Chapter 4

The Muscular System

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I. Introduction

The muscular system of bats differs markedly from that of terrestrial mammals. Not only are differences in relative sizes of muscles involved, but origins, insertions, and functions of homologous muscles frequently differ between these groups of mammals. Each group uses a different type of locomotion, and with each type is associated a dominance of certain types of muscles. In terrestrial mammals the limbs are held beneath the body, more or less vertical to the substrate, and locomotion is due primarily to anteroposterior movements of the limbs. The main propulsion stroke of the limbs is toward the rear of the animals; consequently, flexors and extensors of the limbs are the most important muscles. The situation is entirely different in bats, in which the limbs are held more or less out to the sides of the body. The main movements associated with aerial locomotion in bats involve adduction (the downstroke) and abduction (the upstroke) of the forelimbs. The propulsion stroke is the downstroke of the wings, and the largest muscles are those causing this action. The flight membranes are controlled by both the forelimbs and hind limbs, and the appendages are also used for some sort of quadrupedal locomotion in most bats. Although the appendages of bats are primarily adapted for flight, the evolution of the limbs has apparently been within the limits imposed by their importance in both aerial and terrestrial locomotion.

The following descriptions cover muscles that attach to the pectoral and pelvic girdles and are therefore primarily important in locomotion. These muscles are of particular interest because of their specializations associated with flight and with types of terrestrial locomotion unique to bats. The descriptions of muscles serve as a background for later considerations of the muscular control of flight and of the major muscular specializations for flight.

The descriptions are based on the following four bats of the suborder Microchiroptera: *Eumops perotis* (Molossidae), *Myotis velifer* (Vespertilionidae), *Macrotus waterhousii* (Phyllostomatidae), and *Hipposideros armiger* (Rhinolophidae). *Eumops perotis* is a North American insectivorous bat with long, narrow wings and unusually fast flight. It roosts in crevices in rocks and in manmade structures, and can run rapidly and easily. *Myotis velifer*, another North American species, eats insects and has moderately slow, maneuverable flight. It roosts in caves, crevices, and buildings, and can crawl easily. *Macrotus waterhousii* occurs in the southwestern United States, Mexico, and the West Indies. This species eats insects and some fruit and its flight is highly maneuverable.
It roosts by hanging pendant from the ceilings of caves, mines, or buildings, and is unable to crawl. *Hipposideros armiger* lives in southern Asia and is insectivorous. Its flight is slow and maneuverable and it roosts by hanging in caves, hollow trees, and buildings. *Hipposideros* can crawl slowly. These four bats are used in the following descriptions to illustrate some of the morphological diversity that occurs between different taxa of bats.

Discussions of functions of muscles are based on careful considerations of the anatomical relationships involved. In my judgement this method leads to an accurate general understanding of functional relationships. Only careful experimental work, however, can clarify complex divisions of labor between muscles (Basmajian, 1962).

Descriptive terms are applied as they are to terrestrial mammals; that is to say, the limbs are assumed to extend ventrad, beneath the animals. It should be remembered, however, that this is not the normal posture for the limbs in bats. Indeed, I know of no bat that can bring its hind limbs into this position.

Descriptions of muscles are based on *Eumops*. Additional descriptions are given for those muscles in the other genera that differ from the corresponding muscles in *Eumops*.

### II. Muscles Unique to Bats (Figs. I-3)

**M. occipito-pollicalis**

*Origin.* From lambdoidal crest adjacent to midline.

*Insertion.* On distal half of anterior surface of second metacarpal.

*Remarks.* This muscle is fleshy from the lambdoidal crest to the anterior surface of the shoulder. Between the shoulder and the carpus the muscle is represented first by elastic fibers and then by a tendon. In *Eumops* this muscle is bound to the shoulder by a tendon from a slip from the distal part of the M. clavodeloideus and by connective tissue anchored to the adjacent part of the M. pectoralis. In *Hipposideros* the attachment is by two tendons from slips of the M. clavodeloideus and one tendon from a slip of the M. pectoralis. In each of the other two genera a short tendon anchors the muscle. The insertion in *Hipposideros* is on the medial base of the thumb.

*Action.* This muscle pulls the propatagium craniad and ventrad, thereby increasing the area of the proximal segment of the wing and improving its airfoil.
Fig. 1. Ventral view of Eumops perotis (Molossidae), showing the proportions of the body and selected muscles.
4. THE MUSCULAR SYSTEM

M. CORACOCUTANEUS

**Origin.** From distal part of medial ridge of humerus.
**Insertion.** Into axillary part of plagiopatagium.
**Remarks.** This muscle is relatively largest in *Eumops*. In *Myotis* the origin is on the tip of the coracoid process, in *Macrotus*, on the dorsal surface of the coracoid head of the biceps, and in *Hipposideros*, on fascia in the axilla.
**Action.** This muscle attaches distally to networks of elastic fibers and

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*Fig. 2. Dorsal view of Hipposideros armiger (Rhinolophidae), showing selected muscles. Some of the superficial muscles have been removed from the left side of the shoulder area.*
by anchoring these to the axilla braces and helps maintain the tautness of the proximal part of the plagiopatagium during flight.

**M. humeropatagialis**

*Origin.* From fascia on medial surface and medial epicondyle of humerus and from posteromedial surface of base of ulna.

*Remarks.* The distal part of this muscle gives way to a diverging series of elastic fibers that merge with the network of fibers in the distal part of the plagiopatagium. In the bats under discussion, this muscle

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**Fig. 3.** Ventral view of the left wing of *Eumops perotis* (Molossidae), showing the muscles and part of the system of elastic fibers that brace the wing membranes.

is present only in *Eumops*. In *Macrotus* and *Hipposideros* bundles of elastic fibers take the place of this muscle.

*Action.* This muscle tightens and braces the distal part of the plagiopatagium.

**M. depressor ossis styliformis**

*Origin.* From dorsolateral surfaces of calcaneus and adjacent base of fifth metatarsal.

*Insertion.* Along proximal two-thirds of anterior surface of calcar.

*Remarks.* This muscle is similar in the four genera but is relatively largest in *Eumops*.

*Action.* This muscle helps spread the uropatagium by swinging the calcar laterad, away from the shank.
M. tensor plagiopataghi

Origin. In two parts: the first, from distal three-quarters of medial and anterior surfaces of tibia and from ventral surface of tarsus; the second, from medial surface of internal cuneiform and base of first metatarsal.

Insertion. First part: into part of the plagiopatagium adjacent to anterior surface of shank. Second part: along trailing edge of plagiopatagium, giving way distally to elastic fibers.

Remarks. Among the bats under consideration, this muscle occurs only in Eumops, but is present also in all other molossid bats.

Action. This muscle anchors and braces the trailing edge of the plagiopatagium and the part of this membrane that attaches to the shank.

III. Muscles of the Pectoral Girdle and Limb (Figs. 1–10)

A. Trapezius Group

M. acromiotrapezius and clavotrapezius

Origin. On middorsal line from last cervical to fifth thoracic vertebra.

Insertion. On medial surfaces of distal end of clavicle and entire acromion process, and on rim of scapular spine.

Remarks. In Macrotus the insertion is on the distal third of the clavicle and the acromion process. The two parts of this muscle are separate in Hipposideros. The M. clavotrapezius originates by a broad tendon on the neural ridge on the last cervical vertebra and inserts on the distal part of the clavicle. The origin of the M. acromiotrapezius is on the neural ridge on the fused last cervical and first two thoracic vertebrae. The insertion is on the acromion process.

Action. This muscle pulls the clavicle and scapula medially and tips the vertebral border of the scapula ventrad. The large size of this muscle and its partial insertion on the acromion process suggest that it helps in the upstroke of the wing by bracing the scapula against the pull of the deltoideus, supraspinatus, and infraspinatus muscles.

M. spinotrapezius

Origin. Along middorsal line from thoracic vertebrae eight to thirteen.

Insertion. On middle third of vertebral border of scapula.

Remarks. In Myotis the origin is from thoracic vertebrae seven to
Fig. 4. (A) Dorsal view of the shoulder region of Eumops perotis (Molossidae). (B) Dorsal view of the shoulder region with some superficial muscles removed.
Fig. 5. (A) Ventral view of the shoulder region of Eumops perotis (Molossidae).
(B) Ventral view of the proximal part of the forelimb.
ten, in *Macrotus*, from thoracics ten to thirteen, and in *Hipposideros*, from thoracic ten to the second lumbar vertebra. The insertion is similar in the four genera, but is relatively least extensive in *Hipposideros*, in which it extends along the middle fifth of the vertebral border of the scapula.

**Action.** This muscle pulls the scapula caudad and mediad and tips the vertebral border ventrad. Its function in the wing-beat cycle is probably similar to that of the M. acromiotrapezius.

![Diagram](https://example.com/diagram.png)

*Fig. 6. Semidiagrammatic cross section through the proximal segment of the wing of Myotis evotis (Vespertilionidae). A is the plane of motion. B is the chord line of the airfoil. C is the angle of attack.*

**B. Costo-spino-scapular Group (Figs. 4 and 5)**

**M. LEVATOR SCAPULAE**

*Origin.* From cervical vertebrae four to seven, by four large slips.

*Insertion.* On vertebral border of scapula from the posterior end of the flange to junction of spine and vertebral border.

*Remarks.* The attachments of this muscle are similar in all four genera.

*Action.* This muscle draws the anteromedial border of the scapula ventromediad and slightly craniad and probably acts with the trapezius and rhomboideus muscles to brace the scapula during the upstroke of the wing.

**M. SERRATUS ANTERIOR (ANTERIOR DIVISION)**

*Origin.* By four slips, from a broad band along the middle sections of ribs one to four.

*Insertion.* On rim and anteromedial surface of flange of scapula.

*Remarks.* In *Myotis* the origin is from ribs one to five, in *Macrotus,*
Fig. 7. Lateral view (A) and medial view (B) of the forearm of *Eumops perotis* (Molossidae).
from the first rib and first costal cartilage, and in *Hipposideros*, from the anterodorsal part of the pectoral ring.

**Action.** This muscle is ideally situated to pull the anteromedial border of the scapula ventrad.

M. *SERRATUS ANTERIOR* (POSTERIOR DIVISION)

**Origin.** From a band that widens from 2 mm anteriorly to 10 mm posteriorly along distal surfaces of ribs one to eight.

**Insertion.** On posterior two-thirds of lateral border of scapula, adjacent lateral 3 mm of M. subscapularis, lateral edge of M. infraspinatus, and on posterior, cartilaginous extension of scapula.

**Remarks.** In *Myotis* the origin is from the first costal cartilage and on ribs two to nine. The origin extends from ribs two to ten in *Macrotus*. In *Hipposideros* the area of origin is unusually extensive, including the middle of the posteroventral surface of the pectoral ring and roughly the distal halves of ribs three to eleven (all of the unfused ribs).

**Action.** This muscle and the M. subscapularis are roughly equal in weight and are, next to the M. pectoralis, the largest muscles in bats.
(Table 1). The posterior division of the serratus anterior, the pectoralis, and the subscapularis are by far the most important muscles powering the downstroke of the wings. Unique attachments of the posterior division of the serratus anterior enable this muscle to help in this action.

Fig. 9. Medial view of the carpus of Eumops perotis (Molossidae).

In terrestrial mammals, in which the long axis of the scapula lies more or less at right angles to the vertebral column, the serratus anterior inserts on the vertebral border of the scapula and connects the scapula to the rib cage. During terrestrial locomotion, therefore, the body is cradled between the scapulae by this muscle. In bats, however, in which the long axis of the scapula lies roughly parallel to the vertebral column,
this muscle inserts on the lateral border (axillary border) of the scapula and pulls this part of the scapula ventrad. Because the anterior end of the scapula is braced against the distal end of the clavicle, to which it is attached by ligaments, the point of contact between these bones partially establishes the pivotal axis of the scapula. The scapula probably responds to ventral pull exerted on either its medial or lateral border primarily by rocking on this axis. Consequently, when the serratus an-

Fig. 10. Front view of the shoulder joint showing the relative sizes of the coracoid and glenoid heads of the biceps brachii muscles in Antrozous pallidus (top), a vespertilionid, and Eumops perotis (bottom), a molossid.

TABLE I  RELATIVE WEIGHTS OF THE THREE MAJOR FLIGHT MUSCLES IN SEVERAL BATS*

<table>
<thead>
<tr>
<th>Species</th>
<th>Pectoralis</th>
<th>Serratus anterior (post. division)</th>
<th>Subscapularis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tadarida brasiliensis (4)</td>
<td>67.5</td>
<td>15.3</td>
<td>17.2</td>
</tr>
<tr>
<td>Eumops perotis (4)</td>
<td>67.2</td>
<td>16.7</td>
<td>16.1</td>
</tr>
<tr>
<td>Myotis yumanensis (6)</td>
<td>63.4</td>
<td>18.1</td>
<td>18.5</td>
</tr>
<tr>
<td>M. velifer (7)</td>
<td>64.0</td>
<td>18.6</td>
<td>17.4</td>
</tr>
<tr>
<td>Antrozous pallidus (3)</td>
<td>59.5</td>
<td>21.1</td>
<td>19.4</td>
</tr>
</tbody>
</table>

* Muscles were dried to a constant weight in a drying oven and weighed on an analytical balance. Figures in parentheses indicate the number of specimens weighed.
terior (posterior division) pulls the lateral border of the scapula ventrad; the reciprocal movements are caused by the contraction of the trapezius and rhomboideus muscles.

Owing to a series of modifications of the scapulohumeral articulation in bats, the greater tuberosity of the humerus locks against the scapula at the top of the upstroke of the wing. This locking transfers the work of stopping the upstroke largely to the serratus anterior (posterior division). By anchoring the lateral edge of the scapula this muscle stops the upstroke, and by pulling this edge of the scapula ventrad the muscle moves the locked humerus downward and begins the downstroke of the wing.

**M. rhomboideus**

*Origin.* On thoracic vertebrae one to seven.

*Insertion.* Along postspinal section of medial border of scapula.

*Remarks.* This muscle originates on thoracic vertebrae one to five in *Myotis*, and in *Macrotus* and *Hipposideros*, from thoracics one to six.

*Action.* This muscle pulls the scapula mediad and tips its medial border ventrad. Acting with the trapezius muscles and the anterior division of the serratus anterior, the rhomboideus helps control the upstroke of the wing.

**M. omocervicalis**

*Origin.* From base of transverse process of atlas.

*Insertion.* On end of acromion process.

*Remarks.* In *Macrotus* this muscle is especially large and inserts on the middle of the clavicle. The omocervicalis is absent in *Hipposideros*.

*Action.* Because the scapula of bats is strongly braced by some of the largest muscles associated with flight, the omocervicalis probably functions mainly to move the neck caudad or laterad.

**C. Latissimus–Subscapularis Group (Figs. 2, 4, and 5)**

**M. latissimus dorsi**

*Origin.* Along middorsal line from thoracic vertebrae ten to thirteen and from lumbodorsal fascia to level of fourth lumbar vertebra.

*Insertion.* On distal end of medial ridge of humerus by tendon shared with M. teres major.
Remarks. In *Myotis* the origin is from the eleventh thoracic to the second lumbar vertebra. The origin in *Macrotus* is from the tenth thoracic to the fourth lumbar vertebra, and in *Hipposideros*, from the seventh thoracic to the second lumbar vertebra. In all but *Eumops* the insertion is by a tendon separate from that of the teres major.

Action. The muscle flexes and rotates (pronates) the humerus. Because all joints in the forelimb distal to the scapulohumeral articulation allow movement in but one plane, the entire limb is rotated by the action of this muscle. During the upstroke of the wing the rotational stability of the wing may be maintained in part by the latissimus dorsi and teres major acting as counter rotators against the deltoideus and infraspinatus muscles. The latissimus dorsi is also advantageously situated to help in the propulsion part of the stride of the forelimb in terrestrial locomotion.

M. teres major

Origin. From lateral part of dorsal surface of posterolateral facet of scapula.

Insertion. On distal end of medial ridge of humerus by tendon shared with latissimus dorsi.

Remarks. In *Myotis* this muscle originates from the entire posterolateral facet of the scapula. Some fibers take origin from the surface of the infraspinatus in *Macrotus*. In both *Macrotus* and *Hipposideros* this muscle is larger, relative to the latissimus dorsi, than in the other genera. In all but *Eumops* the tendinous insertion is on the medial ridge of the humerus just distal to the insertion of the latissimus dorsi.

Action. This muscle flexes and rotates the humerus. The sharing of a common tendon of insertion by this muscle and the latissimus dorsi in *Eumops* suggests that in this bat these muscles frequently act together.

M. subscapularis

Origin. From entire ventral surface of scapula including inner surface of flange and ventral surface of posterior, cartilaginous extension.

Insertion. On lesser tuberosity of humerus.

Remarks. Nearly 100 years ago Macalister stated (1872, p. 143) that “probably the largest subscapularis in the animal kingdom are possessed by bats.” In bats the M. subscapularis is surpassed in size only by the M. pectoralis and is roughly equal to the posterior division of the serratus anterior (Table I). In addition to being remarkably large, the subscapularis is highly specialized in being composed of two bipinnate parts,
with the fibers of each part inserting on a central, tendinous sheet. This complex arrangement occurs in muscles with attachments that allow a short contraction to produce the necessary action. Such a muscle contains more fibers than does an undivided muscle of equal mass, and can act more powerfully. In *Eumops* and *Myotis* the large anteromedial flange of the scapula, the complex faceting, and the posterior, cartilaginous extension seem to be modifications serving most importantly to increase the area of origin of the subscapularis.

**Action.** This muscle, together with the M. pectoralis and posterior division of the serratus anterior, adducts and extends the humerus, the two most important actions producing the downstroke of the wings. During terrestrial locomotion this muscle helps support the weight of the anterior part of the body by adducting the humeri.

**D. Deltoid Group (Figs. 2 and 5)**

**M. Clavodeltoideus**

*Origin.* Along distal quarter of ventral surface of clavicle.

*Insertion.* On proximal half of pectoral ridge of humerus.

*Remarks.* In *Myotis* and *Macrotus* the origin is from the distal third of the clavicle. In *Hipposideros* this muscle has an extensive area of origin including the entire posteroventral surface of the clavicle and the ventral part and transverse ridge of the manubrium. This muscle is imperfectly separated from the pectoralis in *Eumops* and *Myotis*; in the other two genera the clavodeltoideus and the pectoralis are clearly separated.

*Action.* This muscle extends and adducts the humerus, movements causing the downstroke of the wing. Also, extension of the humerus at the start of the stride of the forelimb during terrestrial locomotion is probably mostly under the control of this muscle.

**M. Acromiodeltoideus**

*Origin.* From distal three-quarters of spine of scapula and lateral surface of acromion process.

*Insertion.* On lateral surface of pectoral ridge of humerus.

*Remarks.* The origin in *Myotis* is from the lateral surface of the acromion; the insertion is on the distal part of the lateral surface of the pectoral ridge and the adjacent lateral surface of the humerus. The muscle in *Macrotus* is composed of two parts. One part originates on
the anterior end of the acromion process and inserts on the lateral surface of the pectoral ridge. The other part takes origin from all but the end of the acromion and inserts on the lateral surface of the humerus just beyond the pectoral ridge. In *Hipposideros* the origin is from the distal "knob" of the acromion; insertion is along the lateral surface of the pectoral ridge.

*Action.* This muscle elevates (abducts), rotates, and flexes the humerus. Its action is similar to that of the spinodeltoideus and infraspinatus muscles. Together with these muscles and the large muscles binding the medial border of the scapula to the axial skeleton (the trapezius and rhomboideus muscles) the acromioutrapezius controls the upstroke of the wing.

The result of the common action of the deltoideus and infraspinatus muscles is not only to raise the humerus but to rotate it such that the leading edge of the wing is tipped upward. It should be remembered that the humerobrachial and carpal joints allow movement only in the anteroposterior plane; rotation of the humerus, therefore, causes rotation of the entire wing and changes its angle of attack. (The angle of attack is the angle the chord line of the airfoil makes with the plane of motion. See Fig. 6.) High-speed photographs of bats in flight show that during the upstroke the wing is raised and partially flexed and maintains a fairly high angle of attack. Because of this angle, the airstream helps with the upstroke and the wing probably produces some lift during this phase of the wing-beat cycle. The control of the angle of attack and of rotational stability of the wing during the upstroke is of basic aerodynamic importance. This control is seemingly affected by the deltoideus and infraspinatus muscles serving as counter rotators against the latissimus dorsi and teres major muscles.

**M. spinodeltoideus**

*Origin.* From postspinous part of vertebral border of scapula and medial quarter of spine.

*Insertion.* On posterior edge of acromiodeltoideus and on dorsal surface of pectoral ridge of humerus.

*Remarks.* The origin in *Myotis* includes the medial three-quarters of the spine of the scapula as well as the postspinous part of the medial border; insertion is on the lateral surface of the humerus opposite the middle of the pectoral ridge. This muscle is in two parts in *Macrotus*: the first part has attachments similar to those in *Myotis*; the second part originates on the posterior half of the acromion and the anterior
half of the spine of the scapula and inserts on the lateral surface of the humerus at the distal base of the greater tuberosity. In *Hipposideros* the origin is from the proximal part of the “knob” of the acromion, the ligament between the acromion and the medial border of the scapula, and the posterior two-thirds of the medial border. The insertion is along 3 mm of the lateral surface of the humerus opposite the distal end of the pectoral ridge.

*Action.* This muscle raises, flexes, and rotates the humerus. Because the insertion of the spinodeltoideus is farthest from the long axis of the humerus in *Eumops*, this muscle probably acts as a rotator most effectively in this genus. Action of this muscle is discussed under M. acromiodeltoideus.

**M. teres minor**

*Origin.* From lateral edge of scapula just posterior to glenoid fossa.

*Insertion.* On greater tuberosity of humerus.

*Remarks.* This muscle is similar in all four genera but is especially narrow and delicate in *Myotis*.

*Action.* This muscle flexes and rotates the humerus.

**E. Suprascapular Group (Fig. 4)**

**M. supraspinatus**

*Origin.* From supraspinous fossa, medial surface of scapular spine, and ligament that spans supraspinous fossa from anteromedial flange to tip of acromion and base of coracoid process.

*Insertion.* On lateral surface of greater tuberosity of humerus.

*Remarks.* This muscle is similar in all genera and is relatively largest in *Hipposideros*.

*Action.* This muscle raises (abducts), extends, and rotates the humerus. The supraspinatus is ideally situated to bring the greater tuberosity into position to lock against the scapula at the end of the upstroke.

**M. infraspinatus**

*Origin.* Lateral surface of scapular spine and all of infraspinous fossa but lateral third of posterolateral facet.

*Insertion.* On distal part of greater tuberosity of humerus.

*Remarks.* This muscle is bipinnate in all but *Hipposideros*, in which
it is pinnate. Relative to the supraspinatus, the infraspinatus is considerably smaller in *Hipposideros* than in the other three genera.

*Action.* This muscle raises (abducts), flexes, and rotates the humerus. Together with the deltoideus muscles, the infraspinatus helps power the upstroke of the wing. This muscle also partly controls the rotational stability of the wing during the upstroke.

**F. Triceps Group (Figs. 4 and 5)**

**M. Triceps brachii (lateral head)**

*Origin.* Along posterolateral surface of humerus from distal base of greater tuberosity to distal end of pectoral ridge, and from posterior surface of medial ridge and adjacent posterior surface of humerus.

*Insertion.* On proximal end of olecranon.

*Remarks.* Attachments of this muscle are similar in all four genera.

**M. Triceps brachii (medial head)**

*Origin.* Along distal three-quarters of posterior surface of humerus.

*Insertion.* On proximal end of olecranon deep to other tendons of triceps group.

*Remarks.* In *Myotis* the origin is from the distal third of the humerus; the distal tendon enlarges into a thick cartilaginous pad that rests against the proximal surface of the trochlea of the humerus. A small sesamoid bone in the distal part of the pad is connected to the olecranon by a short tendon. This muscle originates in *Macrotus* on the distal end of the medial ridge of the humerus. The tendons of the three parts of the triceps in *Macrotus* merge and form a single, thick, padlike tendon that inserts on the olecranon. The origin of the medial head in *Hipposideros* is from the distal sixth of the posterior surface of the humerus and the insertion is on a large sesamoid bone that lies against the posterior surface of the trochlea and is bound by ligaments to the proximal part of the olecranon.

**M. Triceps brachii (long head)**

*Origin.* Along one-fifth of lateral border of scapula just posterior to glenoid fossa.

*Insertion.* On proximal end of olecranon.

*Remarks on the triceps group.* In all four genera the long head is the largest division of the triceps and is composed of two indistinctly
divided portions that each give rise distally to a tendon. The medial head is the smallest division and is especially reduced in Hipposideros. Several types of specializations allow the tendons of the long and lateral heads of the triceps group to pass smoothly over the posterior surface of the trochlea. In Eumops and Hipposideros these tendons ride in a groove in the posterior surface of a large sesamoid bone that rests against the posterior surface of the trochlea. In Myotis these tendons pass over a cartilaginous pad. All of the triceps tendons in Macrotus form a single, enlarged, padlike tendon that inserts on the olecranon.

Action. These muscles extend the forearm. To develop maximum thrust and lift from the wing-beat cycle, the wing must be extended rapidly at the start of the downstroke and kept fully extended throughout its duration. This action is largely under the control of the lateral and long heads of the triceps. The antagonistic actions of the biceps and triceps muscles are important in maintaining the rigidity of the distal part of the wing during the downstroke.

The long head of the triceps is seemingly of greatest importance in maintaining extension of the wing after the humerus is extended. Because of the position on the scapula of the origin of the long head of the triceps, the distance from origin to insertion is increased when the humerus is extended. This partly compensates for the proximal movement of the point of insertion (the olecranon) when the forearm is extended and allows the long head to function most effectively when the forearm is extended. The central tendons in the belly of the muscle and the fibrous sheath that partially invests it in many bats serve to reduce the elasticity of the muscle. These modifications probably allow the long head of the triceps to affect some degree of extension of the forearm without muscular contraction when the humerus is extended by other muscles.

The small medial head of the triceps is a weak extensor of the forearm and probably serves most importantly in Eumops and Hipposideros to brace the sesamoid bone on which it inserts.

G. Extensor Group of Forearm (Figs. 7-9)

M. BRACHIORADIALIS

Origin. From 2 mm of the anterolateral surface of the distal part of the humerus.

Insertion. Along 10 mm of anteromedial surface of proximal third of humerus.
Remarks. This muscle occurs only in Hipposideros.
Action. Flexion of the forearm.

M. extensor carpi radialis longus

Origin. From short ridge extending from lateral epicondyle of humerus to distal end of shaft.

Insertion. On lateral base of first metacarpal and anterolateral base of second metacarpal.

Remarks. In all but Eumops the origin is from the proximal part of the lateral epicondyle of the humerus. In Hipposideros the insertion is on the anterior surface of the second metacarpal just distal to its base. In all four genera this large muscle is partly enveloped by a glistening fibrous sheath.

Action. This muscle extends the second digit and indirectly extends all digits but the first. The action of this muscle is discussed in the account of the extensor carpi radialis brevis.

M. extensor carpi radialis brevis

Origin. On ridge on lateral epicondyle of humerus.

Insertion. On anterolateral surface of third metacarpal just distal to base.

Remarks. In Eumops this muscle contains a sesamoid bone just distal to its origin. The insertion in Hipposideros is on the lateral surfaces of the base of metacarpals one, two, and three. In all but Hipposideros the tendon of this muscle has a sesamoid bone just short of the insertion.

Action. The extensor carpi radialis longus and brevis are doubtless the most important flight muscles in the forearm. These muscles extend digits one, two, and three. Because digits two and three are attached by membranes to digits four and five, this action extends all of the digits and spreads the distal segment of the wing (chiroptagium). This part of the wing develops the thrust necessary for propulsion during flight; to develop maximum thrust the chiroptagium must be kept fully spread during the downstroke. Due to specializations of their structure and attachments, the slender extensor carpi radialis muscles are able to perform this demanding function effectively.

In all four genera the origins of these muscles are not at the center of rotation of the humerobrachial joint but are at the proximal base of the lateral epicondyle of the humerus (Fig. 7). Therefore, with extension of the forearm, the distance between origin and insertion of these muscles is increased considerably. This increase amounts to roughly
3 mm in *Eumops*. If nonelastic, then, these muscles would automatically spread the chiroptagium with extension of the forearm. Indeed, the elasticity of these muscles is greatly reduced by their heavy tendons that extend to within the proximal fourth of the muscles and by fibrous sheaths that invest most of the bellies of the muscles. With but little muscular effort these muscles can probably function as nonelastic cords. Seemingly, the most important effect of these modifications is to transfer much of the burden of extending the distal part of the wing from the small extensor carpi radialis muscles to the larger, proximally located, triceps muscles.

Extension of the thumb by the extensor carpi radialis longus helps spread and maintain the tautness of the propatagium.

**M. supinator**

*Origin.* From center of lateral epicondyle of humerus.

*Insertion.* Along proximal eighth of anterolateral surface of radius.

*Remarks.* The tendinous origin of this muscle contains a sesamoid bone in all four genera.

*Action.* This muscle probably serves primarily to brace the humero-brachial articulation.

**M. extensor pollicis brevis**

*Origin.* Along lateral surface of proximal part of ulna and anterolateral surface of slender shaft of ulna, and from fascia on M. abductor pollicus longus and M. extensor indicus.

*Insertion.* On metacarpophalangeal joint and distal end of second phalanx of first digit.

*Remarks.* In *Hipposideros* the origin is from the proximal part of the ulna. The distal tendon becomes a broad sheet that divides into three parts over the carpus. The insertions are as follows: (1) on the lateral surface of the first metacarpophalangeal joint; (2) on the lateral part of the base of the second metacarpal; (3) on the base of the third metacarpal.

*Action.* This muscle extends the first three digits.

**M. abductor pollicis longus**

*Origin.* From all but proximal 10 mm of posterior surface of radius.

*Insertion.* On scaphoid bone of carpus.

*Remarks.* This muscle is similar in all four genera.
Action. This muscle helps brace the ventral part of the fifth carpometacarpal articulation. The insertion and function of this muscle are unique in bats, for in most mammals this muscle inserts on the thumb and abducts this digit.

The plagiopatagium probably creates most of the lift developed during the wing-beat cycle; the amount of lift depends in part on the angle of attack of this segment of the wing. The fifth digit forms the distal edge of the plagiopatagium and, together with the hind limbs, determines its angle of attack. Probably due to the great aerodynamic importance of maintaining the plagiopatagium at a fairly constant angle of attack during flight, a series of morphological specializations in bats serve to brace the fifth carpometacarpal joint against any other movement than flexion and extension. At this joint there is almost no “give” of the sort that would allow changes in the angle of attack. The pisiform, which in most bats spans the ventral surface of the fifth carpometacarpal joint, is attached almost immovably by ligaments to the medial base of the fifth metacarpal. The proximal end of the pisiform is bound to the medial surface of the trapezium and the scaphoid but may move slightly against the carpus. By pulling the scaphoid craniad the M. abductor pollicis longus anchors the pisiform and braces the fifth digit against “give” that would change the angle of attack of the plagiopatagium.

M. extensor digitorum communis

Origin. On lateral epicondyle of humerus.

Insertion. On lateral surfaces of second phalanges of digits three to five.

Remarks. The insertion of this muscle on the second digit is lost in *Eumops* and is seemingly in various stages of reduction in the other genera. Only in *Myotis* does this muscle retain a connection with the first phalanx of the second digit. A tiny, vestigial tendon from this muscle inserts on the second metacarpal in *Macrotus*. In *Hipposideros*, whereas the tendons to the other digits insert on the joints between the first and second phalanges, the tendon to the second digit inserts on the proximal third of the metacarpal.

Action. By extending the phalanges of digits three to five this muscle spreads the distal part of the wing. Although this is an important function, this muscle is not especially large, suggesting that the force of the airstream helps keep this part of the wing membrane spread during flight.
M. extensor indicus

Origin. Opposite middle half of forearm from posterior surface of radius and anterolateral surface of ulna.

Insertion. By aponeurosis, on anterolateral surface of carpus.

Remarks. In Eumops the thickest part of the distal aponeurosis inserts on the lateral base of the second metacarpal. In the other genera insertion is entirely on the second metacarpal. In Hipposideros this muscle is unusually large. Its origin extends along most of the ulna and nearly all but the distal quarter of the radius.

Action. By extending the second digit this muscle spreads the distal part of the wing. Its action is thus similar to that of the radial extensors. The unusually large size of the extensor indicus in Hipposideros may be a reflection of the fact that the origins of the radial extensors in this genus are not as advantageously located as in the other bats in terms of allowing these muscles to operate effectively as automatic extensors of the hand (see account of M. extensor carpi radialis brevis). In Hipposideros these muscles may need considerable help from the extensor indicus.

M. extensor digiti quinti proprius

Remarks. Apparently this muscle is not present in Eumops or Hipposideros. In Macrotrus and Myotis the insertion is on the lateral base of the fifth metacarpal. In Myotis the origin is from the lateral base of the ulna and the adjacent surface of the extensor digitorum communis; the origin in Macrotrus is on the lateral epicondyle of the humerus. The insertion in both bats is on the second phalanx of digit five.

Action. In Myotis and Macrotrus, extension of the fifth digit.

M. extensor carpi ulnaris

Origin. From proximal part of ulna and posterolateral surface of distal half of radius.

Insertion. On anterolateral base of third metacarpal.

Remarks. In Myotis the insertion is the same as that in Eumops, but in Macrotrus and Hipposideros the insertion is on the lateral base of the fifth metacarpal.

Action. In Eumops and Myotis this muscle flexes the third digit and thus closes the distal part of the wing. This muscle is probably important in keeping this part of the wing closed during terrestrial locomotion,
when it counteracts the automatic action of the radial extensors when the forearm is extended. In Macrotus and Hipposideros, neither of which uses its forelimbs in terrestrial locomotion to any extent, the extensor carpi ulnaris retains its primitive insertion on the fifth metacarpal and flexes the fifth digit.

II. Pectoralis Group (Figs. 1 and 4)

M. subclavius

**Origin.** On ventral surface of first costal cartilage.

**Insertion.** Along proximal three-quarters of posterodorsal surface of clavicle.

**Remarks.** In Myotis the origin is from the distal end of the first rib. The origin in Hipposideros is on the flaring lateral tuberosity of the pectoral ring.

**Action.** This muscle moves the clavicle caudad and ventrad and probably acts primarily to steady the clavicle against the pull of the dorsal musculature.

M. pectoralis

In the bats under discussion this large sheet of muscle is more or less clearly divided into two parts. One part originates on the clavicle and the other, on the sternum. Because of uncertainty as to the terminology of the divisions of the pectoralis muscle in bats, I refer to the parts as anterior and posterior divisions.

M. pectoralis (anteri or division)

**Origin.** From proximal three-quarters of ventral surface of clavicle.

**Insertion.** Along dorsal edge of pectoral ridge of humerus.

**Remarks.** This muscle is similar in all genera, but in Hipposideros this muscle is larger and its origin is vastly more extensive than in the other genera. The origin in Hipposideros is from the entire ventral surface of the clavicle and from all of the ventral part of the pectoral ring medial to the lateral tuberosity.

**Action.** This muscle pulls the humerus downward and forward and rotates it by tilting the pectoral ridge ventrad. Together with the posterior division of the pectoralis, this is the most important muscle controlling the downstroke of the wings.
M. pectoralis (posterior division)

*Origin.* Along entire sternum and midventral raphe from ventral arm of manubrium to anterior part of xiphoid process, and from a band extending along the medial 5 mm of the seventh costal cartilage.

*Insertion.* On anterior surface of pectoral ridge.

*Remarks.* This muscle has similar attachments in all four genera, but in *Hipposideros* it is smaller, relative to the anterior division of the pectoralis, than in the other bats. Considering both divisions of the pectoralis together, this is easily the largest muscle in bats (Table I).

*Action.* The posterior division of the pectoralis helps produce the downstroke of the wing by adducting the humerus and pulling its leading edge downward.

Because of the very extensive origin of the pectoralis, extending from the distal part of the clavicle to the xiphoid process of the sternum, this muscle alone can control the downstroke of the wing through a considerable range of planes. During the normal wing-beat cycle, both divisions of this muscle doubtless work together. Their common action not only adducts the humerus but pulls it well forward, spreading the wing.

The insertion of the pectoralis muscle is anterior to the long axis of the humerus. Consequently this muscle acts as a rotator of the humerus. Such action controls the angle of attack and the rotational stability of the wing by operating against the counter rotational action of the biceps brachii. Because of the variety of directions from which the fibers of the pectoralis pull on the humerus and the extensiveness of their insertion, however, the action of this muscle alone imparts considerable rotational stability to the humerus.

M. pectoralis abdominalis

*Origin.* From abdominal fascia opposite xiphisternum (Fig. 1).

*Insertion.* On middle of ventral edge of pectoral ridge.

*Remarks.* The insertion in *Macrotus* is between the pectoral ridge and the greater tuberosity of the humerus. In *Hipposideros* the insertion is on the posterior border of the anterior division of the pectoralis.

*Action.* This muscle is primarily a flexor of the humerus. Owing to its length and its attachments, this muscle can pull the humerus through a wide arc and is probably important primarily in producing the backward component (propulsion stroke) of the stride during terrestrial locomotion.
I. Flexor Group of Arm (Figs. 7 and 9)

M. CORACOBRACHIALIS

Remarks. This muscle is absent in *Eumops* but occurs in the other three genera. In these bats the origin is from the tip of the coracoid process of the scapula. The insertion in *Myotis* is on the medial surface of the humerus opposite the distal end of the pectoral ridge. The insertion is on roughly the middle of the medial surface of the humerus in *Macrotus*. This muscle is relatively larger in *Hipposideros* than in the other genera and inserts along the medial surface of the humerus from opposite the middle of the pectoral ridge to near the middle of the humerus.

Action. This muscle is a weak adductor and extensor of the humerus. The loss of this muscle in *Eumops* is probably associated with the specializations of the coracoid head of the biceps in this bat.

M. BICEPS BRACII


Insertion. Into flexor fossa of radius (Chapter 3, Fig. 16).

Remarks. The coracoid head is much the larger of the two divisions of this muscle in *Eumops*, but in *Myotis* the heads are of roughly equal size (Table II). In *Macrotus* and *Hipposideros* the coracoid head is the smaller.

Action. Both heads of the biceps flex the forearm, extend the humerus, and rotate the forelimb. In addition, at least in *Eumops*, the coracoid head adducts the humerus.

During the downstroke of the wing-beat cycle the wing must remain fully extended against the force of the airstream in order to produce the maximum thrust and lift. Photographs of bats in flight show that the biceps tendons are taut and are drawn away from the leading edge of the humerus during the downstroke. Throughout this phase the wing is apparently steadied in a fully extended position partly by the antagonistic actions of the biceps and triceps. The flexing of the wing during the upstroke may be largely passive. The position of the insertion of the biceps tendons gives these muscles much greater mechanical advantage than that of the triceps muscles. Consequently, the forearm probably flexes under the control of the tonus of the biceps.

Because the insertion of the biceps muscles is medial to the long
axis of the radius, these muscles tend to rotate the wing such as to raise its leading edge. Although an analysis of such complex functional relationships is most difficult, on the basis of anatomical evidence it seems probable that the biceps muscles aid in the maintenance of rotational stability during the wing-beat cycle.

Whereas the coracoid process turns more or less laterad in the other genera, it curves mediad in *Eumops*, allowing the coracoid head of the biceps to serve as an adductor of the humerus during the lower part of the downstroke in this bat (Fig. 10). The unusually large coracoid head of the biceps in this genus is probably correlated with this partial change in function.

### Table II

<table>
<thead>
<tr>
<th>Species</th>
<th>Weight of glenoid head (gm)</th>
<th>Weight of coracoid head (gm)</th>
<th>Coracoid head Glenoid head</th>
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<tbody>
<tr>
<td><em>Tadarida brasiliensis</em> (7)</td>
<td>0.0039</td>
<td>0.0081</td>
<td>211.1</td>
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<tr>
<td><em>Eumops perotis</em> (4)</td>
<td>0.0195</td>
<td>0.0339</td>
<td>173.8</td>
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<tr>
<td><em>Myotis yumanensis</em> (7)</td>
<td>0.0022</td>
<td>0.0020</td>
<td>91.0</td>
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<tr>
<td><em>M. velifer</em> (9)</td>
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<td>0.0032</td>
<td>86.5</td>
</tr>
<tr>
<td><em>Antrozous pallidus</em> (3)</td>
<td>0.0107</td>
<td>0.0069</td>
<td>64.8</td>
</tr>
</tbody>
</table>

*Muscles were dried to a constant weight in a drying oven and weighed on an analytical balance. Figures in parentheses indicate the number of specimens measured.*

**M. BRACHIALIS**

**Origin.** On roughly middle half of anterior surface of humerus.

**Insertion.** Into flexor fossa of radius (see Chapter 3, Fig. 16).

**Remarks.** In all but *Eumops* this muscle originates along the third quarter of the humerus.

**Action.** Flexion of the forearm.

**J. Flexor Group of Forearm (Figs. 7 and 9)**

**M. FLEXOR CARPI ULNARIS**

**Origin.** From tip of spinous process of medial epicondyle of humerus.

**Insertion.** On proximal part of pisiform.
Remarks. In *Eumops* heavy fibrous sheets surrounding most of the belly of this muscle reduce its elasticity, and in *Myotis* elasticity is reduced by a tendinous core within the belly of the muscle. The fleshy origin of the muscle in *Macrotus* is on the medial surface of the ulna and most of the distal part of the posterior border of the radius. In *Hipposideros*, in contrast to the other genera, this is the smallest flexor muscle in the forearm and originates along the proximal half of the medial surface of the ulna.

Action. This muscle flexes the fifth digit by acting on the proximal end of the pisiform, to which the fifth metacarpal is bound by ligaments. The degree of flexion or extension of the fifth digit helps govern the tautness of the plagiopatagium and the amount of extension of the chiropatagium.

In *Eumops* and *Myotis* this muscle controls the degree of flexion or extension of the fifth digit automatically, seemingly with but little muscular effort. (This digit, it should be remembered, can extend no further than to roughly right angles with the radius.) In both of these bats the origin of this muscle is on the tip of the elongate spinous process of the medial epicondyle. The tip of this process is well away from the axis of rotation of the humerobrachial joint (see Chapter 3, Fig. 15) and during flexion and extension of the forearm the tip moves through a wide arc. The origin of the flexor carpi ulnaris is thus moved proximad with flexion of the forearm, and distad with extension. Because this muscle is fairly inelastic, movement of its origin is transmitted to the pisiform, and the fifth digit is flexed or extended with corresponding movements of the forearm. This arrangement transfers the work of regulating the extension of the fifth digit to the proximally located flexors and extensors of the forearm (the biceps and triceps brachii, respectively) and allows the size of the flexor carpi ulnaris to be kept to a minimum.

In *Macrotus* and *Hipposideros* the origin of this muscle is on the forearm and the muscle does not act as an automatic flexor of the fifth digit.

**M. palmaris longus**

*Origin*. From base of spinous process of medial epicondyle of humerus.

*Insertion*. On anteromedial surface of carpus, on thumb pad, and on surface of abductor digitorum quinti.

*Remarks*. This muscle is absent in *Myotis*. The origin in *Macrotus* is from the medial epicondyle and the surface of the flexor digitorum
profundus; the insertion is on the anterior surface of the distal end
of the first metacarpal and on the proximal part of the third metacarpal.
In *Hipposideros* the insertion is on the proximal part of the medial
surface of each metacarpal.

*Action.* Flexion of the digits of the hand.

**M. flexor carpi radialis**

*Origin.* On distal part of pronator teres.

*Insertion.* In fascia at medial base of first metacarpal.

*Remarks.* In *Eumops* and *Myotis* this muscle is vestigial and is prob­ably functionless. This muscle is robust in *Macrotus* and originates along
the middle third of the pronator teres. The insertion is on the medial
base of the third metacarpal. This is the largest flexor muscle of the
forearm in *Hipposideros* and originates on the medial epicondyle, the
proximal part of the medial aspect of the radius, and on the surface
of the pronator teres. The insertion is on the medial base of the first
metacarpal.

*Action.* In *Macrotus* this muscle flexes the third, and in *Hipposideros*,
the first digit.

**M. pronator teres**

*Origin.* From base of spinous process of medial epicondyle.

*Insertion.* Along proximal eighth of medial surface of radius.

*Remarks.* This muscle is considerably smaller in *Eumops* than in the
other genera.

*Action.* This muscle probably functions primarily to brace the elbow
joint.

**M. flexor digitorum profundus**

*Origin.* From proximal three-fifths of posterior border of radius and
adjacent border of ulna.

*Insertion.* On medial base of second phalanx of thumb and medial
base of fifth metacarpal.

*Remarks.* This is a large muscle in all four genera and is the largest
flexor muscle of the forearm in *Eumops*. In *Myotis* the origin is from
the spinous process of the medial epicondyle and the insertion is on
the second phalanges of digits one and three and the third phalanx
of digit four. The insertion in *Macrotus* is on the second phalanx of
the thumb and the third phalanx of the third digit. In *Hipposideros*
the insertion is on the second phalanges of digits one and three and on the first phalanx of digit four.

*Action.* Flexion of the digits of the hand.

**K. Extensor Group of Manus (Fig. 8)**

**M. interosseus dorsale**

*Origin.* From posterolateral base of second metacarpal.

*Insertion.* On anteromedial base of first phalanx of third digit.

*Remarks.* This muscle occurs only in *Eumops*.

*Action.* Of the bats considered here, only in *Eumops* is flexion and extension of the first phalanx of the third and fourth digits in the antero-posterior plane. (This same pattern of flexion, however, occurs in all molossid bats.) This muscle extends the first phalanx of the third digit and thus spreads part of the end of the wing.

**L. Flexor Group of Manus (Fig. 9)**

I have had difficulty identifying certain muscles of the hand in bats. The names *M. abductor digiti quinti* and *M. opponens digiti quinti* are tentatively applied; these muscles may not be homologous with those bearing the same names in other mammals.

**M. abductor pollicis brevis**

*Origin.* From trapezium and ligament between this bone and medial base of second metacarpal.

*Insertion.* Into pad on medial surface of first metacarpophalangeal joint.

*Remarks.* This muscle is similar in the four genera but is unusually small in *Macrotus*.

*Action.* Abduction and flexion of first digit.

**M. flexor pollicis brevis**

*Origin.* From medial base of second metacarpal, ligament from trapezium to second metacarpal, and tendon of flexor digitorum profundus.

*Insertion.* On posteromedial part of thumb pad.

*Remarks.* This muscle is relatively largest in *Eumops* and is very small.
in *Macrotus*. The tendon of insertion extends to the base of the second phalanx of the thumb in *Hipposideros*.

*Action.* This muscle flexes the first metacarpal in all but *Hipposideros*, in which the entire thumb is flexed.

**M. adductor pollicus**

*Origin.* Along proximal 3 mm of posteromedial surface of second metacarpal.

*Insertion.* On lateral base of second phalanx of thumb and on tendon of M. extensor pollicis brevis.

*Remarks.* This muscle is absent in *Macrotus* and *Hipposideros*.

*Action.* Adduction and rotation of the thumb.

**M. adductor digitii secundi**

*Origin.* On posteromedial surface of trapezium.

*Insertion.* Along proximal 9 mm of medial surface of second metacarpal.

*Remarks.* This muscle is relatively largest in *Eumops* and is absent in *Macrotus*. One part of this muscle originates on the tendon of the flexor digitii profundus in *Hipposideros*.

*Action.* This muscle flexes the second digit posteriorly, thus folding the chiropatagium.

**M. abductor digiti quinti**

*Origin.* On posterior edge of scaphoid.

*Insertion.* On medial surface of fifth metacarpal and adjacent sesamoid to the fifth metacarpophalangeal joint.

*Remarks.* The origin of the muscle in *Eumops* is by a thick tendon that gives way distally to a fascial sheet that invests the belly of the muscle. In *Myotis* the origin is from the pisiform. This muscle in *Macrotus* is represented by a tendon that extends from the pisiform and the adjacent sesamoid to the fifth metacarpophalangeal joint. In *Hipposideros* the origin is from the scaphoid and the insertion is on the medial base of the second phalanx of the fifth digit.

*Action.* The primary function of this muscle is probably to brace the fifth carpometacarpal joint and to help maintain the camber of the fifth metacarpal. This muscle also flexes the first phalanx of the fifth digit in *Eumops* and *Myotis* and the second, terminal phalanx of this digit in *Hipposideros*.

The fifth digit has the important aerodynamic function of help-
ing to control the angle of attack and camber of the wing during flight. The abductor digiti quinti is one means by which the fifth digit is reinforced against the force of the airstream during the downstroke. The effectiveness of the muscle is increased in several ways. It is fairly inelastic in both *Eumops* and *Macrotus* and in these genera acts like a bowstring to resist forces tending to straighten the laterally bowed fifth metacarpal. In addition, the structure of the carpus is such that the abductor digiti quinti is stretched when the digits are fully extended. Further, contraction of the abductor pollicus longus pulls the scaphoid craniad and in *Eumops* and *Hipposideros* slightly stretches the abductor digiti quinti.

**M. Adductor Digiti Quinti**

*Origin.* On proximal 4 mm of posteromedial surface of second metacarpal.

*Insertion.* Along proximal fifth of anteromedial surface of fifth metacarpal.

*Remarks.* This muscle is present only in *Eumops*, in which it is one of the largest muscles in the hand.

*Action.* This muscle pulls the second and fifth metacarpals together and helps fold the chiropatagium. This action is important mainly during terrestrial locomotion or when the bat is roosting in confined quarters. The retention of this muscle in *Eumops* is apparently associated with the importance of terrestrial locomotion in this bat.

**M. Opponens Digiti Quinti**

*Origin.* From distal part of pisiform.

*Insertion.* On medial surface of fifth metacarpophalangeal joint.

*Remarks.* This muscle, considerably smaller than the abductor digiti quinti, is similar in the four genera.

*Action.* This muscle braces the fifth metacarpal and is similar in function to the abductor digiti quinti.

**Mm. Interossei**

In *Eumops* and *Hipposideros* there are four of these muscles; their attachments are as follows: (1) from posteromedial base of second metacarpal and distal part of tendon of adductor digiti secundi to posterior surface of third metacarpophalangeal joint; (2) from proximal end of pisiform to posterior surface of proximal end of first phalanx
of third digit; (3) from posteromedial base of third metacarpal and anteromedial base of fourth metacarpal to anteromedial surface of fourth metacarpophalangeal joint; (4) from sesamoid bone that lies on postero-medial base of fourth metacarpal to posteromedial surface of fourth metacarpophalangeal joint.

Remarks. The posterior interosseus muscle of the third digit is not present in *Myotis* or *Macrotus*. The interosseus muscles are otherwise roughly alike in the four genera.

Action. These muscles brace the third and fourth carpometacarpal articulations and flex the phalanges of these digits. In *Eumops* the anterior interosseus muscle of the fourth digit extends the first phalanx because in this genus this bone flexes posteriorly rather than medially.

![Fig. 11. Lateral view of the pelvic region in Eumops perotis (Molossidae).](image)

**IV. Muscles Attaching to the Pelvic Girdle and Limb (Figs. 11–14)**

**M. PSOAS MINOR**

*Origin.* From strip 1 mm wide along ventrolateral surfaces of lumbar vertebrae two to four.

*Insertion.* On tip of pubic spine.

Remarks. The origins of this muscle are slightly different in each genus: in *Myotis* the origin is on lumbar vertebrae one to three, in *Macrotus*, on the last thoracic and first three lumbers, and in *Hipposideros*, on lumbar three and four. At least one-third of the length of the muscle is tendinous in *Eumops* and *Myotis*, whereas in the other two genera it is almost entirely fleshy. This muscle is remarkably large in *Hipposideros* and inserts on a prominent knob adjacent to the anteroventral rim of the iliac fenestra.
Fig. 12. (A) Medial view of the hind limb of Eumops perotis (Molossidae). (B) and (C) Progressively deeper muscles of the thigh.
Fig. 13. (A) Lateral view of the hind limb of Eumops perotis (Molossidae).
(B) Deep muscles of the thigh.
Fig. 14. (A) Dorsal view of left foot of Eumops perotis (Molossidae). (B), (C), and (D) Progressively deeper muscles of the ventral surface of the left foot.

Action. This muscle flexes the posterior part of the vertebral column, tending to pull the pelvis downward and forward. This action doubtless comes into play when a bat curls up and “pouches” its uropatagium when catching insects as Myotis and Lasiurus have been shown to do (Webster and Griffin, 1962). The unusually large size of this muscle in Macroto and Hipposideros suggests that this muscle is important in bracing the dorsally arched vertebral column and the pelvis against the shock transmitted to them in the hind limbs when these bats alight on ceilings of caves or buildings.
A. Iliacus Group (Figs. 11 and 12)

M. ILIACUS

*Origin.* From lumbar vertebrae two to five, lateral half of the expanded anterior end of the ilium, and most of lateral rim of ilium.

*Insertion.* On distal end of lesser tuberosity of femur.

*Remarks.* The vertebral part of the origin of this muscle in *Myotis* is from the iliac crest; the insertion is on the middle of the medial ridge of the femur. This muscle in *Hipposideros* originates on the descending ramus of the ilium and inserts along the medial ridge of the femur.

*Action.* This muscle flexes and rotates the femur in such a way as to swing the shank downward and forward. This muscle is an especially strong rotator in *Macrotus* and *Hipposideros*.

In *Eumops* and *Myotis* this muscle helps produce the forward component of the stride used in terrestrial locomotion and during flight serves to change the angle of attack of the uropatagium by swinging the shank downward and forward. In all four genera this muscle can help maintain rotational stability of the hind limbs during flight be acting against counter rotators and extensors.

M. PSOAS MAJOR

*Origin.* From ventrolateral surfaces of lumbar vertebrae three to six, medial half of ventral surface of iliac crest, and from pubis just posterior to spine.

*Insertion.* On anterior surface of lesser trochanter of femur.

*Remarks.* The origin in *Myotis* is on lumbers three to five, in *Macrotus*, on lumbar three to six and from the ilium and pubis as in *Eumops*. In *Hipposideros* the origin is on lumbers five to seven; the muscle passes deep to the descending ramus of the ilium and through the iliac fenestra to the insertion on the lesser trochanter. Some fibers originate from the anterior and dorsal rim of the iliac fenestra.

*Action.* Flexion and rotation of the femur. The function of this muscle is probably similar to that of the iliacus.

M. PECTINEUS

*Origin.* On lateral surface and base of pubic spine.

*Insertion.* Along roughly proximal half of anteroventral surface of femur starting 3 mm distal to lesser trochanter.
Remarks. In Macrotus and Hipposideros the insertion is on the medial ridge of the humerus; in the latter the origin is from the anteriormost part of the pubis.

Action. This muscle is mostly an adductor of the femur in Eumops and Myotis. In these genera this muscle helps support the weight of the body during terrestrial locomotion and works with the other adductors in maintaining dorsoventral stability of the femur during flight. In Macrotus and especially in Hipposideros the origin is displaced cranial and the insertion is on the medial ridge well medial to the axis of rotation of the femur. Due to these differences, the muscle is mostly a flexor and rotator of the femur in these genera.

B. Gluteal Group (Fig. 13)

During flight the force exerted by the airstream against the flight membranes is transmitted to the hind limbs, which anchor the proximal part of the trailing edge of the wing and the anterior and lateral edges of the uropatagium. Movements of the hind limbs during flight affect the angle of attack, camber, and tautness of the membranes. Accordingly, it is of considerable aerodynamic importance that the hind limbs be braced against the pull exerted from a variety of angles due to the changes in positions of the wings during the wing-beat cycle. The gluteal group of muscles in Eumops and Myotis help maintain the dorsoventral stability of the hind limbs in flight by resisting the ventral pull of the wing membranes during the lower part of the downstroke. In Macrotus and Hipposideros, because of the spiderlike postures of the hind limbs, these muscles resist lateral pull by the wing membranes.

M. Tensor Fasciae Latae

Origin. Along posterodorsal edge of iliac crest and neural ridge of first sacral vertebra.

Insertion. On anterior edge of M. gluteus maximus and middle of lateral surface of femur.

Remarks. This muscle is roughly similar in all four genera.

Action. Abduction and flexion of the femur.

M. Gluteus Maximus

Origin. On neural spines and middorsal fascia of last three sacral and first caudal vertebrae.

Insertion. Along middle 3 mm of lateral surface of femur.

Remarks. In Myotis the insertion is along the second fifth of the femur,
and in *Macrotus* and *Hipposideros* the insertion is within the proximal third of the femur.

*Action.* Abduction and flexion of the femur.

**M. Gluteus Medius**

*Origin.* Along posterodorsal rim of iliac crest and from entire iliac fossa.

*Insertion.* On greater trochanter of femur.

*Remarks.* This muscle is similar in all four genera.

*Action.* Flexion, abduction, and rotation of the femur.

**C. Quadriceps Femoris Group (Fig. 13)**

**M. Quadriceps Femoris**

In the bats under discussion, this muscle is composed of two parts. One part, probably composed of the fused vastus lateralis, vastus medialis, and vastus intermedius, originates on the femur. The origin of the second part, the rectus femoris, is on the ilium. It is not clear with what muscles in other mammals the first part is homologous. For the sake of convenience, this part is here called the vastus lateralis.

*Origin.* M. rectus femoris: from ilium immediately anterior to acetabulum. M. vastus lateralis: from greater trochanter, proximal two-thirds of anterolateral surface, and entire anterior surface of femur.

*Insertion.* On patella.

*Remarks.* In all but *Macrotus* the vastus lateralis is larger than the rectus femoris; in *Macrotus* the rectus femoris is the larger and the two divisions have separate tendons of insertion. The vastus lateralis originates in *Myotis* along the proximal third of the femur, and in *Macrotus* and *Hipposideros*, on all but the distal third of the femur.

*Action.* This muscle extends the shank. Acting against the powerful flexors of the shank (the gracilis, semimembranosus and semitendinosus), the quadriceps femoris probably is important in steadying the shank during flight. This muscle also causes extension of the shank at the end of the rearward part of the stride during terrestrial locomotion.

**D. Tibial Extensor Group (Figs. 13 and 14)**

**M. Extensor Digitorum Longus**

*Origin.* From lateral condyle of femur and anterior surface of M. extensor digitorum longus.
Insertion. On dorsal bases of distal phalanges of digits two to five.
Remarks. The insertion in *Myotis* and *Macrotus* is on digits one to five.
Action. Extension of the digits.

**M. extensor hallucis longus**

*Origin.* From lateral condyle of femur and anterior surface of M. extensor digitorum longus.
*Insertion.* On medial surface of base of first metatarsal.
*Remarks.* In *Myotis* the origin is on all but the most proximal 3 mm of the posterior surface of the tibia and from the lateral surface of the distal third of the fibula. The insertion is on the lateral part of the base of the first phalanx of the first digit. This is a delicate muscle in *Macrotus* and originates on the lateral surface of the distal half of the tibia. The origin in *Hipposideros* is along the proximal half of the tibia.
*Action.* This muscle rotates the foot craniad and dorsad. The large size of the muscle in *Eumops* is probably due to the importance of crawling in this bat, and the small size of the muscle in *Macrotus* may be associated with this animal’s inability to crawl.

**MM. extensoris breves**

*Origin.* This muscle is composed of seven slips. The medial slip originates on the anterodorsal surface of the distal end of the fibula, and the lateral slip, from the dorsal surface of the proximal part of the calcaneus. The other five slips originate on the dorsal projection on the distal part of the calcaneus.
*Insertion.* Medial slip: on dorsomedial surface of base of first phalanx of first digit. Lateral slip: on dorsolateral surface of base of first phalanx of fifth digit. The other slips insert on the distal phalanges of digits one to five.
Remarks. This muscle is similar in the four genera.
*Action.* Extension of the digits.

*E. Peroneal Group (Fig. 13)*

**M. peroneus longus**

*Origin.* From lateral condyle of tibia and proximal third of anterolateral surface of fibula.
**Insertion.** On ventrolateral base of fourth metatarsal.

**Remarks.** In *Myotis* this muscle originates on the head and lateral surface of the proximal two-thirds of the fibula. The insertion is on the ventral base of the third metatarsal. The origin in *Macrotus* is from the base and the distal vestige of the fibula, and the insertion is on the base of the second metatarsal.

**Action.** This muscle rotates the foot dorsad and laterad. This action aids the M. gastrocnemius in giving a final push at the end of the stride used in terrestrial locomotion in *Eumops* and *Myotis*.

**M. peroneus brevis**

**Origin.** From middle half of anterolateral surface of fibula.

**Insertion.** On dorsolateral base of fifth digit.

**Remarks.** In *Myotis* the insertion is on the dorsal surface of the shaft of the fifth metatarsal.

**Action.** The action is similar to that of the M. peroneus longus.

**F. Adductor Group (Fig. 12)**

**M. gracilis**

**Origin.** Along ventrolateral edge of pelvis from posteroventrall angle to tip of pubic spine and along posterior 3 mm of insertional tendon of M. psoas minor.

**Insertion.** On posteromedial surface of tibia one-third of way along shank, by a common tendon with the semitendinosus.

**Remarks.** This muscle is roughly equal to the semimembranosus in size in *Eumops*, and these are the largest muscles in the hind limb. The gracilis muscle is also large in the other genera. In *Myotis* the insertion is approximately one-sixth of the way along the shank. The insertion in *Macrotus* is by separate tendon one-tenth of the way along the shank. This is the largest muscle of the pelvic girdle in *Hipposideros*. The origin is unusually extensive, extending along the ventrolateral border of the pelvis from the junction of the pubis and ilium to the posteriormost part of the ischium. The insertion is at the end of the proximal fifth of the tibia.

**Action.** This muscle flexes the shank and adducts the femur. The common tendon of insertion of the gracilis and the semitendinosus in the three genera suggests that these muscles perform their most important functions together. Together they form the strongest functional unit of the musculature of the pelvic girdle.
In *Eumops* and *Myotis* a major function of this muscle may be to maintain partial flexion of the shank against the force of the lateral pull exerted by the plagiopatagium during flight. This flexion is important for spreading the uropatagium and anchoring the proximal part of the plagiopatagium. In these genera, when the claws of the feet have purchase on the substrate, the common action of the gracilis and the semitendinosus extends and adducts the femur. These movements tend to support the weight of the body and move the hind limb through part of the propulsion stroke used in terrestrial locomotion. In *Macrotus* and *Hipposideros*, because of the posture of the hind limbs, the gracilis helps maintain dorsoventral stability of these limbs during the wing-beat cycle. By flexing the shank the gracilis may also help in movements made while the bats are hanging.

**M. adductor longus**

*Origin*. Along lateral surface of ventral half of ascending ramus and posteroverentral angle of ischium and from pubis posterior to spine.

*Insertion*. On roughly proximal third of posteromedial surface of femur.

*Remarks*. In *Myotis* the origin is on the posteroverentral angle of the ischium; the insertion is along the middle third of the femur. This muscle is large and is in two parts in *Macrotus* and *Hipposideros*. The first part takes origin roughly as in *Eumops*; the second part originates along the ascending ramus of the ischium mostly dorsal to the origin of the first part. Considering both divisions, the insertion extends along the posterior surface of the medial ridge and extends well beyond its distal end.

*Action*. Adduction and extension of the femur.

**M. adductor brevis**

*Origin*. Along lateral surface of posteroverentral rim of obturator fenestra.

*Insertion*. Along 4 mm of proximal part of posterolateral surface of femur.

*Remarks*. This muscle originates on the ascending ramus of the ischium in *Myotis*, but otherwise differs but little between the four genera.

*Action*. In *Myotis* this muscle extends, and in the other genera it adducts, the femur.
M. ADDUCTOR MAGNUS

Origin. Along 4 mm of ventral border of obturator fenestra.
Insertion. On posterior part of greater trochanter of femur.
Remarks. In Myotis and Macrotus, the origin is from the ischium posterior to the acetabulum.
Action. In Eumops and Hipposideros, this muscle adducts the femur and rotates it such that the shank swings downward and forward. Because of the different placement of the origin in Myotis and Macrotus, this muscle in these genera acts primarily as an extensor of the femur.

M. OBTURATOR EXTERNUS

Origin. Along posteroinferior rim of obturator fenestra.
Insertion. On posteromedial surface of greater trochanter of femur.
Remarks. This muscle is absent in Hipposideros, but is present and differs little in the other genera.
Action. Adduction and extension of the femur.

G. ISCHIOTROCHANTERIC GROUP (Fig. 12)

M. GEMELLUS

Origin. On dorsal ramus of ischium from near posterior rim of acetabulum to dorsal tuberosity.
Insertion. On posterior part of greater trochanter of femur.
Remarks. This muscle is absent in Myotis and is very small in Macrotus. It is similar in size and attachments in Eumops and Hipposideros.
Action. Extension and rotation of the femur.

H. HAMSTRING GROUP (Fig. 13)

The muscles of this group serve mainly to extend the femur and to flex the shank. In Eumops and Myotis, this action is important in controlling the propulsion part of the stride in terrestrial locomotion. The "pouching" of the uropatagium when Myotis catches insects seemingly involves rapid flexion of the shank and some degree of extension of the femur, actions caused in part by muscles of the hamstring group. The different posture of the limbs in Macrotus and Hipposideros allows these muscles in these genera to aid in maintaining dorsoventral stability.
of the hind limbs during flight. Movements made by these bats while hanging frequently involve flexion of the shank, an action primarily under the control of the hamstring group.

M. CAUDOFEMORALIS

*Origin.* On last sacral and first caudal vertebrae.

*Insertion.* Along proximal half of posterior surface of femur.

*Remarks.* The origin in *Myotis* is from the last sacral vertebra; the insertion is along the proximal third of the femur. In *Hipposideros* the origin is from the dorsal ramus of the ischium, and in this genus and in *Macrotus* the insertion is along the proximal quarter of the femur.

*Action.* Extension of the femur.

M. SEMITENDINOSUS

*Origin.* From dorsal ischial tuberosity.

*Insertion.* On posterior border of tibia, by common tendon with the M. gracilis.

*Remarks.* In all but *Macrotus* insertion is by a common tendon with the M. gracilis. In *Myotis* the insertion is one-sixth of the way along the tibia. This muscle originates by two heads in *Macrotus*: (1) from the dorsal ischial tuberosity; (2) from the middle of the dorsal ramus of the ischium. The insertion is at the distal end of the proximal eighth of the tibia. The origin extends from the posterior angle of the ischium to just posterior to the acetabulum in *Hipposideros*.

*Action.* Extension of the femur and flexion of the shank. This muscle is ideally situated to help power the rearward component of the stride in *Eumops* and *Myotis*.

M. SEMIMEMBRANOSUS

*Origin.* From dorsal tuberosity and ascending ramus of ischium.

*Insertion.* On posteromedial surface of tibia at end of proximal quarter of shank.

*Remarks.* The insertion in *Myotis* is one-sixth, in *Macrotus*, one-eighth, and in *Hipposideros*, one-tenth of the way along the shank.

*Action.* Extension of the femur and flexion of the shank.

M. BICEPS FEMORIS

*Origin.* From tip of dorsal ischial tuberosity.

*Insertion.* On lateral condyle of tibia.
Remarks. This muscle is absent in *Myotis* and *Hipposideros* and is vestigial in *Macrotus*.

Action. In *Eumops* this muscle extends the femur and flexes the shank.

I. Flexor Group of Leg (Fig. 12)

M. gastrocnemius

*Origin.* Medial head: from posteromedial surface of femur just proximal to medial condyle. Lateral head: on posterior surface of head of fibula and lateral condyle of femur.

*Insertion.* On proximal end of calcaneus.

*Remarks.* This muscle differs little between the four genera.

*Action.* Flexion of the foot.

M. plantaris

*Origin.* On proximal two-thirds of posterior surface of tibia and adjacent surface of proximal half of fibula.

*Insertion.* On ventral surfaces of distal phalanges of all five digits.

*Remarks.* In all four genera the large tendon of this muscle broadens into a plantar aponeurosis joined by the tendon of the flexor digitorum fibularis (Fig. 14). The origin of the plantaris in *Myotis* is from the proximal two-thirds, and in *Macrotus* and *Hipposideros*, from the proximal half of the tibia.

Seemingly the primitive pattern in terrestrial mammals is for the plantaris tendon to divide in the plantar region and to give rise to a deep and a superficial aponeurosis. From the deep part originates the flexor digitorum brevis. The aponeurosis of the flexor digitorum fibularis lies deep to the two plantar aponeuroses and gives origin to the Mm. lumbricales. From this plan the bats considered here differ as follows: the superficial plantar aponeurosis is absent; the flexor digitorum brevis does not originate on the plantaris; the deep plantar aponeurosis is fused distally to that of the flexor digitorum fibularis; the lumbricales originate on the ventral surface of the plantar aponeurosis.

*Action.* Flexion of the digits of the foot. The fusion of the tendons of the plantaris and the flexor digitorum fibularis suggest that these muscles usually work together. These muscles form the strongest muscular unit in the shank and probably act primarily when the claws grip the substrate.
M. POPLITEUS

Origin. From medial part of head of fibula.
Insertion. On proximal half of posterolateral surface of tibia.
Remarks. This muscle is vestigial in Myotis and inserts on the tibia just distal to the head. In Macrotus this muscle fills most of the concavity in the posterior surface of the tibia adjacent to the head and inserts along the proximal eighth of the tibia. The popliteus is absent in Hipposideros.
Action. This muscle binds the fibula to the tibia.

M. TIBIALIS POSTERIOR

Origin. From distal two-thirds of medial surface of fibula and anterior surface of M. flexor digitorum fibularis.
Insertion. On ventral surface of tarsus.
Remarks. In Myotis this muscle originates along the distal third, in Macrotus, along the distal three-quarters, and in Hipposideros, along the distal half of the shank.
Action. Extension of the foot.

M. FLEXOR DIGITORUM FIBULARIS

Origin. From nearly entire length of posteromedial surface of fibula.
Insertion. On ventral surfaces of distal phalanges of all five digits.
Remarks. The aponeurosis of this muscle and that of the plantaris are fused at their distal ends in all but Eumops, in which the fusion involves the entire aponeurosis.
Action. Flexion of the digits of the foot.

J. Flexor Group of Foot (Fig. 14)

M. FLEXOR DIGITORUM BREVIS

Origin. On proximal end of calcaneus.
Insertion. On lateral surfaces of second phalanges of digits two to four.
Remarks. The identification of this muscle is tentative. Each tendon divides at the proximal end of the first phalanx and sends a tendon on either side of the common tendon of the plantaris and flexor digitorum fibularis. In Macrotus an additional tendon inserts on the fifth digit.
Action. Flexion of the digits served.
M. **ABDUCTOR HALLUCIS BREVIS**

*Origin.* On distal part of medial tarsal bone.

*Insertion.* On medial sesamoid of first metatarsophalangeal joint.

*Remarks.* This muscle is similar in the four genera.

*Action.* Abduction of the first digit.

M. **ABDUCTOR OSSIS METATARSI QUINTI**

*Origin.* From ventrolateral part of calcaneus.

*Insertion.* On lateral border of plantar aponeurosis.

*Remarks.* In *Hipposideros* this muscle inserts on the expanded lateral part of the base of the fifth metatarsal.

*Action.* This muscle pulls the plantar aponeurosis laterad and proximad in all but *Hipposideros*; in this genus the action is abduction of the fifth digit.

M. **ABDUCTOR DIGITI QUINTI**

*Origin.* On ventral surface of distal end of calcaneus and lateral part of base of fifth metatarsal.

*Insertion.* On lateral sesamoid of fifth metatarsophalangeal joint.

*Remarks.* This muscle is divided in *Hipposideros* and one tendon inserts on each side of the fifth metatarsophalangeal joint.

*Action.* Abduction of the fifth digit.

M. **ADDUCTOR HALLUCIS**

*Origin.* From ventral bases of second and third metatarsals and raphe between this muscle and the M. adductor digiti quinti.

*Insertion.* On lateral base of first phalanx of first digit and lateral sesamoid of first metatarsophalangeal joint.

*Remarks.* This muscle is vestigial in *Hipposideros*.

*Action.* Adduction of the first digit.

M. **ADDUCTOR DIGITI QUINTI**

*Origin.* From ventral bases of metatarsals two and three and raphe between this muscle and adductor hallucis.

*Insertion.* On medial base of first phalanx of fifth digit and medial sesamoid of fifth metatarsophalangeal joint.

*Remarks.* This muscle is absent in *Hipposideros*.

*Action.* Adduction of fifth digit.
MM. LUMBRICALES

*Origin.* From ventral surface of plantar aponeurosis.

*Insertion.* Along dorsal surfaces of second phalanges of digits one to five.

*Remarks.* There are nine lumbricales. They send a tendon spiraling around each side of digits two to five, and one tendon around the medial surface of the first digit.

*Action.* Flexion of the digits.

M. INTEROSSEI

*Origin.* By 10 slips, one from the lateral and one from the medial base of each metatarsal.

*Insertion.* On lateral and medial base of first phalanx of each digit and the sesamoid bones of each metatarsophalangeal joint.

*Action.* Flexion of the digits.

V. CHIROPTERAN MUSCLE SPECIALIZATIONS FOR FLIGHT

In the evolution of bats the muscles that enabled terrestrial mammals to crawl, run, or climb were modified into a system effective primarily in controlling wings during flight. Many of the typically chiropteran muscular specializations are clearly associated with specific demands of flight, such as the necessity for lightness of the appendages, particularly the wings. Many fairly minor morphological changes were of major importance in perfecting the bat as a flying animal.

A. WEIGHTS OF MAJOR FLIGHT MUSCLES IN BATS

The pectoralis muscle, the largest and most important flight muscle in bats, comprises less than 10% of the total weight of these animals (Table III). Relative to the pectoralis of birds (Table IV), that of bats is small and is less variable in weight. Among the bats I have studied, the variation in pectoral size is from 5.4% of the body weight in *Natalus stramineus* (Natalidae) to 8.5% in *Pteropus* sp. (Pteropodidae) and *Artibeus lituratus* (Phyllostomidae). Hartman (1963) found that within a single family of birds (the flycatchers, Tyrannidae) the pectoralis varies from 12 to 22% of the body weight, and that whereas the pectoralis is 5.7% of the body weight in a grebe (*Podilymbus* sp.), this muscle is 33% of the body weight in a dove (*Leptotila*). The above
data support the conclusion that there is a greater similarity between styles of flight in bats than in birds.

**Table III** Percentage of the total weight that the pectoralis muscle comprises in selected bats

<table>
<thead>
<tr>
<th>Species</th>
<th>Body weight (gm)</th>
<th>Pectoralis weight (gm)</th>
<th>Pectoralis weight Body weight</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pteropus</em> sp. (1)</td>
<td>836.4</td>
<td>70.84</td>
<td>8.5</td>
</tr>
<tr>
<td><em>Pteronotus davyi</em> (3)</td>
<td>9.9</td>
<td>0.61</td>
<td>8.4</td>
</tr>
<tr>
<td><em>Sturnira lilium</em> (22)</td>
<td>14.8</td>
<td>1.02</td>
<td>6.8</td>
</tr>
<tr>
<td><em>Artibeus hirsutus</em> (21)</td>
<td>31.2</td>
<td>2.19</td>
<td>6.9</td>
</tr>
<tr>
<td><em>A. jamaicensis</em> (6)</td>
<td>30.9</td>
<td>2.15</td>
<td>6.9</td>
</tr>
<tr>
<td><em>A. lituratus</em> (18)</td>
<td>46.8</td>
<td>4.06</td>
<td>8.5</td>
</tr>
<tr>
<td><em>Natalus stramineus</em> (3)</td>
<td>6.0</td>
<td>0.32</td>
<td>5.4</td>
</tr>
<tr>
<td><em>Lasius borealis</em> (22)</td>
<td>10.2</td>
<td>0.86</td>
<td>8.4</td>
</tr>
<tr>
<td><em>Molossus ater</em> (19)</td>
<td>28.7</td>
<td>2.37</td>
<td>8.3</td>
</tr>
</tbody>
</table>

*Weights were taken from preserved animals. Numbers in parentheses indicate the number of specimens weighed and averaged.

**Table IV** Percentages of the total weights that the pectoralis muscle comprises in selected birds

<table>
<thead>
<tr>
<th>Species</th>
<th>Weight of pectoralis muscle expressed as percentage of total weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pintail duck (<em>Anas acuta</em>)</td>
<td>21.3</td>
</tr>
<tr>
<td>Black vulture (<em>Coragyps atratus</em>)</td>
<td>14.3</td>
</tr>
<tr>
<td>Duck hawk (<em>Falco peregrinus</em>)</td>
<td>18.2</td>
</tr>
<tr>
<td>Bobwhite quail (<em>Colinus virginianus</em>)</td>
<td>21.6</td>
</tr>
<tr>
<td>Killdeer (<em>Charadrius vociferans</em>)</td>
<td>21.5</td>
</tr>
<tr>
<td>Laughing gull (<em>Larus atricilla</em>)</td>
<td>12.6</td>
</tr>
<tr>
<td>Rock dove (<em>Columbia livia</em>)</td>
<td>20.3</td>
</tr>
<tr>
<td>Lesser nighthawk (<em>Chordeiles acutipennis</em>)</td>
<td>19.6</td>
</tr>
<tr>
<td>Chestnut-sided warbler (<em>Dendroica pennsylvanica</em>)</td>
<td>13.6</td>
</tr>
<tr>
<td>Field sparrow (<em>Spizella pusilla</em>)</td>
<td>18.3</td>
</tr>
<tr>
<td>Coot (<em>Fulica americana</em>)</td>
<td>8.2</td>
</tr>
</tbody>
</table>


The three largest muscles that power the downstroke in bats are the pectoralis, the posterior division of the serratus anterior, and the subscapularis (Vaughan, 1959, p. 117). The relative weights of these muscles are fairly uniform even between distantly related bats (Table I). The pectoralis is approximately 65% of the total weight of these muscles;
the other two muscles roughly equal each other in weight. The slight
differences between the relative weights of the three major flight muscles
in different bats are probably associated both with differences in the
structure of the bones of the pectoral girdle and with differences in
styles of flight. Because most bats fly at night and depend on echoloca-
tion for the perception of obstacles, maneuverability is of great impor-
tance. The consistency of the relative weights of the major flight muscles
suggests that an optimal division of muscular labor for controlling ma-
neuverable flight has evolved in bats. Wide departures from the usual
pattern would perhaps impair maneuverability.

In the three vespertilionid bats listed in Table II, the coracoid head
of the biceps is appreciably smaller than the glenoid head, whereas in
the molossids measured the coracoid head is roughly twice the weight
of the glenoid head. This striking difference in relative weights of mus-
cles lends support to the supposition, considered in the description of
the biceps brachii muscles, that the coracoid head of this muscle is
better adapted to help power the downstroke in molossids than it is
in other bats (see Vaughan, 1966).

B. Reduction of the Weight of the Wing

Concentration of weight near the center of gravity and reduction of
the weight of the wings are adaptations for flight common to all flying
animals. These specializations occurred in the pterosaurs, the large flying
reptiles of the Mesozoic Era, and are apparent today in insects, birds
and bats. Many of the most important adaptive features of the chirop-
teran wing are associated with a reduction or redistribution of the weight
of the wing.

Propulsion is obtained in all flying animals by movements of the wings,
and the kinetic energy produced by such movements depends upon
the speed of the wing and its weight. The amplitude of a stroke and
its speed are progressively greater toward the wing tip. Consequently,
reduction of the weight of the distal parts of the wing results in reducing
the kinetic energy developed during a wing stroke. A considerable ad-
vantage in metabolic economy is thus gained, for the less kinetic energy
developed during each stroke the less energy necessary to control the
wings. In addition, light wings can be controlled with speed and preci-
sion during the extremely rapid maneuvers used when bats chase flying
insects.

The most important modifications serving to lighten the wings of bats
involve both skeleton and musculature and serve to transfer the burden
of controlling the wings from small, distally situated muscles, to large, proximally situated muscles. In general, the mechanical arrangements of the muscles of the forelimb are such that extension of the humerus by the large muscles that power the downstroke causes automatic extension of the forearm and spreading of the distal part of the wing (extension of the digits).

Several muscles of the forearm are especially important. The extensor carpi radialis longus and brevis tend to extend the metacarpals automatically when the forearm is extended, an action facilitated by the placements of the attachments of these muscles and by adaptations that reduce their elasticity (see accounts of these muscles). The flexor carpi ulnaris regulates the degree of flexion or extension of the fifth digit automatically during corresponding movements of the forearm. These thin and largely tendinous muscles act mostly to transfer force exerted on them indirectly by more proximally situated muscles. Along the upper arm (brachium) lie the biceps and triceps muscles; these cause flexion and extension of the forearm, respectively. The bellies of these muscles are proximally located and are made relatively inelastic by investing sheaths of connective tissue. The triceps muscles are stretched when the humerus is extended and thus in part use force exerted on them by more proximally placed muscles to extend the forearm. The biceps muscles are aided in their action of flexion of the forearm by being stretched when more proximally placed muscles flex the humerus. It is apparent, then, that some of the most important flight muscles of the forearm and upper arm, the muscles that control extension and flexion of the hand and forearm, serve partly to transfer distally the force exerted on them by the large muscles originating near the center of gravity on the scapula or axial skeleton. Because of this functional arrangement, these light, slender muscles can effectively perform their demanding functions.

There is considerable variation in the size of the musculature of the forearm in bats. For example, the musculature of the forearm is larger and heavier, relative to the total weight of the animal, in the primitive Hipposideros armiger than it is in the more advanced genus Molossus ater. The lightness in the advanced species results both from greater perfection of automatic devices and from the simplification of the musculature by the loss of certain muscles.

The hind limbs in most bats are lightly built and the largest muscles are situated near the center of gravity. In contrast to the forelimbs, however, there are no automatic devices in the hind limbs that contribute to lightness of the distal musculature.
C. Muscular Control of the Wing-beat Cycle

The wings of all flying animals produce both the forward propulsion (thrust) and lift necessary for flight, and the largest muscles of these animals control the wings. In bats, as in most birds, the downstroke of the wings is the propulsion stroke, whereas the upstroke is relatively passive and requires relatively little power. The ventral muscles that adduct the wing are accordingly the most important flight muscles in bats.

There is an intricate division of labor between the several most important adductors that power the downstroke in bats. Seemingly, the arrangement is such that when the greater tuberosity of the humerus locks against the scapula at the top of the upstroke and transmits the force of this stroke to the scapula, the serratus anterior (posterior division) stops the upstroke and starts the downstroke by steadying the lateral border of the scapula and tipping it slightly ventrad. The action of this serratus muscle is probably of considerable importance in allowing for a greater time interval between contractions of the other major muscles controlling the downstroke. The common action of the pectoralis, subscapularis, and clavodeltoideus then extends the humerus and pulls it downward, completing the downstroke. The rotational stability and angle of attack of the wing during the downstroke is probably under the control of these muscles and perhaps the biceps brachii, which in high-speed photographs of bats in flight appears to be under tension during the downstroke.

The upstroke of the wing involves primarily abduction (elevation) of the humerus and partial flexion of all segments of the wing but the phalanges. During the upstroke the trapezius, rhomboideus, and anterior division of the serratus anterior muscles brace the scapula and anchor its medial border, while the spinodeltoideus, acromiodeltoideus, supraspinatus, and infraspinatus elevate the humerus and govern the rotational stability and angle of attack of the wing. The force of the airstream probably helps raise the wing.

A similar end—the effective control of the wings—has been achieved by different means in bats and birds. In birds but two muscles, the pectoralis and supracoracoideus, are of major importance in powering the wing-beat cycle (see George and Berger, 1966, pp. 22–24). Both muscles originate on the sternum. The sternum is greatly enlarged and bears a prominent keel in most birds, and the claviculae, coracoids, and scapulae are braced solidly and almost immovably against the axial skeleton. The avian scapula is long and bladelike and much of its muscu-
ature serves most importantly to bind this bone to the rib cage and vertebral column. This morphological plan makes the bird’s body deeper than it is wide, and keeps the center of gravity low, an advantageous feature in terms of aerodynamic stability.

In bats a very different arrangement occurs. No less than four muscles (pectoralis, subscapularis, posterior division of the serratus anterior, clavodeltoidus) are important in controlling the downstroke, and at least an equal number serve directly to raise the wing during the upstroke. Only one of these muscles originates on the sternum. In further contrast, the sternum is not greatly enlarged nor does it bear a large keel in most bats, and the scapula is large, complexly faceted, and has considerable freedom of movement. Indeed, the unique chiropteran arrangement for muscular control of the downstroke is based on the ability of the scapula to rock slightly on its long axis. Reviewing briefly, then, in birds most of the power for the wing-beat cycle is provided by but two muscles, both originating on the sternum, and the scapula is firmly bound to the axial skeleton. In bats, in contrast, a relatively large number of muscles control the wing-beat cycle, only one of these muscles originates on the sternum, and mobility of the scapula is essential to the control of the cycle.

Why are the adaptations for the control of the wings so different in bats and birds? The differences may have resulted from a predilection of bats, during the period of their early evolution, to rest and escape danger by day in narrow cracks and crevices. Any modifications causing a considerable increase in dorsoventral thickness of the body, such as occurred in birds, would have made it difficult for bats to use such confining retreats. The assemblage of muscular and osteological specializations typical of bats avoids great enlargement of the pectoralis muscle and a resultant increase in dorsoventral thickness. The reptilian posture of the hind limbs typical of most bats may also have developed in response to crevice dwelling. Flight and movement within a crevice demand the same general type of limb posture, and it is possible that the course of the early evolution of bats was “guided” by both of these types of locomotion (Vaughan, 1959, p. 134).

REFERENCES

Stereoradiograph of fossil bat, about 50 million years old, described in Chapter 1. Two times natural size. Cf, fourth caudal vertebra; Hl, left humerus, partly opaque to x-rays; Tir, right tibia, distal end; Wr, right wrist.