Wood (1867), although it is not clear how to distinguish this condition from an extended middle head.

M. biceps brachii

Origin: The long head originates from the supraglenoid tuberosity. The short head originates from the coracoid process.

Insertion (Fig. 10): Inserts on the bicapital tuberosity on the radius, distal to or slightly overlapping the insertion of brachialis on the ulna. The short head merges into and inserts with the long head.

Remarks: In sciurids, the short head of biceps is usually present, but has been reported absent in *Sciurus vulgaris* (Hoff-

mann and Weyenbergh, 1870) and in *Spermophilus variegatus* and *S. beecheyi* (Bryant, '45). The biceps always inserts on the radius (Parsons, 1894; Alezais, 1900; Hill, '37; Brizze, '41; Bryant, '45). In other rodents, the short head of biceps is absent in some hystricognaths and *Castor* (Parsons, 1894), *Zapus* and *Jaculus* (Klingener, '64), and *Alacraga* (Howell, '32). Insertion on both radius and ulna, or just on ulna, is common (Parsons, 1894; Alezais, 1900; Hill, '37; Rinker, '54; Klingener, '64; Ryan, '89).

M. brachialis

Origin: Arises extensively as a single head from the lateral surface of the humerus distal to the origin of the lateral head of triceps. Distal to the deltoid ridge, the origin extends more medially, adjoining the insertion of the coracobrachialis.

Insertion (Fig. 8): Inserts on the ulna distal to the coronoid process.

Remarks: The recognition of a small medial head of brachialis, seen in other rodents (Parsons, 1894; Hill, '37; Rinker, '54; Klingener, '64; Woods, '72), does not seem warranted for squirrels. Parsons (1894) described the two heads in sciurids as "so closely blended as to be indistinguishable," and Bryant ('45) remarked that brachialis "has two incompletely separated heads."

Flexor group of the forearm

M. epitrochleo-anconeus

Origin (Fig. 10): Arises from the extensor side of the medial epicondyle of the humerus. *Petaurista* has a more extensive origin that includes the epicondylar ridge.

Insertion: Inserts on the medial surface of the olecranon process deep to the dorsoepitrochlearis.

M. flexor carpi ulnaris

Origin (Fig. 10): Arises from the base of the medial epicondyle of the humerus, either on its own or in common with the other forearm flexors, and from the medial surface of the olecranon, deep to the insertion of dorsoepitrochlearis.

Insertion: Inserts on the distal tip of the pisiform bone. In the flying squirrels, flexor carpi ulnaris inserts both on the pisiform and on the styloform cartilage.

Remarks: In squirrels, the epicondylar head is almost always present, but has been reported absent in *Spermophilus* (Parsons, 1894). Gupta ('66) and Johnson-Murray ('77) described two tendons of insertion in flying squirrels, one inserting on the styloform car-

tilage. This latter is the tendon of the palmaris longus (Thorington et al., '97a). In flying squirrels, the flexor carpi ulnaris serves the additional function of retracting the wing tip when the animals are not gliding (Thorington et al., '97a). In other rodents, the epicondylar head is absent in geomyids (Hill, '37), *Oryzomys* (Rinker, '54), dipodoids (Klingener, '64), microtines (Stein, '86), and heteromyids (Ryan, '89).

M. palmaris longus

Origin: Arises from the medial epicondyle of the humerus with flexor digitorum sublimis. It is completely separable from the flexor in *Spermophilus columbianus*, *Callosciurus*, *Funisciurus*, *Paraxerus*, and *Sciurus*.

Insertion: Inserts on the palmar fascia of the hand. In flying squirrels, it also inserts on the styloform cartilage. In *Petaurista*, a broad tendon separates into two parts before inserting on the palmar fascia.

Remarks: In other mammals, this muscle is usually innervated by the median nerve. In sciurids and hystricomorphs, it is innervated by the ulnar nerve (Woods, '72).

M. flexor carpi radialis

Origin: Arises from the medial epicondyle of the humerus, distal to the origin of pronator teres, either separately or with the other flexor muscles. It is completely separate in *Spermophilus columbianus*, *Heliosciurus*, *Paraxerus*, *Callosciurus*, and *Funisciurus*.

Insertion: Inserts on the base of the second metacarpal.

M. pronator teres

Origin: Arises from the proximal portion of medial epicondyle of the humerus, separate from the other forearm flexors in all genera except *Eoglaucomyis*.

Insertion (Fig. 10): Inserts on the medial surface of the radius, over approximately the middle third of the bone. Pronator teres inserts more distally in *Eoglaucomyis*, *Callosciurus*, and *Xerus*. The length of the insertion varies. *Spermophilus*, *Ratufa*, *Funambulus*, *Sciurus*, *Protoxerus*, *Eoglaucomyis*, and *Glaucomyis* have relatively long insertions, but the insertion is relatively short in the other genera. In *Glaucomyis* and *Ratufa*, the proximal portion of the insertion curves medially toward the insertion of biceps.

M. flexor digitorum sublimis

Origin: Arises from the medial epicondyle of the humerus, between the condyloradial and central heads of flexor digitorum profun-

muscle, either separately or in common with the other forearm flexors. It arises separately in *Spermophilus columbianus*, *Callosciurus*, *Paraxerus*, and *Funisciurus*.

Insertion: Inserts on digits 2–5. The tendon to each digit is perforated by the corresponding tendon of the flexor digitorum profundus. It divides over the distal end of the metacarpal and reunites deep to the profundus tendon over the first phalanx. Each inserts as a single broad tendon on the palmar surface of the base of the second phalanx.

Remarks: Contrary to the normal innervation by the median nerve in other mammals, this muscle is commonly innervated by the ulnar nerve in squirrels. We found only ulnar innervation in *Xerus*, *Protoxerus*, *Ratufa*, and *Petaurista*, and Woods ('72) found it in *Sciurus* and *Eutamias*. We found only median innervation in *Funisciurus* and *Glaucomys* and in two specimens of *Callosciurus*. We found both median and ulnar innervation in one specimen of *Callosciurus*. Thus ulnar innervation of the flexor digitorum sublimis has been observed in both subfamilies and five of the seven tribes of the Sciurinae, and median innervation in flying squirrels and two tribes of the Sciurinae. The insertion of this muscle is commonly restricted to digits 2–4 in other rodents (Parsons, 1894; Rinker, '54; Klingener, '64; Stein, '86; Ryan, '89).

M. flexor digitorum profundus

Origin: Arises by four heads. The condylo-radial head arises from the posterior portion of the medial epicondyle of the humerus, anterior to the origin of epitrochleo-aneoneus. The central head arises from the anterior portion of the medial epicondyle, deep to the other forearm flexors. These two heads arise separately in *Spermophilus columbianus*, *Paraxerus*, *Funisciurus*, and *Callosciurus*. Only the central head is separate in *Sciurus*. In other genera, these arise in common with the other forearm flexors. The radial head arises from the medial surface of the radius, deep to the insertion of pronator teres. The ulnar head arises from the medial surface of the ulna, deep to the origin of flexor carpi ulnaris.

Insertion: All four heads converge to a single tendon in the carpal tunnel and diverge into four tendons at the level of the metacarpals. These tendons insert on the terminal phalanges of digits 2 through 5. The tendon to digit 2 commonly bifurcates and sends a branch to digit 1. This tendon to

digit 1 was absent in *Myosciurus*, *Sciurus*, *Callosciurus*, and *Petaurista*.

Remarks: The innervation of this muscle is also variable. Innervation of the ulnar head by the ulnar nerve, and the other heads by the median nerve, is probably most common, as in other rodents (Hill, '37), but we observed innervation of the two condylar heads by both median and ulnar nerves in two specimens of *Glaucomys*, and of the condyloradial head in *Funisciurus*.

The tendon to digit 1 was not found by Parsons (1894) in *Callosciurus* or *Pteromys*, and by Alezais (1900) in *Marmota*. It was found in *Sciurus* by Alezais (1900). Bryant ('45) found it in all of his specimens, including *Sciurus* and *Marmota*.

M. pronator quadratus

Origin (Fig. 10): Arises from the medial surface of the ulna near its distal end.

Insertion (Fig. 10): Inserts on the medial surface of the radius near its distal end. In *Callosciurus*, *Spermophilus*, *Paraxerus*, *Sciurus*, *Atlantoxerus*, and *Xerus*, the origin is more extensive than the insertion.

Remarks: This muscle is absent in the pygmy squirrels *Nannosciurus* and *Myosciurus* and in the smaller flying squirrels *Glaucomys*, *Pteromys*, and *Hylopetes*. In the larger flying squirrels *Petaurista*, *Eupetaurus*, *Eoglaucomys*, and *Belomys*, it is a narrow, thin, interosseous muscle, in contrast to the robust pronator quadratus of tree and ground squirrels.

Miscellaneous muscles

M. omohyoid

Origin: Arises from the ventral portion of the cranial border of the scapula, in the cranial notch.

Insertion: Inserts on the hyoid.

Lateral retractor of pouch

We found this muscle present in *Spermophilus* and *Sciurotamias*.

Origin: Arises from the metacromion of the scapula, between the insertion of trapezius and atlantoscapularis ventralis and the origin of spinodeltoid.

Insertion: Inserts on the cheek pouch in *Spermophilus* and *Sciurotamias*. There is a similar muscle taking origin on the scapula and inserting on the cheek in *Heliosciurus*, *Callosciurus*, and *Funambululus*, although these squirrels lack cheek pouches.

Remarks: Bryant ('45) found this muscle in *Spermophilus*, *Cynomys*, *Ammospermophilus*, and *Tamias*, but not in *Marmota*.

The lateral retractor of the cheek pouch in squirrels is formed of facial musculature. In hamsters, it is derived from the auricular slip of the trapezius muscle. In geomyids and heteromyids, both facial musculature and trapezius muscle contribute to the lateral retractor (Hill, '35; Priddy and Brodie, '48; Klingener, '64, '70). The presence of an auricular portion of trapezius in *Marmota* and *Xerus* suggests that another form of cheek retractor could readily have evolved in sciurids.

DISCUSSION

Our goal in this study was to locate derived myological features of phylogenetic or functional significance. Forelimb musculature alone is an inadequate base for a phylogenetic analysis, but it is clear that some of the myological differences we describe have important phylogenetic implications. An adequate understanding of how muscles function during locomotion requires a great deal of information not currently available for squirrels. These include differences in muscle masses, distributions of slow and fast twitch muscle fibers, differences in recruitment patterns, etc. (Jenkins and Weijs, '79; Armstrong, '81; Fleagle, '82; Stalheim-Smith, '84; Larson, '93). However, even if we had all of this information for squirrels, it would be difficult to interpret it in view of the diverse locomotor behaviors of these animals, which include walking, bounding on horizontal to vertical surfaces, digging, leaping, gliding, landing, and head-first descent of vertical surfaces. Nonetheless, comparative anatomy provides data for initial hypotheses about the functional differences between animals, and it seems appropriate to speculate on the biological significance of the data presented.

The 19 genera of squirrels we selected for morphological comparison are geographically and ecologically diverse. The two genera of pygmy tree squirrels, *Myosciurus* of Africa and *Nannosciurus* of Southeast Asia, occupy the bark gleaner niche (Emmons, '80). *Atlantoxerus* and *Xerus* are genera of African ground squirrels. Like many of the North American ground squirrels, *Spermophilus*, they live in burrows, but also climb readily (Herzig-Straschil, '78; Herzig-Straschil and Herzig, '89; O'Shea, '91). The two tribes of African tree squirrels are represented by the highly arboreal *Protoxerus* and *Heliosciurus*, and by the less arboreal members of the genera *Funisciurus* and *Paraxerus* (Kingdon, '74; Emmons, '80). *Funambulus*, the Indian striped squirrels, are

traditionally, but probably incorrectly, allocated to the same tribe as the African squirrels *Funisciurus*, *Paraxerus*, and *Myosciurus*. Like chipmunks, they are active both on the ground and in trees. *Ratufa*, the giant tree squirrels of Southeast Asia, are highly arboreal and seldom come to the ground (MacKinnon, '78; Payne, '80; Thorington and Cifelli, '90). *Callosciurus*, also of Southeast Asia, are usually highly arboreal, but the species we studied, *C. notatus*, frequently comes to the ground like North American tree squirrels of the genus *Sciurus* (MacKinnon, '78; Payne, '80). The six genera of flying squirrels we dissected include *Petaurista*, the giant flying squirrels of Southern Asia; *Eoglaucomys*, the large Himalayan flying squirrels; *Belomys* and *Hylotropes*, smaller flying squirrels of Southern Asia; *Pteromys*, the northern flying squirrels of Eurasia; and *Glaucomys*, the North American flying squirrels. In addition, we examined a few muscles in a forearm of the large woolly flying squirrel, *Eupetaurus cinereus*, and one specimen of the Chinese rock squirrel, *Sciurotamias davidianus*.

Arboreality is presumed to be primitive for the Sciuridae because the earliest fossil squirrel, *Douglassia jeffersoni*, has so many features of an arboreal squirrel (Emry and Thorington, '82). Accordingly, it is likely that the forelimb anatomy of tree squirrels is primitive for the family. The similarity of musculature among tree squirrels in five tribes of the Sciurinae is in keeping with this assumption. Only in the Ratuini is there a noteworthy derived myological feature, the insertion of the subclavius on the supraspinatus muscle in addition to the insertion on the clavicle (Fig. 11). This muscle stabilizes the distal end of the clavicle, which serves as a strut for positioning the shoulder joint. The extended insertion of the subclavius presumably strengthens this role. The division of the rhomboid (Figs. 1, 3, 5) into anterior and posterior sections occurs in *Funambulus* and *Heliosciurus gambianus*, which are not closely related to one another. Functional reasons for this morphology are unclear. There are other differences among the tree squirrels in the relative positions of origins and insertions of muscles, but these are subtle and do not distinguish any of the tribes from each other. The scansorial and arboreal locomotion of tree squirrels in all five tribes is accomplished with the same basic arrangement of forelimb muscles. One feature shared by all tree squirrels, but not by other sciurids, is a well-developed teres

major fossa at the posterior angle of the scapula (Fig. 3). The teres major functions in retroflexion of the shoulder—decreasing the angle between the humerus and the axillary border of the scapula. In terrestrial locomotion, retroflexion occurs during the support phase as the forelimb is retracted, but the weight of the animal probably contributes to this movement and little force is required by the teres major. In a climbing animal, however, gravity works against retroflexion and the teres major must overcome it (Jenkins and Weijjs, '79). This may explain why tree squirrels have the enlarged fossa and why Stalheim-Smith ('84) found that the tree squirrel *Sciurus niger* has a much stronger teres major than does the prairie dog *Cynomys gunnisoni*.

Pygmy tree squirrels are bark gleaners and forage on large tree trunks with their limbs placed far more laterally than is seen in larger tree squirrels. The limbs are elongated, particularly the forearm, and the thumb is reduced or absent (Anthony and Tate, '35; Emmons, '79; Thorington and Thorington, '89). The atlantoscaphularis dorsalis (Fig. 3) is lost in *Myosciurus* and is greatly reduced in *Nannosciurus*. This muscle functions to rotate the scapula during retraction of the limb, but it may be in a poor position to effect this when the limbs are held laterally. The spinodeltoid is extensive in pygmy squirrels and probably plays a major role in retroflexion of the shoulder joint. Pronator quadratus (Fig. 10) is lost in these two animals, correlating with the elongation of the forearm and presumably with a reduction in the amount of pronation and supination at the wrist.

Terrestrial locomotion takes several forms within the Sciurinae. Cursorial terrestrial squirrels (*Rheithrosciurus* and *Epixerus*) and the terrestrial Asiatic squirrel *Rhinosciurus* were not included in this study because of the unavailability of specimens. The two tribes of burrowing ground squirrels, Xerini and Marmotini, were included. These animals both climb less and dig more than do tree squirrels. A distinctive derived muscle in the Marmotini is the superficial layer of the clavodeltoid, which inserts on the ulna and forms a clavobrachialis (Fig. 7). This is found only in some genera (*Marmota*, *Spermophilus*, and *Cynomys*) forming a single clade of the Marmotini (Bryant, '45), and is absent in others (*Tamias*, *Sciurotamias*, and *Ammospermophilus*). This muscle has a completely different function from the rest of the

deltoid, to flex the elbow in support of the normal function of the brachialis. These muscles flex the elbow without causing supination of the forearm, in contrast with the biceps, which causes both flexion and supination. In comparing *Sciurus* and *Cynomys*, Stalheim-Smith ('84) noted that the biceps of *Sciurus* generated more than twice the torque as that of *Cynomys*. Tree climbing probably requires both strong elbow flexion and forearm supination, while digging may require flexion without supination. The atlantoscaphularis dorsalis is lost repeatedly in the xerine ground squirrels, and in four subgenera of the marmotine genus *Spermophilus*. It is not clear to us why this muscle would be lost in burrowing squirrels. It would appear to function as a rotator of the scapula, a movement that may be more effectively accomplished by the occipitoscaphularis in these animals.

Flying squirrels exhibit a number of derived myological features. The trapezius lacks a cranial origin and, in association with this, the insertion of the cleido-occipitalis on the nuchal line is more extensive than in other squirrels (Fig. 1). The cranial fibers of trapezius in tree squirrels probably function both to assist in head movements and in protraction of the shoulder joint. The absence of these fibers in flying squirrels does not greatly affect the protraction of the scapula, but it does eliminate the use of the trapezius in cranial movement. The more extensive insertion of the cleido-occipitalis in flying squirrels presumably assumes this function. Occipitoscaphularis has a restricted lateral origin on the nuchal line and tends to insert on the vertebral border and not on the spine of the scapula. The insertion of atlantoscaphularis dorsalis extends to or onto the vertebral border of the scapula (Fig. 3). Both these muscles are positioned to have better leverage than in tree squirrels for rotating the scapula during retraction of the limb. In larger flying squirrels, the lateral head of triceps has a muscular origin, and in the giant flying squirrel *Petaurista*, it has an extensive muscular origin, contrasting with the tendinous origin in other squirrels (Fig. 8). As a result of this, there appears to be an increase in the number of long muscle fibers in these flying squirrels. A very important aspect of flying squirrel locomotion is safe landing after a glide. The triceps absorbs the impact, and the lateral head may play a special role in this if it is composed of fast twitch fibers, as in other mammals (Armstrong, '81). The radial and ulnar heads of

the forearm flexors have more restricted origins than usual for squirrels, reflecting the elongation of the radius and ulna for gliding, and the pronator quadratus is greatly reduced or absent. Flying squirrels exhibit greatly reduced mobility between the distal ends of radius and ulna, yet they pronate and supinate their forearms readily. Pronation and supination occur at the elbow and are effected by pronator teres and supinator muscles, thereby reducing the function of the pronator quadratus (Thorington, '84). The flying squirrels are characterized by the derived morphology of the abductor pollicis, the flexor carpi ulnaris, and the palmaris longus, associated with the extension and retraction of the styloform cartilage and the wing tip of the plagiopatagium (Thorington et al., in press).

Derived features of forelimb musculature in squirrels may characterize groups of genera or tribes, like the clavobrachialis (Fig. 7) and the scapular insertion of subclavius (Fig. 11), or they may evolve independently in several tribes, like the loss of the atlantoscaphularis dorsalis. No derived myological features of the forelimb appear to be synapomorphies of two or more tribes. This clearly suggests that tribal divergence occurred prior to this evolutionary differentiation. Adapting to burrowing and terrestrial locomotion appears to require little modification of the forelimb musculature from that of tree squirrels. Only a few modifications are required in the evolution of pygmy squirrels as well. We see the greatest divergence in forelimb musculature from that of tree squirrels among the flying squirrels.

This survey of forelimb musculature raises a number of questions. Is there a change of function of the subclavius muscle in *Ratufa* which parallels the additional insertion on the supraspinatus? Is there a difference in the ways that tree squirrels and flying squirrels bound up vertical trunks, especially in the degree of retroflexion of the shoulder joint, which correlates with the prominent teres fossa in tree squirrels and its absence in flying squirrels? Is scapular rotation different in flying squirrels from in tree squirrels? Does the lateral head of triceps play an important role in absorbing the impact of landing after a glide? In fact, is there any difference in landing speeds and momentum between jumping tree squirrels and gliding flying squirrels? How does the clavobrachialis function in ground squirrels? Does it act at the same time as brachialis, or does it function differently? The atlantoscaphularis dorsalis is absent in some and present in

other closely related species of *Spermophilus*. How does the absence of this muscle affect scapular rotation? Does the absence of pronator quadratus in pygmy tree squirrels reflect a difference in how they pronate and supinate their forearms, as it does in flying squirrels? We conclude this study with more questions, but more focused questions than before, about the functional anatomy of these interesting animals.

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LITERATURE CITED

- Alezais, H. (1900) Contribution a la Myologie des Rongeurs. Paris: F. Alcan, 400 pp.
- Anthony, H.E., and G.H.H. Tate (1935) Notes on South American Mammalia. I. *Sciurillus*. Am. Mus. Novit. 780:1-13.
- Armstrong, R.B. (1981) Recruitment of muscles and fibres within muscles in running animals. In M.H. Day (ed): Vertebrate Locomotion. London: Academic Press, 471 pp.
- Askins, R. (1977) Family Sciuridae. In B. Lekagul and J.A. McNeely (eds): Mammals of Thailand. Bangkok: Kurusapha Ladpraop Press, 758 pp.
- Black, C.C. (1963) A review of the North American Tertiary Sciuridae. Bull. Mus. Comp. Zool. 130:109-248.
- Black, C.C. (1972) Holarctic evolution and dispersal of squirrels (Rodentia: Sciuridae). Evol. Biol. 6:305-322.
- Brizzee, K.R. (1941) Osteology and myology of the pectoral and pelvic girdles and limbs of the Uinta ground squirrel, *Citellus armatus*. M.S. Thesis. Salt Lake City: University of Utah, 158 pp.
- Bryant, M.D. (1945) Phylogeny of Nearctic Sciuridae. Am. Midl. Nat. 33:257-390.
- Campbell, B. (1939) The shoulder anatomy of the moles. A study in phylogeny and adaptation. Am. J. Anat. 64:1-39.
- Cheng, C. (1955) The development of the shoulder region of the opossum, *Didelphis virginiana*, with special reference to the musculature. J. Morphol. 97:415-471.
- Corbet, G.B., and J.E. Hill (1992) The Mammals of the Indomalayan Region: A Systematic Review. Oxford: Natural History Museum Publications, Oxford University Press, 481 pp.
- DeBrujin, H., and E. Unay (1989) Petauristinae (Mammalia, Rodentia) from the Oligocene of Spain, Belgium, and Turkish Thrace. Ser. Nat. Hist. Mus. L.A. County 33:139-145.

- Ellis, L.S., and L.R. Maxson (1980) Albumin evolution within New World squirrels (Sciuridae). *Am. Midl. Nat.* 104:56-62.
- Emmons, L.H. (1979) A note on the forefoot of *Myosciurus pumilio*. *J. Mammal.* 60:431-432.
- Emmons, L.H. (1980) Ecology and resource partitioning among nine species of African rain forest squirrels. *Ecol. Monogr.* 50:31-54.
- Emry, R., and W.W. Korth (1996) A new genus of squirrel (Sciuridae: Rodentia) from the Chadronian of western North America. *J. Vert. Paleo.* 16:775-780.
- Emry, R.J., and R.W. Thorington, Jr. (1982) Descriptive and comparative osteology of the oldest fossil squirrel, *Protosciurus* (Rodentia: Sciuridae). *Smithson. Contrib. Paleobiol.* 47:1-35.
- Fleagle, J.G. (1982) Locomotor behavior and muscular anatomy of sympatric Malaysian leaf-monkeys (*Presbytis obscura* and *Presbytis melalophos*). *Am. J. Phys. Anthropol.* 46:297-308.
- Gupta, B.B. (1966) Notes on the gliding mechanism in the flying squirrel. *Occasional Papers of the Museum of Zoology, University of Michigan*, 645:1-7.
- Hafner, D.J. (1984) Evolutionary relationships of the Nearctic Sciuridae. In J.O. Murie and G.R. Michener (eds): *The Biology of Ground-Dwelling Squirrels: Annual Cycles, Behavioral Ecology, and Sociality*. Lincoln: University of Nebraska Press, 459 pp.
- Hafner, M.S., L.J. Barkley, and J.M. Chupasko (1994) Evolutionary genetics of New World tree squirrels (tribe Sciurini). *J. Mammal.* 75:102-109.
- Herzig-Straschil, B. (1978) On the biology of *Xerus inauris* (Zimmerman, 1780) (Rodentia, Sciuridae). *Z. Säugetierkd.* 43:262-278.
- Herzig-Straschil, B., and A. Herzig (1989) Biology of *Xerus princeps* (Rodentia, Sciuridae). *Madoqua* 16:41-46.
- Hight, M.E., M. Goodman, and W. Prychodko (1974) Immunological studies of the Sciuridae. *Syst. Zool.* 23:12-25.
- Hill, J.E. (1935) The retractor muscle of the pouch in the Geomyidae. *Science* 81:160.
- Hill, J.E. (1937) Morphology of the pocket gopher, mammalian genus *Thomomys*. *Univ. Calif. Publ. Zool.* 42: 81-172.
- Hoffmann, C.K., and H. Weyenbergh, Jr. (1870) *Die Osteologie und Myologie von Sciurus vulgaris L., Verglichen mit der Anatomie der Lemuriden und des Chomomys und Ueber die Stellung des Letzteren im Natürlichen Systeme*. Haarlem: Loosjes Erben, 136 pp.
- Hoffmann, R.S., C.G. Anderson, R.W. Thorington, Jr., and L.R. Heaney (1993) Family Sciuridae. In D.E. Wilson and D.M. Reeder (eds): *Mammal Species of the World: A Taxonomic and Geographic Reference*. 2nd Ed. Washington, DC: Smithsonian Institution Press, 1,206 pp.
- Howell, A.B. (1926) *Anatomy of the Woodrat*. Baltimore: Williams & Wilkins, 225 pp.
- Howell, A.B. (1932) The saltatorial rodent *Dipodomys*: The functional and comparative anatomy of its muscular and osseous systems. *Proc. Am. Acad. Arts Sci.* 67:377-536.
- Howell, A.B. (1937) Morphogenesis of the shoulder architecture, Part VI. Therian Mammalia. *Quarterly Review of Biology*, 12:440-463.
- Howell, A.B., and W.L. Straus, Jr. (1933) The muscular system. In C.G. Hartman and W.L. Straus, Jr. (eds): *The Anatomy of the Rhesus Monkey*. Baltimore: Williams & Wilkins, 383 pp. (Reprinted with corrections by Hafner, New York, 1961.)
- Jenkins, F.A., Jr., and W.A. Weijs (1979) The functional anatomy of the shoulder in the Virginia opossum (*Didelphis virginiana*). *Zool. Soc. Lond.* 188:379-410.
- Johnson-Murray, J.L. (1977) Myology of the gliding membranes of some Petauristine rodents (genera: *Glaucomys*, *Pteromys*, *Petinomys*, and *Petaurista*). *J. Mammal.* 58:374-384.
- Kingdon, J. (1974) *East African Mammals: An Atlas of Evolution in Africa*. Vol II, Part B: Hares and Rodents. New York: Academic Press, 703 pp.
- Klingener, D. (1964) The comparative myology of four dipodoid rodents (Genera *Zapus*, *Napaeozapus*, *Sicista*, and *Jaculus*). *Univ. Mich. Misc. Publ. Mus. Zool.* 124:1-100.
- Klingener, D. (1970) Superficial facial musculature of *Aplodontia*. *J. Mammal.* 51:35-41.
- Larson, S.G. (1993) Functional morphology of the shoulder in primates. In D.L. Gebo (ed): *Postcranial Adaptation in Nonhuman Primates*. DeKalb: Northern Illinois University Press, 281 pp.
- Lavocat, R. (1973) Les Rongeurs de Miocène d'Afrique Orientale. I Miocène inférieur. *Mém. Trav. E.P.H.E. Inst. Montpellier* 1:1-284.
- Lehmann, W.H. (1963) The forelimb architecture of some fossorial rodents. *J. Morphol.* 113:59-76.
- Lewis, T.H. (1949) The morphology of the pectoral girdle and anterior limb in *Aplodontia*. *J. Morphol.* 85:533-558.
- MacKinnon, K.S. (1978) Stratification and feeding differences among Malayan squirrels. *Malay. Nat. J.* 30:593-608.
- McEvoy, J.S. (1982) Comparative myology of the pectoral and pelvic appendages of the North American porcupine (*Erethizon dorsatum*) and the prehensile-tailed porcupine (*Coendou prehensilis*). *Bull. Am. Mus. Nat. Hist.* 173:337-421.
- McKenna, M.C. (1962) *Eupetaurus* and the living Petauristine sciurids. *Am. Mus. Novit.* 2104:1-38.
- Mein, P. (1970) Les Sciuropteres (Mammalia, Rodentia) Neogenes d'Europe occidentale. *Geobios* 3:7-77.
- Moore, J.C. (1959) Relationships among the living squirrels of the Sciurinae. *Bull. Am. Mus. Nat. Hist.* 118: 153-206.
- Nomina Anatomica (1966) Prepared by the International Anatomical Nomenclature Committee. New York: Excerpta Medica Foundation, 112 pp.
- O'Shea, T.J. (1991) *Xerus rutilus*. Mammalian species. *Am. Soc. Mammal.* 370:1-5.
- Oshida, T., R. Masuda, and M.C. Yoshida (1996) Phylogenetic relationships among Japanese species of the family Sciuridae (Mammalia, Rodentia), inferred from nucleotide sequences of mitochondrial 12S ribosomal RNA genes. *Zool. Sci.* 13:615-620.
- Parsons, F.G. (1894) On the myology of the sciuriform and hystricomorph rodents. *Proc. Zool. Soc. Lond.* 18:251-297.
- Parsons, F.G. (1896) Myology of rodents. II. An account of the Myomorpha, together with a comparison of the muscles of the various suborders of rodents. *Proc. Zool. Soc. Lond.* 20:159-192.
- Payne, J.B. (1980) Competitors. In D.J. Chivers (ed): *Malayan Forest Primates*. New York: Plenum Press, pp. 261-278.
- Peterka, H.E. (1936) A study of the myology and osteology of tree sciurids with regard to adaptation to arboreal, glissant and fossorial habits. *Trans. Kans. Acad. Sci.* 39:313-332.
- Priddy, R.B., and A.F. Brodie (1948) Facial musculature, nerves and blood vessels of the hamster in relation to the cheek pouch. *J. Morphol.* 83:149-180.
- Reed, C.A. (1951) Locomotion and appendicular anatomy in three soricoid insectivores. *Am. Midl. Nat.* 45:513-671.
- Rinker, G.C. (1954) The comparative myology of the mammalian genera *Sigmodon*, *Oryzomys*, *Neotoma*, and *Peromyscus* (Cricitinae), with remarks on their intergeneric relationships. *Univ. Mich. Misc. Publ. Mus. Zool.* 83:1-124.
- Rinker, G.C. (1963) A comparative myological study of three subgenera of *Peromyscus*. *Univ. Mich. Misc. Publ. Mus. Zool.* 632:1-18.

- Ryan, J.M. (1989) Comparative myology and phylogenetic systematics of the Heteromyidae (Mammalia, Rodentia). Univ. Mich. Misc. Publ. Mus. Zool. 176:1–103.
- Schaller, O. (1992) Illustrated Veterinary Anatomical Nomenclature. Germany: Ferdinand Enke Verlag Stuttgart, 614 pp.
- Stalheim-Smith, A. (1984) Comparative study of the forelimbs of the semifossorial prairie dog, *Cynomys gunnisoni*, and the scansorial fox squirrel, *Sciurus niger*. J. Morphol. 180:55–68.
- Stein, B.R. (1981) Comparative limb myology of two opossums, *Didelphis* and *Chironectes*. J. Morphol. 169:113–140.
- Stein, B.R. (1986) Comparative limb myology of four arvicolid rodent genera (Mammalia, Rodentia). J. Morphol. 187:321–342.
- Stein, B.R. (1990) Limb myology and phylogenetic relationships in the superfamily Dipodoidea (birch mice, jumping mice, and jerboas). Z. Zool. Syst. Evolutionsforsch. 28:299–314.
- Swidersky, D.L. (1993) Morphological evolution of the scapula in tree squirrels, chipmunks, and ground squirrels (Sciuridae): An analysis using thin-plate splines. Evolution 47:1854–1873.
- Thorington, R.W., Jr. (1984) Flying squirrels are monophyletic. Science 225:1048–1050.
- Thorington, R.W., Jr., and R.L. Cifelli (1990) The unusual significance of the giant squirrels (*Ratufa*). In J.C. Daniel and J.S. Serrao (eds): Conservation in Developing Countries: Problems and Prospects. Proceedings of the Centenary Seminar of the Bombay Natural History Society. Bombay: Oxford University Press, 656 pp.
- Thorington, R.W., Jr., and K. Darrow (1996) Jaw muscles of Old World squirrels. J. Morphol. 230:145–165.
- Thorington, R.W., Jr., and E.M. Thorington (1989) Postcranial proportions of *Microsciurus* and *Sciurillus*, the American pygmy tree squirrels. In K.H. Redford and J.F. Eisenberg (eds): Advances in Neotropical Mammalogy. Gainesville, FL: Sandhill Crane Press, 614 pp.
- Thorington, R.W., Jr., A.L. Musante, C.G. Anderson, and K. Darrow (1996) Validity of three genera of flying squirrels: *Eoglaucmys*, *Glaucmys*, and *Hylopetes*. J. Mammal. 77:69–83.
- Thorington, R.W., Jr., K. Darrow, and C.G. Anderson (in press) Wingtip anatomy and aerodynamics in flying squirrels (Sciuridae). J. Mammal.
- Vianey-Liaud, M. (1974) *Palaeosciurus goti* nov. Sp., écoreuil terrestre de l'Oligocène moyen du Quercy. Données nouvelles sur l'apparition des Sciuridés en Europe. Ann. Paleontol. (Vert.) Paris 60:103–122.
- Wood, J. (1867) On human musculature variations and their relation to comparative anatomy. J. Anat. Physiol. 1:44–59.
- Woods, C.A. (1972) Comparative myology of the jaw, hyoid, and pectoral appendicular regions of New and Old World hystricomorph rodents. Bull. Am. Mus. Nat. Hist. 147:115–198.

APPENDIX. Specimens dissected

Family Sciuridae

Subfamily Sciurinae: Tree, ground, and pygmy squirrels

Tribe Ratufini: Indo-Malayan giant squirrels

Ratufa affinis: USNM 522980

Ratufa bicolor: USNM 546334

Ratufa indica: USNM 548661

Tribe Protoxerini: African giant and sun squirrels

Protoxerus stangeri: USNM 481817, 481821

Heliosciurus gambianus: USNM 381419, 481830

Heliosciurus rufobrachium: USNM 463538, 463544, 463545, 541537

Tribe Funambulini: Indian and African tree and pygmy squirrels

Subtribe Funambulina: Indian striped squirrels

Funambulus palmarum: USNM 448821, 448824

Subtribe Funisciurina: African striped squirrels and tree squirrels

Funisciurus anerythrus: USNM 463536

Paraxerus ochraceus: USNM 251930

Paraxerus palliatus: USNM 548034

Subtribe Myosciurina: African pygmy squirrels

Myosciurus pumilio: USNM 514360, 220760

Tribe Callosciurini: Oriental squirrels

Callosciurus notatus: USNM 521141, USNM uncatalogued (IMR 84702, 86338, 86351)

Nannosciurus melanotis: USNM 154407

Tribe Sciurini: Holarctic and neotropical tree and pygmy squirrels

Sciurus carolinensis: USNM 396002, 497249, 497250, 522976

Tribe Marmotini: Holarctic ground squirrels

Spermophilus columbianus: OJSMNH uncatalogued (EY821)

Spermophilus richardsonii: USNM 398236

Spermophilus variegatus: OJSMNH 414

Sciurotamias davidianus: USNM 541398

Tribe Xerini: African ground squirrels

Xerus rutilus: CM 86231

Atlantoxerus getulus: USNM 477053, 477054

Subfamily Pteromyinae: Flying squirrels

Belomys pearsoni: USNM 359595

Eoglaucmys fimbriatus: FMNH 140501

Eupetaurus cinereus: USNM uncatalogued forelimb

Glaucmys volans: USNM 457978, 457979

Hylopetes spadiceus: USNM uncatalogued (IMR 89902, 89799)

Petaurista philippensis: USNM 334352, 334359

Pteromys volans: USNM 547926
