# Post-Cranial Osteology of Bats

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Fossil bats give few clues to the early evolution of the Chiroptera. Adaptations for flight were well established by early Eocene, and osteological characters of Recent Chiroptera show only minor changes since the Eocene.

Examination of the post-cranial skeleton reveals these important general features: (1) arch, anteroposterior compression and partial fusion of the vertebral column; (2) well developed pectoral girdle with large clavicles and a small keel present on the sternum; (3) secondary humeroscapular association; (4) modification of the forearm for flight with the ulna rudimentary and the metacarpals and phalanges elongated to spread the flight membranes; (5) weak hind limbs, incomplete fibula; and (6) well developed hind feet.

## POST-CRANIAL OSTEOLOGY
### VERTEBRAL COLUMN

According to Romer (1966), mammals generally possess seven cervical, twelve to fourteen rib-bearing thoracic, five to seven lumbar, two to five sacral, and show a high degree of variation in the number of caudal vertebrae. The Chiroptera appear to be typical in the number of vertebrae present and differ only slightly from Romer's generalization. Table 1 presents specific information on vertebrae number for various bats. Grassé (1955) offers the following generalization for vertebrae number in bats: seven cervicals, eleven to twelve thoracics, five to seven lumbars, three to four sacrals and the number of caudals variable. Table 1 would, however, indicate the following to be the case: the number of cervicals present is consistently seven, thoracics vary from eleven to thirteen, the lumbars range from four to seven, sacrals vary from one to five and the number of caudals range from none to seventeen.

The general contour of the vertebral column is typically mammalian in configuration as described by Romer (1966). The cervical region curves downward from the head; the curve is so great in some cases as to bring the back of the skull to the level of the first thoracic (H. Allen, 1893). The column begins to arch dorsally at the juncture of the seventh cervical and the first thoracic and downward through the lumbar region to the sacrum. The arching phenomenon is influenced by the fusion in various regions of the vertebral column, present in some bats.

Fusion occurs in three major areas of the chiropteran axial skeleton

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(Miller, 1907; Bourlière, 1955; Grassé, 1955) and may be a function of age (Dobson, 1878). The first area is the cervico-thoracic junction. In the Nycteridae, Megadermatidae, Rhinolophidae, Molossidae and some of the Vespertilionidae this fusion joins the seventh cervical and the first thoracic. These two vertebrae and the second thoracic are united in the Hipposideridae, but only the first and second thoracics are involved in the Thyropteridae.

A second area of fusion occurs in the lumbar region. In the Hipposideridae the lumbars are solidly fused. The last thoracic and all the lumbars are fused, boundaries obliterated and laterally compressed in the Natalidae and Furipteridae. In *Chilonycteris*, thoracics ten through twelve are fused with lumbars one and two (Walton & Walton, 1970). Where lumbar or thoraco-lumbar fusion occurs, the dorsal arching of the column is restricted to the anterior part of the thoracic region.

The third area of fusion is the sacral region. The number of vertebrae in this fusion is difficult to determine in adult specimens of many bats (Walton & Walton, 1968), and there is some confusion as to whether all those involved are true sacral vertebrae. This problem is discussed later in this section. Among fossil Chiroptera, there is little information on vertebral fusion. Jepsen (1966) does state, however, that no fusion is exhibited by *Icaronycteris*.

The atlas appears to be normal in its structure. Transverse processes are present and generally well developed in most bats. There is no neural spine, although a small tubercle is present on the anterior surface (H. Allen, 1893). The vertebrarterial canal is large and conspicuous.

The axis is the only cervical vertebra to possess a spinous process (Bell, 1836; Dobson, 1878; Flower, 1885). The spinous process is so well developed in *Pteropus* and *Epomophorus* as to equal the length of the body of the axis including the odontoid process. The odontoid process shows its greatest development in the *Pteropidae* (H. Allen, 1893). It does appear, however, to be quite small and tuberculoid in *Miniopterus* (Barbu, 1960). The transverse processes are present, but are much reduced in *Rhinopoma* (Wassif & Madkour, 1963).

All of the cervical vertebrae appear short and broad with slender neural arches. The posterior five lack neural spines, but exhibit well-developed transverse processes (Fig. 3).

The vertebrae of the thoracic region all bear ribs, but lack neural spines (Bell, 1836; Dobson, 1878; Flower, 1885). Rudimentary spines are, however, reported for *Rhinopoma* (Wassif & Madkour, 1963) and *Miniopterus* (Barbu, 1960). In *Eumops* the first thoracic is the largest in the series and bears a conspicuous, knob-like spine, but on subsequent

thoracics, medial and lateral ridges are formed (Vaughan, 1959). Small transverse processes are present, but tend to become smaller posteriorly. The neural arches are thin, and conspicuous spaces or gaps exist between successive neural arches. These gaps are most noticeable between the anterior members of the series and are probably associated with the dorsal arching of the column that occurs in this region.

The lumbar vertebrae are similar to the thoracic (Bell, 1836). Transverse processes and neural spines are obsolete (Flower, 1885) and the region has limited mobility (Dobson, 1878). The presence or absence of transverse processes varies throughout the order. *Rhinopoma* exhibits small transverse processes on all vertebrae (Wassif & Madkour, 1963); but in *Macrotus* they appear on lumbars three through five, and are present only on the last lumbar of *Myotis* (Vaughan, 1959). Neural spines also vary: *Rhinopoma* retains short, broad spines on all lumbars (Wassif & Madkour, 1963); *Eumops* has a neural ridge which is spine-like on the last two lumbars, and *Macrotus* lacks all trace of a spine on the last lumbar (Vaughan, 1959). Ventrally, ridges and/or spines are sometimes present. The sixth lumbar in *Macrotus* bears a mid-ventral spine (Vaughan, 1959); the Mystacinidae possess two minute ventral processes on the third lumbar (Miller, 1907), and the last lumbar fuses into the sacroiliac joint in *Mystacops*; *Saccopteryx* possesses two ventral processes on the fourth lumbar; the fifth and sixth lumbars in the Rhinolophidae have a distinct double or bifid hypophysis (Mille, 1970); and there is a distinct, low ventral ridge on all lumbars in *Chilonycteris* (Walton & Walton, 1970).

The mammalian sacrum is generally defined as those fused vertebrae between the lumbar and caudal vertebrae. A few of the anterior caudals may become fused with the sacral vertebrae (Grassé, 1955). Flower & Lydekker (1891) suggest that the sacral vertebrae should be those between the sacroiliac joint and the ischial-sacral ligaments. They acknowledge that this criterion makes the sacrals difficult to ascertain. Through embryological evidence, Flower (1885) and Wassif & Madkour (1963) distinguish between sacral and pseudosacral vertebrae. Flower (1885) defines the true sacrals as those which have a separate lateral ossification for connection to the ilium. This separate center of ossification in the embryo resembles that of the ribs. The remainder of the vertebrae in this region then become pseudosacrals. Romer (1966) defines the sacral region in mammals as those vertebrae which have lost the sacral ribs present in reptiles.

Grassé (1955) notes the fusion of the anterior caudals with the sacrals in some bats. Flower & Lydekker (1891) and Dobson (1878)
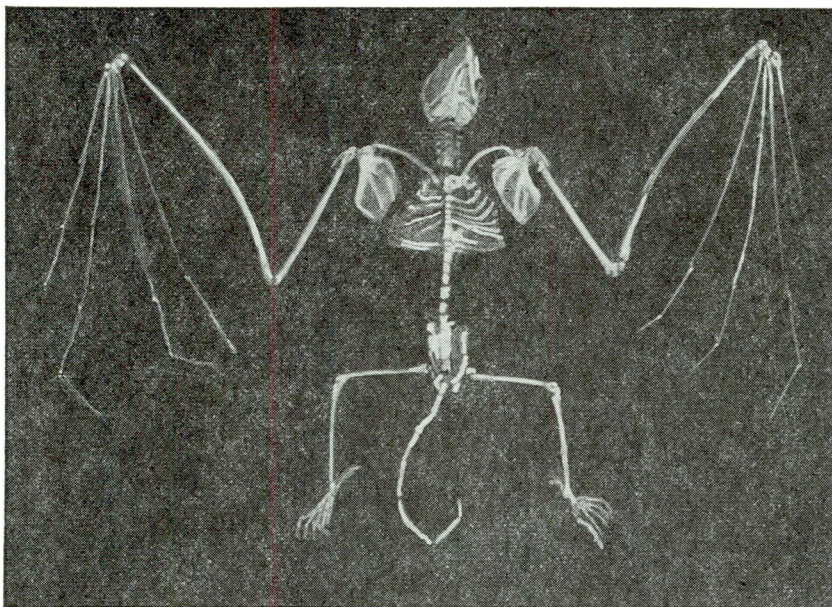
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FIG. 1. Ventral view of the bat *Nyctinomous* (=*Tadarida*).

define those vertebrae which have a connection with the ischium as caudals. Walton & Walton (1968) refer to a fused sacral region as distinct from the caudal region in the Phyllostomatidae. They note that the first two sacral vertebrae enter the sacroiliac joint. Barbu (1960) defines the os sacrum of *Miniopterus* as five fused vertebrae. Wassif & Madkour (1963) consider the sacral region of *Rhinopoma* to comprise the first four vertebrae. They name the last two vertebrae pseudo-sacrals; these are actually two caudal vertebrae which become fused into the sacrum in the embryo.

It should be noted at this point that the one sacral vertebra reported for *Pteropus* by Bell (1836) probably represents fusion of several vertebrae for Flower (1885) reports five present in *Pteropus*. The only clear instance of the presence of a single sacral vertebra is in the Eocene form *Paleochiropteryx taupaidon*. Another Eocene bat, *Icaronycteris index*, which apparently predates *Paleochiropteryx tupaidon,* has three sacrals (Jepsen, 1966). The general number of sacral vertebrae in fossil chiropterans is three or four (Dechaseaux, 1958).

In defining the sacrum, general vertebral characters must be considered. Each sacral vertebra has a reduced neural canal and centrum present. Caudally, these become more dorsoventrally compressed.

Lateral and dorsal processes as well as the amount of fusion are highly variable. The anterior end of the sacrum enters the sacroiliac joint, and the sacroischial joint may, in some cases, be a caudoischial joint.

The chiropteran sacrum is generally fused, and sutures between vertebrae may or may not be evident. The least amount of fusion is seen in the Vespertilionidae; the Pteropidae, Noctilionidae and Desmodontidae show the greatest amount of fusion in this region (Walton & Walton, 1968). The sacrum is generally dorsoventrally compressed and lacks spinous processes. A urostyle-like structure is present, however, in the Pteropidae, Emballonuridae, Noctilionidae, Desmodontidae and Phyllostomatidae (Walton & Walton, 1968). This urostyle arches above the mid-line in the Pteropidae, Noctilionidae and Desmodontidae (see Figs. 4 and 6). The lateral processes are reduced or absent except on those vertebrae which enter the sacroiliac and sacroischial joints. Centra and neural canals become reduced posteriorly. The last few vertebrae may have centra represented by a mere ridge. Fusion with the ilium in the sacroiliac joint is permanent and occurs early in the embryo (Wassif & Madkour, 1963).

When present, caudal vertebrae are simple, cylindrical bones generally lacking processes and always lacking neural canals. Considerable variation is shown in the length of the individual vertebrae (Bell, 1836; Dobson, 1878; Flower, 1885; Flower & Lydekker, 1891; H. Allen, 1893). In some cases the anterior caudals are united to the ischial tuberosities. The first caudal may be large and sacral-like with lateral and spinous processes (H. Allen, 1893). The first four caudals of *Rhinopoma* possess neural spines, and transverse processes are present on the first three (Wassif & Madkour, 1963). In *Miniopterus* the second caudal bears a haemal process on the mid-ventral line, and the neural spine on the first caudal is in the form of a crest (Barbu, 1960). *Chilonycteris* exhibits a neural spine on the first caudal, and transverse processes are reduced to ridges (Walton & Walton, 1970). Inspection of the caudal vertebrae of many different species indicates that the presence of various processes on the anterior-most caudals (usually caudals one through three) is a common characteristic.

In *Rhinopoma*, the fourth caudal may be longer than the combined length of the first three caudals and a gradual increase occurs from the fourth to the ninth (Wassif & Madkour, 1963). The third caudal is larger than the first two in *Miniopterus* (Barbu, 1960); in *Chilonycteris* the third caudal is equal in length to the first two caudals and the third through the fifth are essentially equal in length (Walton & Walton, 1970). In *Myzopoda* (Thomas, 1904), *Thyroptera* and *Furipterus* (Miller, 1907) the last caudal is represented as a cartilaginous rudiment.

## THE STERNUM

The chiropteran sternum is composed of two basic parts: the manubrium and the body (mesosternum and xiphoid portions). The manubrium usually bears two lateral processes and a vertical process. The clavicles and costal cartilages of the first ribs articulate with the lateral processes. The body of the sternum normally exhibits a low median ridge which may be raised into a low keel (Figs. 2 and 6). There is no clear boundary between the mesosternum and the xiphoid portion, although the posterior tip of the body of the sternum may be laterally expanded and bear a cartilaginous extension. The ventral margin of the median ridge of the body of the sternum may be smooth or serrate.

There is one vertical lobe on the presternum of all the families except the Pteropidae and Nycteridae. There are two large distinct lobes in the Pteropidae (Fig. 2). In the Nycteridae there is a large ventrally directed lobe and a smaller anterior lobe which is directed anteroventrally. Both lobes are directed ventrally in the Pteropidae. In the Furipteridae the single vertical lobe is forked and appears in the form of a "Y" (Fig. 2). The ventral margin of the vertical process exceeds the base of the manubrium in length in the chilonycterines. The vertical lobe is poorly developed in the Megadermatidae, Rhinolophidae and Hipposideridae.

The lateral lobes are generally directed laterally, but in the Noctilionidae, Phyllostomatidae, Desmodontidae, Natalidae and Furipteridae the processes are directed anterolaterally.

A single foramen pierces the lateral lobes of the manubrium in some of the Phyllostomatidae. In the Rhinolophidae and Hipposideridae two foramina pierce the lateral lobes. These, however, are not homologous to those in the Phyllostomatidae, but are formed as the result of incomplete fusion of the lateral processes with the second rib and costal cartilage. The manubrium of the rhinolophids and hipposiderids is more flattened and shield-like than in other families (Fig. 2). A secondary lateral process from the lateral lobes of the presternum is present in the Megadermatidae, Rhinolophidae and Hipposideridae, but the point of connection between the first costal cartilage and lateral processes is so greatly obscured that the secondary lateral processes may be derived from the cartilage. There is a tendency for the first costal cartilage in all bats to assume the appearance of bone; this tendency is most notable in the three above-mentioned families. A distinct notch in the posterior margin of the lateral lobes is seen in some of the Vespertilionidae and some of the Phyllostomatidae. In the Natalidae and Furipteridae there is a secondary lateral projection from the ventral terminus of the first costal cartilage.

On the body of the sternum a median ridge is generally present and raised into a distinct keel. In the Furipteridae the mesosternal portion is laterally expanded and the median ridge is almost completely obscured. In the Mystacinidae the median ridge is obscured between ribs 2-5.

The position of the greatest vertical height of the keel on the body of the sternum is highly variable. With only one exception the greatest height always occurs on the mesosternal portion. The exception occurs in the Furipteridae where the greatest height is found on the xiphoid portion. Serration of the keel is found in some of the Phyllostomatidae.

The body of the sternum is relatively shortest in the Rhinolophidae and Hipposideridae where the large shield-like manubrium appears to dominate the sternal configuration.

### THE RIBS

The ribs are equal in number to the thoracic vertebrae and are noted for their proportional length (Bell, 1836). All are double headed and Vaughan (1959) reports that the heads of the last two or three merge. The ribs tend to be flattened and somewhat close together according to Flower & Lydekker (1891); broad and flat with wide interspaces according to H. Allen (1893); and flattened and separated by narrow intervals according to Dobson (1878). The disagreement on the spacing of the ribs is undoubtedly caused by the fact that in some bats certain ribs are partially ankylosed together (Dobson, 1878; Miller, 1907; Grassé, 1955; Walton & Walton, 1968). In the Rhinolophidae and Hipposideridae, the ribs are greatly flattened (Dobson, 1878).

The first rib is generally the shortest, but is broad and flat. In *Natalus* and *Hipposideros* the first and second ribs are coalesced (H. Allen, 1893), and partially so in the Rhinolophidae (Miller, 1907). The costal cartilages associated with these two ribs are also broad and flat; that of the first is always larger. The breadth of the first costal cartilage may exceed the breadth of the first rib. The space between the other ribs is well defined, but may be narrow and nearly obliterated as in *Natalus* and *Hipposideros* (H. Allen, 1893).

Ribs often become ankylosed to the vertebrae and in old individuals of some forms become contiguous (H. Allen, 1893). In *Myotis, Eumops* and *Macrotus* the medial surface of the neck of each rib is in contact with the vertebrae (Vaughan, 1959).

The first rib always connects ventrally with the manubrium of the sternum. In *Myzopoda*, ribs two through eight join the body of the sternum, nine through eleven have cartilaginous extensions that do not reach the sternum, and the twelfth and thirteenth are floating ribs (Thomas, 1904). In *Eumops* the first seven are vertebrosternal, the

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next four are vertebrocostal and the last two are vertebral; there are six vertebrosternal, three vertebrocostal and two vertebral in *Myotis*; *Macrotus* has six vertebrosternal, three vertebrocostal and two vertebral ribs (Vaughan, 1959). *Miniopterus* has six vertebrosternal, three verte-brocostal and three vertebral ribs (Barbu, 1960); and *Rhinopoma* exhibits seven vertebrosternal, two vertebrocostal and three vertebral ribs (Wassif & Madkour, 1963). In *Chilonycteris* the first seven ribs are vertebrosternal (Walton & Walton, 1970).

There is considerable variation in the shape of the rib cage. Generally, it has a dorsoventrally flattened, bell shape; and the degree of flattening varies, also. The shape of the rib cage is associated closely with the variation in sternal form.

There apparently are twelve ribs (twelve thoracic vertebrae are present in *Icaronycteris*) and none are coalesced (Jepsen, 1966). Where known, fossil bats exhibit the general rib cage described above.

### PECTORAL GIRDLE AND LIMB

The general outline of the scapula is that of an oval, the length about twice the width. The posterior tip, the smaller end of the oval, is blunt and a cartilaginous extension may be present. The greatest width of the scapula occurs about the level of the base of the acromial process. The spine is short but distinct and may be deflected posteriorly at its medial end. The supraspinous fossa is always conspicuously smaller than the infraspinous fossa. A ventrally directed flange from the coracoid border may be present. The acromial process is large and conspicuous. The glenoid fossa faces laterad, and a facet for articulation with the trocheter or greater tuberosity of the humerus may be present. Three distinct facets are present in the infraspinous fossa and four in the subscapular fossa. The coracoid process is well developed, but the angu-lation of the process, degree of taper, and configuration of the distal tip are variable (see Figs. 2 and 6).

A deep notch in the coracoid border is present in the Emballonuridae, Nycteridae, Megadermatidae, Rhinolophidae, Hipposideridae, Phyllo-stomatidae, Desmodontidae, Natalidae, Vespertilionidae and Molos-sidae. It is shallow in the Pteropidae, Rhinopomatidae, Furipteridae, Thyropteridae and Myzopodidae, and very shallow in the Mystacinidae.

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FIG. 2. A. Left profile of the sternum of *Cynopterus;* B. Left profile of the sternum of *Phylloncyteris;* C. Left profile of the sternum of *Tadarida;* D. Right profile of the sternum of *Furipterus;* E. Ventral view of the shield-like sternum of *Hipposideros;* F. Dorsal view of the left scapula of *Mystacina;* G. Dorsal view of the left scapula of *Thyroptera;* H. Dorsal view of the left scapula of *Rhinolophus;* I. Dorsal view of the left scapula of *Rhinopoma;* J. Right humerus of *Rhinopoma;* K. Left humerus of *Noctilio.*
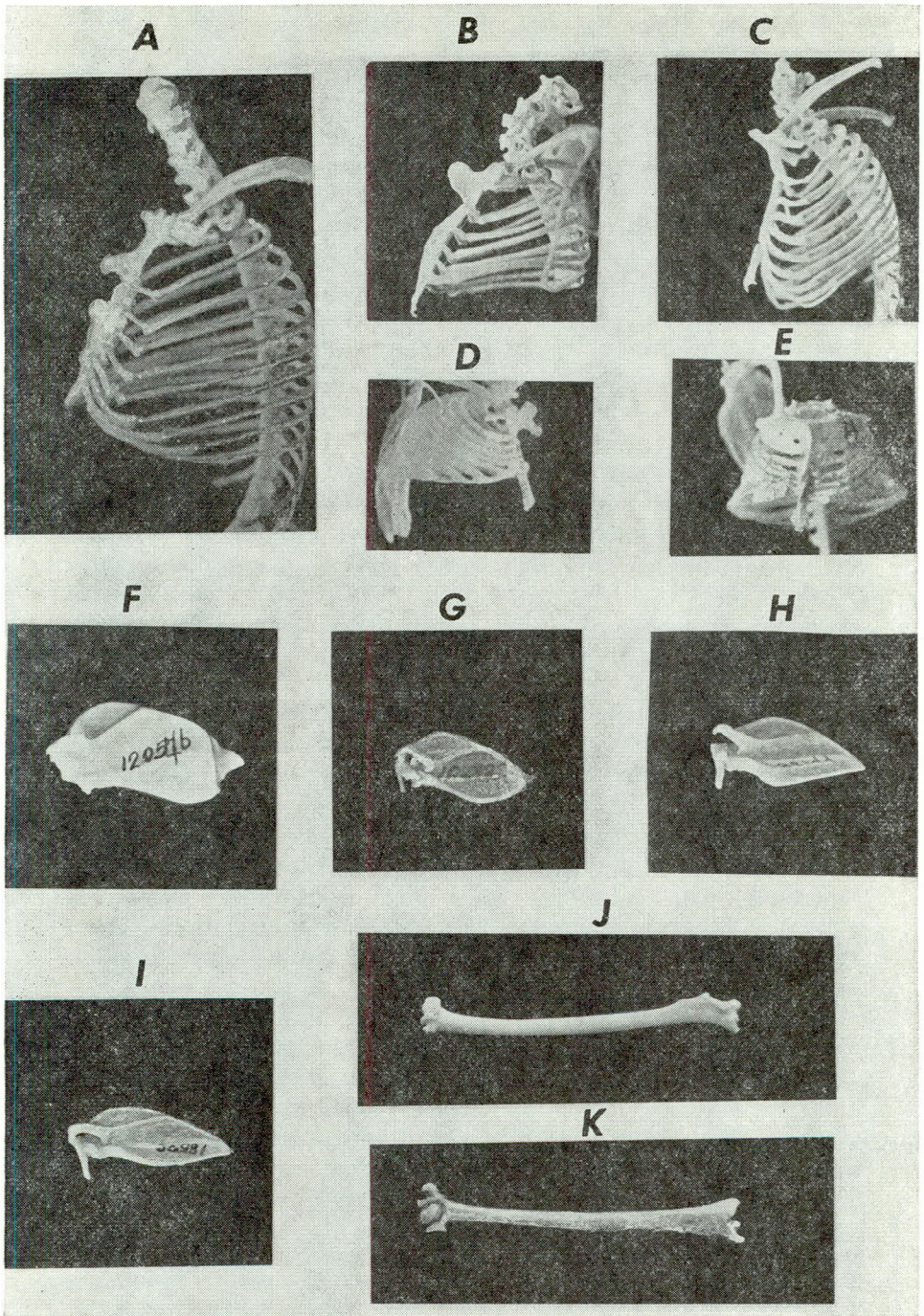
FIG. 2

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A ventrally directed flange from the coracoid border is present in the Emballonuridae, Noctilionidae, Nycteridae, Megadermatidae, Rhinolophidae, Hipposideridae, Natalidae, Myzopodidae, Vespertilionidae and Molossidae. The flange is present or absent in the Pteropidae and Phyllostomatidae, but lacking in all other families.

In the Mystacinidae, a flange from the coracoid border is directed dorsolaterally and joins with a medially directed process from the acromial process to form a span of bone over the supraspinous fossa. This arrangement is peculiar to the Mystacinidae (Fig. 2).

In the Molossidae, a dorsolaterally directed flange from the coracoid border extends toward a medially directed process from the acromial process, but there is no union over the supraspinous fossa as in the Mystacinidae.

A notch in the axillary border is present in the Pteropidae, Nycteridae, Megadermatidae, Rhinolophidae and Hipposideridae. It is either present or absent in the Phyllostomatidae and Vespertilionidae, and absent in all other families. A post-glenoid pit is present in the axillary border of the Pteropidae, Rhinopomatidae, Emballonuridae, Noctilionidae, Nycteridae, Natalidae, Furipteridae, Thyropteridae and Mystacinidae. It is present or absent in the Phyllostomatidae and lacking in all other families.

The coracoid process is untapered except in the Pteropidae, Natalidae, Furipteridae and Molossidae. The length of the coracoid process is generally great, the length as much as one-half the length of the scapula. Relative to the size of the scapula, the smallest coracoid process occurs in the Mystacinidae. The distal tip of the coracoid process is complex in the Phyllostomatidae, Desmodontidae and Vespertilionidae. The tip is generally directed laterally, but in the Vespertilionidae and Molossidae the distal tip is directed posterolaterally to posteriorly. For a discussion of the functional significance of the direction of the coracoid process see Vaughan (1959; 1966).

The acromial process normally recurves anteroventrally. In the Furipteridae, however, it recurves dorsomedially. It fails to recurve in the Mystacinidae and Molossidae. There is a medially directed flange from the acromial process in the Noctilionidae, Natalidae, Thyropteridae, Mystacinidae and Molossidae. In the Molossidae there is also a laterally directed projection from the acromial process which is

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FIG. 3. A. Dorsal view of axis and anterior view of atlas of *Artibeus;* B. Dorsal view of atlas, axis and two posterior cervical vertebrae of *Pteropus;* C. Left clavicle of *Mormoops;* D. Left clavicle of *Molossus;* E. Left clavicle of *Pteropus;* F. The proximal end of the right humerus of *Molossus;* G. Anterior view of the distal end of the left humerus of *Mormoops.*
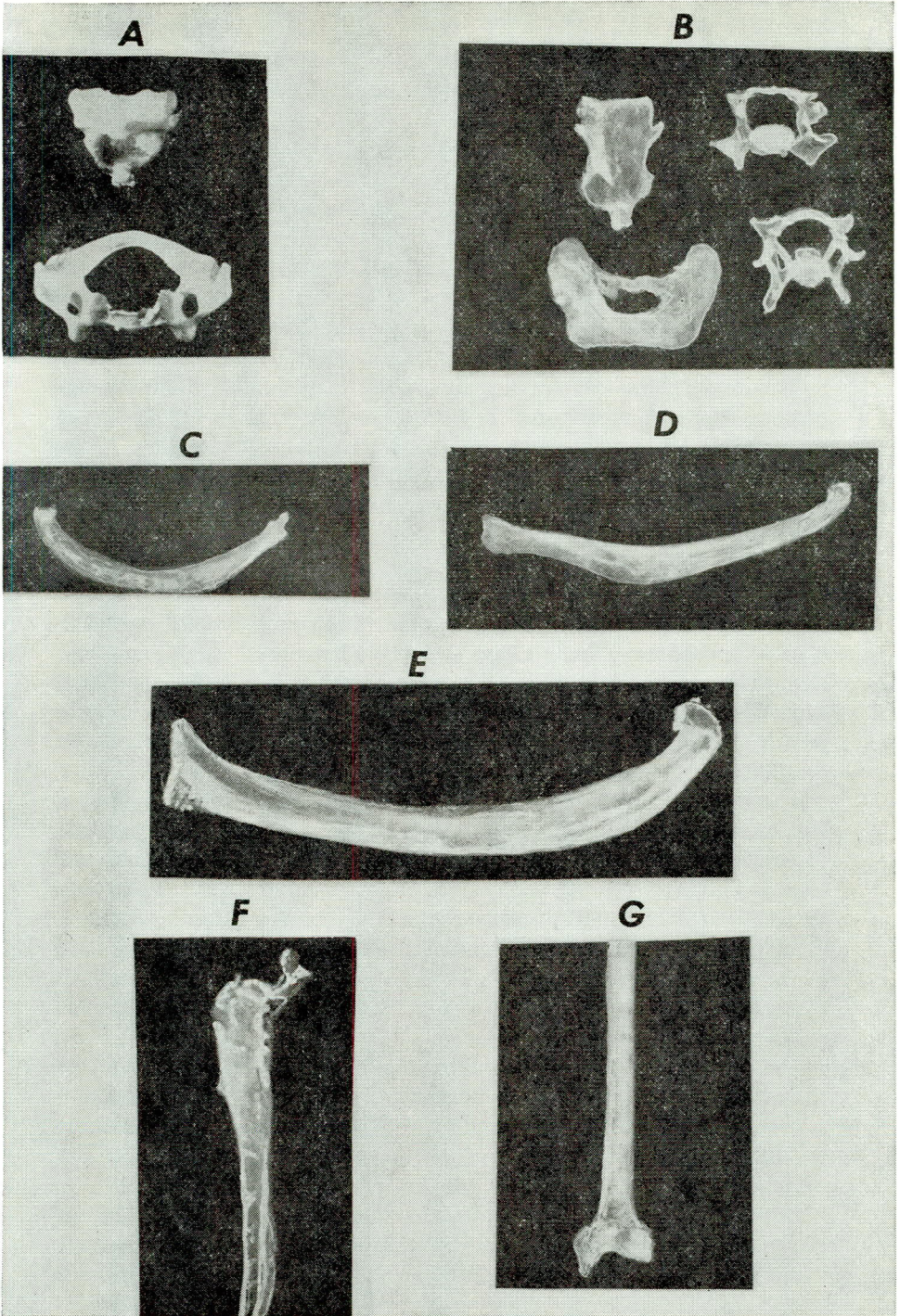
FIG. 3

reminiscent of the metacromion. The acromial process in this family is in line with the spine.

There are three distinct facets in the infraspinous fossa of all the families except the Pteropidae and Nycteridae. In these two families the ridge in the infraspinous fossa is so greatly suppressed as to obliterate clear boundaries of the three facets. These three facets were recognized and named by Vaughan (1959). In three families, Noctilionidae, Phyllostomatidae and Thyropteridae, the ridge of the infraspinous fossa may be raised into a distinct secondary spine. Four distinct facets in the subscapular fossa are present in all families.

The dorsoventral compression of the body and modifications accompanying flight (Vaughan, 1959; 1966) have resulted in elongation of the chiropteran scapula in an anteroposterior plane rather than maintaining the more conventional dorsoventrally lengthened configuration. Possible pathways in attaining the typical chiropteran scapular form are discussed by Walton (1969).

The clavicle is very large, quite long and curved (see Fig. 4). It articulates distally with the scapula and proximally with the lateral process of the manubrium of the sternum. The great size of the clavicle became established quite early in the evolution of the Chiroptera. Dechaseaux (1958) states in a review of fossil bats that the clavicle is generally as long as the rib cage. Bell (1836) states that the clavicle may be half as long as the humerus, and Miller (1907) compares the length of the clavicle to that of the scapula and longest rib.

The sternal end of the clavicle is slightly expanded. The articulation surface is smooth in *Eumops* while that of the scapular end is knoblike (Vaughan, 1959). The ends of the clavicle were not expanded in the Eocene *Icaronycteris* (Jepsen, 1966). In some modern bats, particularly the Rhinolophidae and Hipposideridae, the clavicle forms a complex joint with the manubrium, first costal cartilage, first rib and, in the case of the Hipposideridae, with the second costal cartilage and second rib (Walton & Walton, 1968). This joint is termed the sterno-claviculo-costal joint by H. Allen (1893).

The clavicles leave the manubrium at almost right angles to one another (Miller, 1907), curve anterolaterally, and hook posteroventrally to articulate with the scapula. The point of articulation on the scapula is on the anterolateral boundary of that bone dorsal to the base of the coracoid process.

Despite the large and conspicuous dimensions of the chiropteran clavicle, there are few detailed descriptions of this bone. Vaughan (1959) points out the functional importance of the bone. In addition to the significance of this bone noted by Vaughan (1959), the possi-

bility that this bone is important as a lever arm for movement of the entire pectoral assemblage should be considered. The fusion of cervico-thoracic vertebrae with strengthening of the sterno-claviculo-costal joint would seem to indicate that the sternum is the base of pectoral movement with the clavicle as a limiting lever arm.

The head of the humerus always projects medially from the long axis of the shaft, but only in the Pteropidae and Emballonuridae is the head the most proximal portion of the humerus. The head is generally circular in outline. In the Emballonuridae, Noctilionidae, Rhinolophidae and Hipposideridae it is an elongated oval; it is elliptical in the Mega-dermatidae and Mystacinidae, and variable in the Phyllostomatidae.

With the exception of the Pteropidae, the greater tuberosity always rises above the level of the lesser tuberosity. Only in the Pteropidae and Emballonuridae does the head rise above the greater tuberosity. The extreme development of the greater tuberosity is found in the Molossidae (Fig. 3); the greater tuberosity dominates the proximal end of the humerus and the lesser tuberosity is greatly reduced.

The pectoral and deltoid ridges are compressed into an anteriorly directed flange except in the Pteropidae. The flange is, however, quite low in the Desmodontidae. The humeri of the Pteropidae and Desmo-dontidae are superficially quite similar.

A distinct ridge on the shaft originating from the distal base of the lesser tuberosity is present and conspicuous in most families. It is absent in the Pteropidae and inconspicuous in the Rhinopomatidae, Noctilionidae and Desmodontidae.

The presence of a prominent spinous process from the medial epi-condyle is consistent throughout the Chiroptera. This spinous process is directed distally. Only in some of the Phyllostomatidae is the process completely lost, at least the distally directed portion. The spine is nor-mally displaced from the medial epicondyle, but in *Mormoops* it lies very close to the trochlea rim and projects well beyond the distal articular surfaces (Fig. 3). The appearance of this process in *Mormoops* is more nearly emballonurid-like than typically phyllostomatid-like.

What appears to be a vestige of the olecranon fossa is present in the Rhinopomatidae, Emballonuridae, Rhinolophidae, Hipposideridae and, perhaps, the Vespertilionidae. There is deep fossa, which may be homologous to the radial fossa, present in the Vespertilionidae, Mysta-cinidae and Molossidae.

The shaft of the humerus varies from nearly straight to slightly sigmoid in shape. It is never as long as the radius; it averages between one-half and two-thirds the length of the radius.

The distal articular surfaces are generally not in line with the shaft.

The capitulum is quite large, and the trochlea is somewhat reduced.

The double or secondary articulation between the greater tuberosity of the humerus and the scapula is well documented and discussed in some detail by Miller (1907). Recent studies on *Chilonycteris*, however, suggest that humero-scapular associations other than those currently described do exist and that further studies of this association are warranted (Walton & Walton, 1970).

The radius is greatly elongated and no rotation of the forearm occurs (Bell, 1836). Length of the radius is so great that in some species it equals the length of the head and body and is at least a third longer than the humerus (Flower & Lydekker, 1891). The main support for the forearm is provided by the radius and articulation with the humerus is largely by the radius (H. Allen, 1893; Miller, 1907; Dechaseaux, 1958). The radius is provided with two facets on its proximal end and the main ridge of the distal articular surface of the humerus fits between these two facets (H. Allen, 1893; Vaughan, 1959). The degree of radial involvement with the trochlea of the humerus appears to be related to the degree of terrestrial activity; the association is marked in *Cheiromeles, Molossus* and *Kerivoula* (H. Allen, 1893). In *Rhinopoma* the elbow joint is formed almost completely by the humerus and radius (Wassif & Madkour, 1963).

The shaft of the radius is generally arched slightly and is greatly bent in *Hipposideros* (H. Allen, 1893). In *Eumops* the shaft arches forward, and this curvature aids in producing horizontal camber to the wing (Vaughan, 1959). The shaft is slightly curved in its proximal third in *Rhinopoma* (Wassif & Madkour, 1963). The middle of the shaft is generally round in cross section, but may take a variety of shapes toward either end.

Proximally on the shaft, a fossa is present for the insertion of the biceps muscle group, but the size of the fossa is variable (H. Allen, 1893). In *Eumops* the fossa is in the form of a deep pit; in *Myotis* it is a large irregular triangular depression; the depression is not medially enclosed in *Macrotus* (Vaughan, 1959) and *Chilonycteris* (Walton & Walton, 1969).

The distal articular surface is generally concave and bordered anteriorly by two processes: the lateral or styloid process and the medial or pseudostyloid process. These two processes are pointed in *Eumops*, low knobs in *Myotis* and two small tubercles in *Macrotus* (Vaughan,

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Fig. 4. A. Lateral view of the pelvis of *Noctilio*; B. Lateral view of the left femur, tibia, fibula and calcar of *Mormoops;* C. Lateral view of the left knee, tibia and fibula of *Molossus;* D. Medial view of the left radius and ulna of *Molossus.*
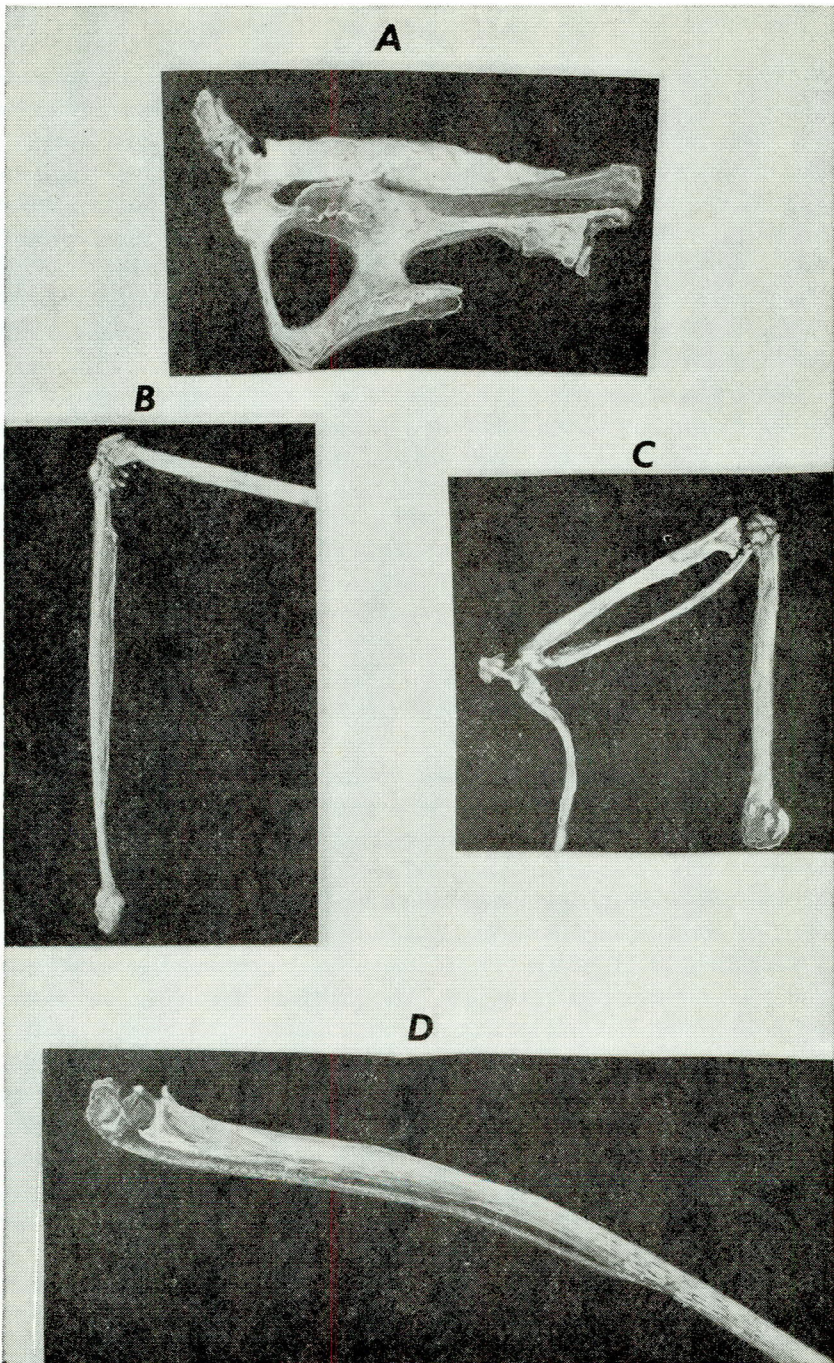
Fig. 4

1959). They are fused into a styloid-pseudostyloid ridge in *Chilonyc-teris* (Walton & Walton, 1970). In *Macrotus* and *Chilonycteris* there is a well developed posterior pseudostyloid process on the postero-medial rim of the articular surface. The styloid process is noted in *Rhinopoma* (Wassif & Madkour, 1963) and on the posterolateral boundary of the distal end of the radius in *Eumops* there is a distinct ridge (Vaughan, 1959). There is a large *processus ulnaris radii* in *Miniopterus* (Barbu, 1960). In *Chilonycteris* there is a flange located on the posterolateral surface of the radius just proximal to the distal epiphysis (Walton & Walton, 1970).

There is a locking mechanism involving the spinous process of the medial epicondyle of the humerus and the proximomedial part of the radius (Vaughan, 1959). The locking mechanism at the joint limits lateral movement so that the joint becomes a hinge only for stretching and flexing the forearm (Winge, 1941). At the distal end of the radius, a locking device occurs between the distal epiphysis and the scapholunar and cuneiform (Vaughan, 1959). Furrows and crests are much in evidence on both the distal and proximal epiphyses and are associated with taunt, strong ligaments (Winge, 1941). The locking devices and strong ligaments reduce the need for heavy distally placed musculature to arrest extension of the limb and laterally placed weight is reduced (Vaughan, 1959).

The ulna is generally quite small, rudimentary, separated proximally from the radius, but united with that bone at about its midpoint (Fig. 6) and has a much reduced olecranon process (Bell, 1836; Dobson, 1878; Miller, 1907). A detached sesamoid bone (ulnar patella) is present in the tendon of the triceps just proximal to the proximal end of the ulna (Fig. 6). It is lacking, however, in *Icaronycteris* (Jepsen, 1966).

According to H. Allen (1893) the ulna is composed of two basic parts: a proximal and distal part. The proximal portion is free at the weak olecranon and this process is continuous with an arched rod-like shaft which unites distally with the radius. Among the vespertilionines, however, the shaft may terminate in the forearm muscle, while in *Corynorhinus, Nyctophilus* and *Chalinolobus* a shaft is entirely absent. The ulna may be represented distally as a plate, hook-like process, cone-like projection, or may be entirely lacking. Among the Mega-chiroptera the distal end is present as a thin cartilaginous strand, but may become fused to the radius in old individuals (Miller, 1907).

Several workers (Dodson, 1878; Flower, 1885; Flower & Lydekker,

FIG. 5. A. Lateral view of the left tibia, fibula and palmar side of the foot of *Artibeus;* B. Left calcar and left foot of *Noctilio.*
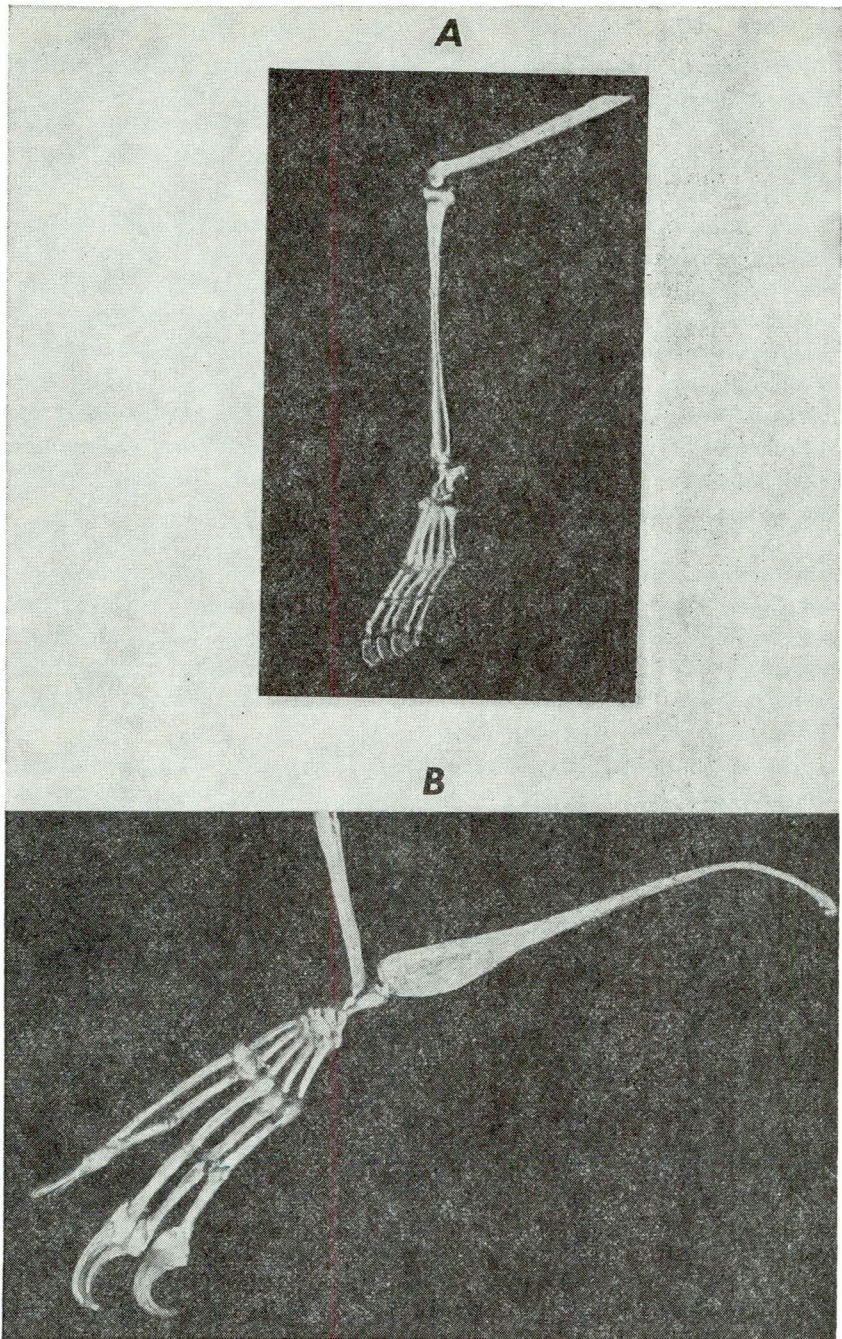
FIG. 5

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1891; Grassé, 1955; Dechaseaux, 1958; Vaughan, 1959; Wassif & Madkour, 1963) either state that only the proximal end of the ulna is present, or fail to make reference to a distal part. Barbu (1960), however, does term the hook-like process on the distal end of the radius the *processus ulnaris radii.*

The sesamoid present in the elbow is apparently unique to the Chiroptera. Winge (1941) notes the presence of small sesamoids in the lateral ligaments of the elbow throughout the order. This is supported in the study of *Chilonycteris* by Walton & Walton (1968) where there is a second sesamoid bone associated with the lateral epicondyle of the humerus (Fig. 6). The absence of the ulnar patella in *Icaronycteris* and the presence of a rather typical ulna does not support the speculation of H. Allen (1893) that the sesamoid may represent a detached portion of the olecranon. The ulnar patella is nearly equal in size to the olecranon (Miller, 1907).

The carpals are generally divided into two rows: proximal and distal. The proximal row comprises the scapholunar and the cuneiform and the distal row the trapezium, trapezoid, magnum and unciform. There is considerable question surrounding the pisiform and this is discussed below. Grassé (1955) considers a third row composed of a single bone referred to as the *os transversum*, but he notes that this is homologous to the pisiform in other mammals.

The scaphoid and lunar become fused during embryonic development (Grasse, 1955) and are present as a single bone in adults. Bell (1836), Dobson (1878), Flower (1885) and Flower and Lydekker (1891) included the cuneiform in this fusion and considered the proximal row as a single bone. H. Allen (1893), Grassé (1955), Vaughan (1959), Barbu (1960) and Wassif & Madkour (1963) consider the proximal row to include the fused scaphoid and lunar (scapholunar) and the unfused cuneiform. A large scapholunar is reported in *Icaronycteris* (Jepsen, 1966). Fusion of the scaphoid and lunar does not occur in the primates or most insectivores, but does occur in carnivores (Flower, 1885; Grassé, 1955).

The scapholunar and cuneiform fit into the distal radial socket (Vaughan, 1959; Wassif & Madkour, 1963). The articulation at this joint is described by Vaughan (1959) as tongue-in-groove and serves to limit movement of the radiocarpal joint. Movement is primarily flexion and extension (Grassé, 1955). There is an indication in *Chilonycteris* that other movement is allowed in the wrist, thus reducing the effectiveness of the lock found here (Walton & Walton, 1970).

The centrale normally associated with the proximal row of carpals is lacking in bats (Flower, 1885). According to Grassé (1955), the

centrale may fuse with the scapholunar early in embryonic life. Reference to it is made by Wassif & Madkour (1963), but they are apparently offering the name centrale radiale as an alternate name for the scapholunar. No indication of the origin of the name centrale radiale is presented, nor implied homologies.

The four bones of the distal row (trapezoid, trapezium, magnum and unciform) vary considerably in relative size throughout the order (Dobson, 1878; Flower & Lydekker, 1891; H. Allen, 1893). In the Pteropines the trapezium and magnum are the largest (Dobson, 1878; H. Allen, 1893); and the magnum bears a hatchet-shaped prolongation that is arranged in such a manner that the magnum is wedged between the second and fifth metacarpal. This process of the magnum is also present in the rhinolophines, but is lacking in other Microchiroptera (H. Allen, 1893). The trapezium is much smaller than the magnum, and the unciform is as large as the magnum in the Microchiroptera (Dobson, 1878). In *Rhinopoma* the trapezium is large and involved in a fusion with the fourth and fifth metacarpals (Wassif & Madkour, 1963).

The pisiform is generally considered a small bone. Bell (1836) states that it lies on the ulnar side of the joint. Dobson (1878) notes that it is smaller in the Megachiroptera than in the Microchiroptera; but H. Allen (1893) states that the bone is lacking in both the pteropines and rhinolophines. Allen does concede, however, that it is possible for the pisiform to be represented in the pteropines and rhinolophines as the hatchet-shaped process of the magnum. In *Miniopterus* the pisiform is included in the proximal row of bones (Barbu, 1960). Wassif & Madkour (1963) state that in *Rhinopoma* the pisiform is a sesamoid. The pisiform described by Vaughan (1959) spans the ventral surface and reinforces the carpus. Jepsen (1966) identifies the pisiform from the dorsal aspect of the carpus of *Icaronycteris*.

The chiropteran carpus is rotated ninety degrees from the position in cursorial mammals; the carpals are wider than long, and arranged in two rows. The pisiform is variously reported as absent, small, large, sesamoid, in the proximal carpal row and spanning the ventral surface of the carpus. The scaphoid and lunar are fused into the scapholunar and with the cuneiform form the radiocarpal joint. The magnum bears a prominent process in the pteropines and rhinolophines, and is probably of importance in a locking mechanism involving metacarpals two and five. The arrangement and form of the carpals restricts movement to flexion and extension. Vaughan (1959) notes locking devices between the radius and scapholunar and between the trapezoid and the second metacarpal.

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Sesamoid bones are found at various positions through the wrist. H. Allen (1893) states that sesamoids are found at points where great movement is permitted. They are particularly well developed in the extensors of the first, second and third metacarpals in the phyllosto-mines. In *Phyllostoma hastatum* there is one on the radial side of the radiocarpal joint, another covers the carpometacarpal joint of the thumb, and a third lies over the articulation of the magnum (Dobson, 1878). In *Chilonycteris psilotis*, two sesamoids are present ventrally at the metacarpophalangeal joints of digits one, three, four and five and a single sesamoid at this joint in digit two (Walton & Walton, 1970). In

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FIG. 6

A.  Dorsal view of the pelvis of *Desmodus rotundus*. Parts or areas indicated by letters are as follows: a. ilium; b. sacrum; c. pubic spine; d. sesamoid bone; e. acetabulum; f. obturator foramen.

B.  Ventral view of the pelvis of *Desmodus rotundus*. Parts or areas indicated by letters are as follows: a. ilium; b. intervertebral foramina; c. pubic spine; d. sacrum; e. acetabulum.

C.  Diagrammatic representation of the caudal view of male and female pelves. Parts or areas indicated by letters are as follows: A. a. dorsal ischial tuberosity; b. ascending ramus of the ischium; c. symphysis pubis.

D.  B. a. dorsal ischial tuberosity; b. ascending ramus of the ischium; c. ventral ischial tuberosity.

E.  Generalized phyllostomatid scapula; dorsal and ventral aspects. Parts or areas indicated by letters are as follows: a. glenoid fossa; b. acromial process; c. notch of coracoid border; d. supraspinous fossa; e. coracoid border; f. vertebral border; g. axillary border; h. anteromedial facet of the infraspinous fossa; k. intermediate facet of the infraspinous fossa; l. posterolateral facet of the infraspinous fossa; m. spine; n. coracoid process; o., p., q., r., four facets of the subscapular fossa.

F.  Dorsolateral view of the right elbow. The parts labeled are as follows: up. ulnar patella; l. lateral condyle of the humerus; s. sesamoid bone; h. humerus; u. ulna; r. radius.

G.  Lateral view of the pelvis of *Desmodus rotundus*. Parts or areas indicated by letters are as follows: a. ilium; b. pubic spine; c. pubis; d. ventral ischial tuberosity; e. obturator foramen; f. ischium; g. dorsal ischial tuberosity; h. acetabulum; i. sesamoid bone; j. sacrum.

H.  Generalized phyllostomatid sternum; ventral and profile views. Parts and areas indicated by letters are as follows: a. presternum or manubrium; b. mesosternum with keel; c. xiphoid portion; d. vertical process of the manubrium; e. lateral process of the manubrium; f. expanded costal cartilage of the first rib; g. notch in posterior margin of the lateral process of the manubrium; h. point of articulation with the clavicle.

I.  Generalized phyllostomatid humerus; anterior and dorsal aspects. Parts and areas indicated by letters are as follows: a. greater tuberosity; b. lesser tuberosity; c. shaft; d. medial epicondyle; e. spinous process of the medial epicondyle; f. trochlea; g. capitulum; h. lateral epicondyle; k. pectoral-deltoid flange; l. head.
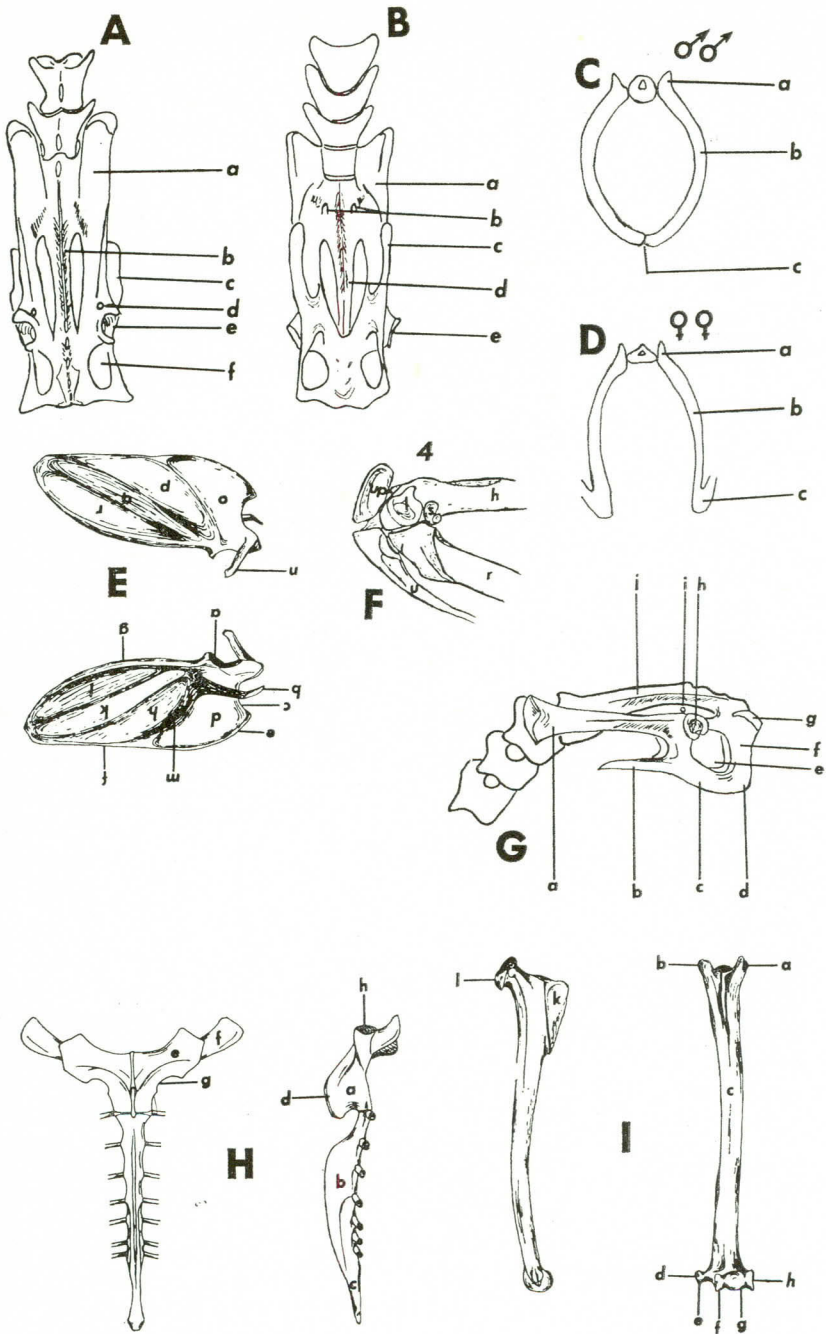
Fig. 6

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*Eumops* there is a sesamoid at the proximal base of metacarpals two and four (Vaughan, 1959). In *Rhinopoma* a sesamoid is located at the metacarpophalangeal joint of the pollex (Wassif & Madkour, 1963), and there are three sesamoids in the wrist of *Myotis myotis*: one lies between the scapholunar and cuneiform, another on the posterior face of the scapholunar-trapezium articulation, and the third associated distally with the trapezoid-magnum articulation (Grassé, 1955).

The metacarpals are slender, cylindrical bones expanded distally at the articulation with the phalanges. There is considerable variation in the relative length of the metacarpals, but a general pattern of length (longest to shortest) can be expressed as 3-4-5-2-1.

Andersen (1912) divided the pteropids into four groups based on relative lengths of the third, fourth and fifth metacarpals, but he noted so much deviation from these groupings that it seems difficult to ascribe much definition to them. Much of the variation occurs in the lengths of metacarpals four and five, but examples were noted where length of the fourth or fifth exceeded the third. Lawrence & Novick (1963) note wide variations of the same type in the pteropids.

Among the Microchiroptera there is substantial variation in length of metacarpals three, four and five. There are instances where length of the fifth metacarpal may exceed the third and the fourth may exceed the fifth. Throughout the families of bats, the metacarpals are comparatively shortest in the rhinolophines and pteropines (H. Allen, 1893).

The carpometacarpal joint of the first digit is highly flexible and allows a wide range of movements (Grassé, 1955). The remaining metacarpals are tightly packed at their proximal ends and support each other. Articulation of metacarpals two through five with the carpals is such that all movement is restricted except in an anteroposterior plane.

The degree of rigidity at the metacarpophalangeal joints is highly variable. Generally, the greatest rigidity occurs in the fifth digit and the least in the third. All joints tend to be most rigid in the Rhinolophidae (H. Allen, 1893).

Except in the family Furipteridae, the pollex has two phalanges. A claw is borne on the distal phalanx. The second or index finger contains three phalanges in the Megachiroptera and a claw is generally present on the terminal phalanx (Miller, 1907). The claw is lacking in *Dobsonia, Eonycteris, Nesonycteris* and *Notopteris* (Bourlière, 1955). Among the Microchiroptera, Miller (1907) states that the families Emballonuridae, Nycteridae, Rhinolophidae, Hipposideridae, Natalidae, Furipteridae and Thyropteridae have only the metacarpal present on the second digit. All others have one bony phalanx except *Rhinopoma* where two are present. In the rhinolophids and hipposiderids, the meta-

carpal that represents this digit lies close to the metacarpal of the third
digit, serving to strengthen the wing's leading edge (Miller, 1907).

The usual number of phalanges present in digits three, four, and five
is three, except in the Megachiroptera, Rhinopomatidae, Emballonu-
ridae, Noctilionidae, Nycteridae, Megadermatidae, Rhinolophidae,
Hipposideridae, Natalidae and Furipteridae where only two are present.
Miller (1907) presented evidence that the third phalanx may be repre-
sented by cartilage in those Microchiroptera which possess only two
phalanges. The homology of the terminal cartilage and the third phalanx
is questioned. The validity of this homology was first accepted by H.
Allen (1889), but later questioned (1893). H. Allen (1889) presented
evidence of a membraneous fourth phalanx in some cases, and reported
that in none of the Megachiroptera were there flexible (non-osseus)
segments. The third digit is generally longest, and its three phalanges
are ossified in the Phyllostomatidae, Desmodontidae, Thyropteridae and
Myzopodidae (Miller, 1907).

Terminal cartilages are noted in many species of bats, and these take
on varying lengths and shapes. Miller (1907) notes that the distal
phalanx of the fourth and fifth digit is always cartilaginous. In *Rhino-
poma* the distal phalanx of digits two, three, four and five carry a small
claw-shaped cartilage that fails to ossify in the adult animal (Wassif &
Madkour, 1963). In *Eumops* and *Myotis* the terminal phalanx of digits
three, four and five is cartilaginous, while in *Macrotus* it is cartilaginous
in digits four and five (Vaughan, 1959). The fourth digit may bear pro-
jections into the edge of the flight membrane. The terminal phalanx
is L-shaped in *Vesperus fuscus* (=*Eptesicus fuscus*) and *Vesperus
noctula* (=*Noctula noctula*); T-shaped in *Vespertilio murinus* (=*My-
otis murinus*); and appears as an inverted T in *Artibeus perspicillatus*
(=*Artibeus jamaicensis*) (H. Allen, 1889). In the vespertilionines
(except *Corynorhinus*) the fifth digit is provided with an accessory
cartilage that projects from the margin of the wing membrane (H.
Allen, 1893).

### PELVIC GIRDLE AND LIMB

The development of the chiropteran innominate may be traced to
the earliest fossil records of the Eocene. Fossil pelves of *Paleochirop-
teryx, Archeonycteris, Icaronycteris index* (Jepsen, 1966) and Tertiary
rhinolophids and hipposiderids differ insignificantly from modern bats
(Dechaseaux, 1958). In the earliest record (*Icaronycteris*) a well
formed innominate with a pubic symphysis, pubic spine, and general
conformation equal to that of modern bats is described (Jepsen, 1966).
Even in Tertiary hipposiderids, the preacetabular foramen is formed and
distinct (Friant, 1963).

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The modern mammalian innominate consists of two portions, the upper or dorsal portion composed of the ilium, and the ventral or lower portion which is divided into an anterior pubis and a posterior ischium. In bats, the ventral portion projects forward slightly and the pubis and ischium are at right angles. The lower region is not in line with the ilium but is caudad to it and, therefore, the ischium is dorsad to the pubis (Flower, 1885).

In contrast to the well developed pectoral girdle of the bat, the pelvis appears small and weak. Compared to body size and weight, however, the pelvis is not uniquely small. It may be considered weak in comparison with the pelves of other mammals (Bell, 1836; Dobson, 1878; Flower, 1885).

The dorsal portion (ilium) of the mammalian pelvis is usually expanded for the accommodation of the muscles utilized in walking. Since the bat utilizes an aerial mode of locomotion, the hind limbs and their corresponding musculature are underdeveloped (Dobson, 1878). Consequently, the ilium of the chiropteran pelvis is rather narrow. The three-sided ilium found in mammals is more rod-like in bats (Flower, 1885) and the three surfaces (sacral, gluteal and iliac) of the ilium are reduced in bats, and frequently the iliac fossa is absent. The ilium articulates with the anterior sacral elements in formation of the sacro-iliac joint in bats as in all mammals, and this joint is ankylosed in a few chiropteran families, adding rigidity to the pelvis (see Fig. 6).

The lower ischial and pubic elements are delicate in construction in bats. The ischium is the narrowest and most delicate except in the Rhinopomatidae where the pubis is the narrowest element (Walton & Walton, 1968). The ischium is a continuous bone composed of a dorsal and an ascending ramus which come together at more or less right angles. There may be a slight depression present in the lateral surface of the dorsal ramus adjacent to the acetabulum. Both ventral and dorsal ischial tuberosities are present (Flower, 1885). The dorsal ischial tuberosity often joins the last sacral or first caudal vertebra by means of ligaments, and in some families an ankylosed fusion occurs with this vertebra (Fig. 6). Portions of the dorsal ischial ramus may enter the fusion also. In the Pteropidae, Noctilionidae and Desmodontidae, there is a fusion of the two innominates at the dorsal ischial tuberosities directly below the sacroischial junction (Fig. 4). This yields further rigidity of the pelvis (Walton & Walton, 1968). Mammals generally have a strong double ligamentous union between the ischium and the caudal vertebrae (Flower, 1885). This union, Flower notes, is bony only in the Edentata. He makes no note of the bony union in some of the Chiroptera.

The pubis is composed of dorsal and ventral rami which come together at right angles, and projecting from the anterior surface of the pubis is a pubic spine (Figs. 4 and 6), also referred to as the iliopectineal spine (Dobson, 1875; Flower & Lydekker, 1891; Barbu, 1960; Wassif & Madkour, 1963) or acicular process (Miller, 1907; Koopman & Cockrum, 1967). It is a continuous ossified process of the pubis and through embryological studies by Barbu (1960) and Wassif & Madkour (1963), it has been established that this process ossifies early and in continuity with the pubic bone of each innominate. This projection differs from the epipubic bone found in the Monotremata and Marsupialia (Flower, 1885). The epipubic bone articulates with but does not fuse with the pubis. There is a pectineal tuberosity present in the Marsupialia but it occupies a position dorsad to that of the chiropteran pubic spine (Flower, 1885); therefore homology is doubtful. This spine varies considerably in length throughout the Chiroptera. It is poorly developed in the Myzopodidae, Pteropidae, Vespertilionidae, Mystacinidae and Thyropteridae; moderately developed in the Rhinolophidae, Desmodontidae, Megadermatidae, Furipteridae, Noctilionidae and Molossidae; and well developed (equal to more than one-third the length of the ilium) in all other families (Walton & Walton, 1968).

In the family Hipposideridae, the innominate is unique among mammals in its possession of a preacetabular foramen (Dobson, 1878). It is formed by a supplemental bridge of bone which connects the anterior tip of the pubic spine with the anterolateral end of the ilium. Sutures are not evident in this junction and this structure is reported in fossil hipposiderids (Friant, 1963).

The obturator foramen is generally oval in shape. This is not changed from the fossil record (Heller, 1935). The foramen exceeds the size of the acetabulum by four to five times in most modern bats. In the families Natalidae, Hipposideridae, Rhinolophidae and Nycteridae, however, the reduction in size of the pubic and ischial elements reduces the size of the obturator foramen to about twice that of the acetabulum (Walton & Walton, 1968).

The acetabulum is formed where the three innominate elements fuse together dorsally. The acetabulum is generally directed dorsolaterad for the accommodation of the femur. A small sesamoid bone is found embedded in the anterior cartilaginous rim of the acetabulum (Fig. 6) in the Emballonuridae, Noctilionidae, Hipposideridae, Phyllostomatidae, Desmodontidae and Molossidae. This small bone may be present in other families, but may often be lost in skeletal preparations (Walton & Walton, 1968).

The innominates are united ventrally in a symphysis pubis in all

mammals (Flower, 1885). In bats only males possess a symphysis (Fig. 6). Wassif & Madkour (1963) and Flower (1885) describe a loose union of the pubes in male specimens, but they state that only in the family Rhinolophidae do the males possess a true symphysis. Winge (1941) notes that due to lateral extension of the hind limbs in flight, the symphysis is loosened and broad. There is, however, a true symphysis pubis present in all male bats, but the union of the pubes may not be close. Ossification does occur quite often at ligamentous unions and there is some indication that ossification is a function of age.

The innominate is set obliquely to the sacrum in mammals (Flower, 1885). The chiropteran innominate is parallel to the vertebral column in the families Pteropidae, Emballonuridae, Rhinopomatidae, Noctilionidae and Desmodontidae. In all other families it is angled slightly. The angle, however, is never as severe as in other mammals.

The mammalian femur is more or less cylindrical and elongated. The proximal epiphysis has a rounded head situated at an angle to the shaft, which fits into the acetabulum (Flower, 1885). The head is set off from the shaft by a short constriction termed the neck (Romer, 1966). There are two projections on the proximal epiphysis termed trochanters (greater and lesser) and in the case of the Perissodactyla, Edentata and some of the Rodentia, there is a third trochanter (Flower & Lydekker, 1891). The distal epiphysis is thickened and composed of lateral and medial condyles (Flower, 1885).

The chiropteran femur is similar in construction to the basic mammalian pattern. The form of the femur varies little throughout the order (Dobson, 1878). It is approximately the same length as the tibia. The shaft is cylindrical with a hemispherical head at the proximal end. The head is rarely inclined at a slant to the shaft, except in some of the fossil forms such as *Icaronycteris* (Jepsen, 1966). The neck of the femur is very short or absent. There are only two trochanters present: the greater and lesser. These are round and nearly equal in size (Dobson, 1878). In the families Natalidae, Hipposideridae, some of the Phyllostomatidae and some of the Vespertilionidae, the trochanters are drawn backward, and in the Molossidae they are of unequal size, the greater being the larger (H. Allen, 1893).

The shaft of the femur is straight. Some fossil bats of the families Rhinolophidae and Hipposideridae have femora which arch slightly (Revilliod, 1917). There is a slight curve in the femur of *Eumops* reported by Vaughan (1959). The necessity of a straight femur is important in the adaptation to flight as the leg must extend the flight membranes laterally (Winge, 1941). Low ridges arise on the shaft of the femur for muscle attachment (Vaughan, 1959; Wassif & Madkour,

1963; Walton & Walton, 1970). These ridges are most distinct in the Desmodontidae (Miller, 1907). Savage (1951) records ridges on the femora of Miocene phyllostomatids. In many modern species a short lateral ridge arises on the shaft where a third trochanter is found in other mammals (H. Allen, 1893). This notation, however, is not to imply homology of the two. Other than these ridges, the shaft is narrow and cylindrical. The distal epiphysis has distinct articular facets (lateral and medial condyles) which are separated by deep grooves: the patellar groove on the anterior surface and the intercondylar notch on the posterior surface (Winge, 1941). The knee is locked in place by these facets upon extension of the leg.

The femur of fossil bats tends to be more robust and the ridges for muscle attachment are well developed generally. The size relationship to the tibia and the basic construction in fossil bats is similar to that in modern forms (Savage, 1951; Dechaseaux, 1958; Jepsen, 1966).

The patella is a large sesamoid bone found in all mammals except the Marsupialia. It is consistently present in bats although Winge (1941) reports it absent in some species. It is joined by ligaments to the patellar groove of the femur and the cnemial process of the tibia.

The tibia is slender but well developed. It has lost many of the grooves associated with muscle attachments that are found in mammals with quadrupedal locomotion. The tibia is broadest at the upper end. The lateral condyle projects abruptly from the main axis and is covered by cartilage. The fibula, when present, articulates with this condyle. There is a small medial condyle covered with cartilage located opposite the lateral condyle. A distinct cnemial process or tubercle of the tibia (Wassif & Madkour, 1963) appears on the anterior surface of the proximal epiphysis of the tibia for the attachment of the ligament to the patella.

The shaft may be round or triangular in cross section. It tends to be more triangular proximally and flattened distally. The shaft of the tibia in fossil phyllostomatids is triangular in cross section (Savage, 1951). The shaft in modern bats is usually straight, smooth and approximately equal in length to the femur (Fig. 4). This is the same in fossil forms except those of the Brown Coal Deposits which have a bent tibia (Heller, 1935). Although the shaft is smooth, low ridges and tuberosities are present for some muscle attachment. A small tubercle is present on the posterior surface of the shaft just below the proximal epiphysis from which the hamstring muscles extend. The tuberosity is most prominent in the pteropines (H. Allen, 1893). In modern species, low ridges lie on the lateral and medial surfaces. The number, length and height of these varies among species.

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The distal epiphysis or medial malleolus is slightly expanded and articulates with the astragalus of the tarsus (H. Allen, 1893).

The fibula is generally a slender, weak bone when present. It may, however, be absent or rudimentary, a condition not altogether uncommon in mammals (Flower, 1885). In some mammals, the fibula ankyloses with one or both ends of the tibia. The condition of the fibula appears to be related to the means of locomotion employed by the animal (Winge, 1941).

The fibula has apparently undergone some changes in structure from the condition seen in fossil bats. It is complete and more robust in fossil specimens. This condition is noted for *Icaronycteris index*, and the fibula is also longer than the tibia in this species (Jepsen, 1966).

In modern bats the fibula is generally threadlike and round in cross section. It may or may not articulate directly with the lateral epicondyle of the tibia. This connection is often ligamentous. The distal epiphysis articulates with the astragalus or calcaneus. The distal tip is termed the lateral malleolus.

Dobson (1878), Flower (1885) and Flower & Lydekker (1891) describe the fibula as incomplete in all chiropteran families except the Molossinae (=Molossidae). Miller (1907) describes a complete fibula for the families Rhinopomatidae, Emballonuridae, Rhinolophidae, Desmodontidae, Vespertilionidae, Molossidae, and Mystacinidae. The fibula is, however, large and complete only in the Molossidae (Fig. 4), Mystacinidae and Desmodontidae. The Thyropteridae lack the proximal half of the bone and in the Nycteridae the entire fibula is absent. All other families either have a very thin complete fibula or the proximal end is cartilaginous (Walton & Walton, 1968). The distal end may be well developed for articulation with the tarsus and, as in the case of *Chilonycteris psilotis*, have distinct ridges along one or more surfaces (Walton & Walton, 1970).

The tarsus is short in bats and composed of seven bones. The arrangement of bones differs little from the typical mammalian pattern. The first row consists of two bones: the astragalus and calcaneus. These bones are elongated in the bat and expanded proximally (H. Allen, 1893). Both the tibia and fibula usually articulate with the astragalus. In the Rhinopomatidae and Pteropidae, however, the calcaneus enters the ankle joint; the fibula articulates with this bone (Grassé, 1955; Wassif & Madkour, 1963). Articulation of the fibula with the calcaneus also occurs in the Rhinolophidae (H. Allen, 1889). The calcaneus of the Noctilionidae is uniquely enlarged, distally expanded and flattened (Miller, 1907).

There is an additional bone, the calcar (Fig. 4 and 5), associated

with the first row of tarsal bones. The origin and construction of the calcar is in question. It is generally described as a detached portion of the calcaneus, although no embryological studies confirm this. Dobson (1878), Flower (1885) and Grassé (1955) describe the calcar as a detached, enlarged tuberosity of the calcaneus, while Bell (1836) and H. Allen (1893) note that the origin and homology are unknown. G. M. Allen (1939) describes the development of the calcar in relation to the development of the uropatagium. He states that in the primitive condition the tail is quite long and the uropatagium absent. The latter then develops simultaneously with a narrow flange (calcar) from the calcaneus for the purpose of spreading the membrane. The tail then shortens and becomes incorporated in the membrane. In the fossil *Icaronycteris index* a long tail is present and the calcar is absent (Jepsen, 1966). The calcar is found in various later fossils (Dechaseaux, 1958). Calcarial construction is cartilaginous at early stages (Dobson, 1878; Flower, 1885; Flower & Lydekker, 1897). Ossification occurs partially or completely, however, and may be a function of age (Grassé, 1955). In the Rhinopomatidae and some of the Pteropidae the calcar is absent entirely, of short to medium length in the Phyllostomatidae, well developed in all other families (G. M. Allen, 1939) and greatly lengthened in the Noctilionidae (Fig. 5) where it is supported by an enlarged calcaneus (Miller, 1907).

The second row of bones in the tarsus is composed of the cuboid, navicular and associated sesamoid bones. The cuboid is larger than the navicular and may be elongated. One or two sesamoid bones may be associated with the cuboid. Grassé (1955) considers the navicular analogous to the scaphoid of the wrist.

The third row of tarsal bones is composed of three cuneiforms (external, middle and internal) and their associated sesamoid bones. The internal cuneiform articulates with the first metatarsal; the middle and external cuneiform articulate with the second and third metatarsals, respectively. There is a small bone termed the medial tarsal which is ventral to the cuneiforms and may contact any of the three cuneiforms. It is not consistently present in bats, although its presence has not been thoroughly investigated. It may be homologous to the sesamoid bone found in rodents and carnivores on the ventral side of the tarsus (Flower & Lydekker, 1891).

The metatarsals are short, but of equal length (Bell, 1836; Gressé, 1955). They may be cylindrical or laterally flattened. There are one or two sesamoid bones located at the metacarpophalangeal joint of each digit (Grassé, 1955; Walton & Walton, 1970).

The phalangeal formula for the foot is 2-3-3-3-3 except in the

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Hipposideridae, Thyropteridae and Myzopodidae where it is 2-2-2-2-2 (Miller, 1907; Grassé, 1955). Toes of bats are of equal length. In those bats with the 2-3-3-3-3 formula the first phalanx of the first digit is elongated to make the first digit equal the others. The other phalanges are of equal length; laterally flattened and sesamoid bones may be present at any of the joints.

The claws are well developed on all digits. They are laterally flattened, arched and of equal size.

In mammals the hind limb generally is constructed similarly to the forelimb. It has three segments: thigh, leg and foot. It works in a fore and aft plane and the knee serves as a fulcrum for the lever thus formed (Romer, 1966). The chiropteran hindlimb, though generally considered rather weak (Dobson, 1878; Flower, 1885), operates on a similar principle. In terrestrial locomotion the hind limb of bats functions similarly to other mammals (Winge, 1941). It is used primarily in flight to control membrane placement. The limb is extended laterally and slightly caudad to support the plagiopatagium and spread the uropatagium. In this position, the bat cannot afford lateral movements of the knee; therefore, the knee becomes more of a hinge with raised articular facets which fit into rather deep sockets. Winge (1941) suggests that the hind limbs originally were used to start the leap before flight and that this aided in the development of the wing membrane. This would explain why the hind limbs are still enclosed in the membranes.

The chiropteran hind limb is delicate and weak in construction except for the stout, short leg of the Molossidae and Mystacinidae and the strong leg of the Desmodontidae (Miller, 1907). In comparison to the forelimb, the hindlimb is short; the combined length of the femur, tibia and foot rarely equals that of the radius (Dobson, 1878). The hind limb is rotated 180 degrees and the knee is directed dorsad and caudad much as it is in a grasshopper (Miller, 1907). In most mammals, the hind limb is vertical to the ground and ventral to the animal. Due to the rotation of the limb in bats, the lateral surface of the limb is homologous to the medial surface in other mammals (Vaughan, 1959). This places the rudimentary fibula on the inner side and slightly behind the tibia (Bell, 1836).

At rest, the bat is suspended by the hindlimbs, and there exists an interesting association of the femur and innominate. As the leg is extended into the resting position, the greater trochanter of the femur rests against the outer surface of the posterior acetabular rim. In some bats, there is a slight depression in the lateral surface of the dorsal ramus of the ischium directly adjacent to the rim of the acetabulum for

accommodation of the greater trochanter. The possibility that this is a locking device must be considered. Grassé (1955) describes resting support as strictly a function of the toes. The tendons in the foot lock the toes in place by means of a "tendon collar." This is generally accepted as correct, but a mechanical lock such as that seen at the proximal end of the femur with the innominate may allow the bat to hang from the knee as well as from the foot.

The hindfoot of the bat is plantigrade and directed caudad on a flat surface. The dorsal surface faces dorsad and the palmar surface faces ventrad (Grassé, 1955). At rest, the ankle is twisted slightly; therefore, the articulations at the ankle are loose and a true hinge joint is absent. The foot is relatively unspecialized in most families. It is rather short and broad in the Mystacinidae and Molossidae, however, for support of the stout legs (Miller, 1907).

## CONCLUSIONS

The post-cranial osteology of the Chiroptera is so constructed as to increase the efficiency of flight as a means of locomotion in the animal.

The vertebral column arches ventrally through the cervical region, dorsally through the thoracic region and descends posteriorly through the lumbar, sacral and caudal regions, when the latter is present. Fusions occur in the cervico-thoracic, lumbar (thoraco-lumbar) and sacral regions. This increases the rigidity of the skeleton. The sternum is well developed and keels may be present on the manubrium and/or the body of the sternum. The rib cage is generally bell shaped and ankylosis of some of the ribs may occur. The number of ribs is equal to the number of thoracic vertebrae.

The pectoral girdle is very well developed. The clavicles are large, long and curved. The scapula is generally large and oval; the length about twice the width. The supraspinous fossa is smaller than the infra-spinous fossa. Dorsoventral compression of the body and modifications due to flight have elongated the chiropteran scapula in an anteroposterior plane.

The forelimb is elongated. The humerus is sturdy and forms a double articulation with the scapula, when it is locked into position upon exten-sion. The radius is greatly elongated and may be arched. It locks into place at the elbow and the radio-carpal joint. There is an ulnar patella present at the elbow. The ulna is rudimentary, never complete. It is separate from the radius proximally but fuses with it distally. The carpus is rotated 90 degrees from its position in cursorial mammals. The bones are all well developed, and varying numbers of sesamoid bones occur. The metacarpals and phalanges are greatly elongated and lock into place

upon extension. Their numbers vary, and sesamoid bones may be present at all joints.

The pelvic girdle is not small in relation to the body size, but may be considered weak. It is generally fused to the sacrum at the sacroiliac joint, and may be at the sacroischial or caudoischial joint. A symphysis pubis is present in all males, and a pubic spine is consistent in the order, although its size differs.

The hindlimb is poorly developed, rotated 180 degrees caudally, and its primary purpose is to spread the flight membranes although it is used for hanging in the roost. The femur and tibia are the same length and lock in position at the knee upon extension; the greater tuberosity of the femur locks against the anterolateral portion of the ischium when the bat is at rest. There is a patella present. The fibula is poorly developed and is complete in only a few families. The tarsus is loose and is twisted when the bat is hanging. Extending from the calcaneus is a separate bone which is elongated to support the uropatagium termed the calcar. It may be cartilaginous. All digits of the foot are of equal length and the muscles of the toes "lock" them in place when the bat is hanging in the roost.

Knowledge of post-cranial osteology contributes to a better understanding of the biology of bats. The flight patterns are determined, in part, by osteological locking mechanisms. Vaughan (1969) relates the importance of these mechanisms. It should also be noted that locking mechanisms play an important role in the roosting habits of the bat. They determine the angle of hanging in the roost and in this manner may influence the choice of the roosting site.

The spread of the plagiopatagium and uropatagium in flight is dependent upon lateral extension of the forelimbs and hindlimbs. The manner and direction of limb extensions is of consequence is determining such things as speed and angle of flight (see Vaughan, 1969), feeding and watering patterns (see Glass, 1969), and approaches to roosting (see Dalquest & Walton, 1969).

Feeding mechanisms in the bat are highly evolved (Glass, 1969). Use of the wings and legs is intricately involved in the feeding processes of insectivorous, frugivorous, nectivorous, sanguivorous, carnivorous and piscivorous chiropterans. Limb utilization in this aspect, however, is fully understood in few cases.

Future investigation of chiropteran genera in the areas of embryological development, habits and paleontology would aid the study of chiropteran osteology.

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## TABLE I

| Genus and/or species | Cervical | Thoracic | Lumbar | Sacral | Caudal |
|---|---|---|---|---|---|
| BELL, T. 1836 | | | | | |
| Vespertilio | | 11 | 5 | | 12 |
| Pteropus | 7 | 12 | 4 | 1 | 0 |
| Phyllostoma | | | 5 | | |
| Rhinolophus | | | 6 | | |
| Noctula | | | 7 | | 6 |
| DOBSON, G. E. 1878 | | | | | |
| Phyllostoma hastatum | | 13 | | | |
| Artibeus perspicillatus | | 12 | | | |
| FLOWER, W. H. 1885 | | | | | |
| Epomophorus franqueti | 7 | 13 | 5 | | |
| Pteropus rubricollis | 7 | 12 | 5 | | |
| | | | | | coalesced |
| | | | | | coalesced |
| | | | | | coalesced |
| Pteropus medius | 7 | 14 | 5 | | |
| Phyllorhina tridens | 7 | 11 | 7 | | 16 |
| Phyllorhina diadema | 7 | 11 | 7 | | 18 |
| Phyllorhina caffra | 7 | 12 | 6 | | 12 |
| Megaderma frons | 7 | 12 | 4 | 3 | 11 |
| Vesperugo serotinus | 7 | 11 | 5 | 3 | 11 |
| Vesperugo noctula | 7 | 11 | 5 | 3 | 11 |
| Vesperugo pipistrellus | 7 | 12 | 4 | 3 | 11 |
| Vesperugo nanus | 7 | 11 | 5 | | 13 |
| Miniopterus schreibersi | 7 | 12 | 5 | | 15 |
| Molossus obscurus | 7 | 11 | 6 | 4 | 11 |
| Desmodus rufus | 7 | 11 | 6 | | |
| | | | | | coalesced |
| THOMAS, O. 1904 | | | | | |
| Myzopoda aurita | 7 | 13 | 5 | 4 | 8 |
| REVILLIOD, P. 1917 | | | | | |
| Paleochiropteryx tupaidon | | | | 1 | |
| VAUGHAN, T. A. 1959 | | | | | |
| Eumops perotis | | 13 | 6 | 5 | 10 |
| Myotis velifer | | 11 | 5 | 5 | 10 |
| Macrotus californicus | | 12 | 6 | 5 | 7 |
| BARBU, P. 1960 | | | | | |
| Miniopterus schrebersi | 7 | 12 | 5 | 5 | 10-11 |
| WASSIF & MADKOUR, 1963 | | | | | |
| Rhinopoma | 7 | 12 | 6 | 4 | 17 |
| JEPSEN, G. L. 1966 | | | | | |
| Icaronycteris index | 7 | 12 | 7 | 3 | 13 |
| WALTON & WALTON | | | | | |
| Chilonycteris psilotis | 7 | 12 | 6 | 5 | 7 |
| Pteropus | 7 | 13 | 4 | 5 | |
| Cynopterus titthaecheilus | 7 | 14 | 5 | 5 | |
| Macroglossus minimus | 7 | 13 | 4 | 5 | |
| Rhinopoma microphyllum | 7 | 12 | 6 | 4 | 17 |
| Saccopteryx bilineata | 7 | 12 | 6 | 5-6 | |

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## TABLE I (cont.)

| Genus and/or species | Cervical | Thoracic | Lumbar | Sacral | Caudal |
|---|---|---|---|---|---|
| Peroptcryx | 7 | 13 | 6 | 4-5 | |
| Noctilio | 7 | 11 | 6 | 4 | |
| Nycteris javanica | 7 | 12 | 5 | 3 | |
| Megaderma spasma | 7 | 13 | 4 | 3-5 | |
| Rhinolophus | 7 | 12 | 6 | 3 | |
| Hipposideros | 7 | 11-12 | 6 | 3 | |
| Chilonycteris | 7 | 12 | 6 | 5 | 7 |
| Mormoops | 7 | 13 | 6 | 5 | |
| Macrotus | 7 | 12 | 6 | 5 | 7 |
| Phyllostomus | 7 | 12 | 6 | 5 | 7 |
| Glossophaga | 7 | 12 | 5 | 5 | |
| Lonchophylla | 7 | 12 | 4-5 | | |
| Carollia | 7 | 12 | 5-6 | 3-5 | |
| Rhinophylla | 7 | 11 | 4 | 4 | |
| Sturnira | 7 | 12 | 5 | | |
| Artibeus | 7 | 13 | 4 | 3-5 | |
| Vampyrops | 7 | 13 | 4 | 5 | |
| Phyllonycteris | — | — | — | — | — |
| Desmodus rotundus | 7 | 11 | 6 | 5 | 2 |
| Natalus mexicanus | 7 | 18 solidly fused | | 5 | |
| Furipterus morrens | 7 | 12 | fused | | 9 |
| Thyroptera discifera | 7 | 12 | 4 | 4 | 9 |
| Myotis evotis | 7 | 11 | 5 | 4 | 11 |
| Lasiurus cinereus | 7 | 11 | 5 | 4 | |
| Plecotus | 7 | 11 | 5 | 4 | 10 |
| Eptesicus | 7 | 11-12 | 5 | 3-4 | |
| Euderma | 7 | 11 | 5 | 4 | 10 |
| Histiotus montanus | 7 | 11 | 5 | 3 | 10 |
| Antrozous | 7 | 11 | 5 | 4 | |
| Mystacops | 7 | 13 | 5 | 5 | |
| Molossus major | 7 | 13 | 6 | 4 | |
| Tadarida | 7 | 13 | 6 | 4 | |