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COMPARATIVE OSTEOLOGY OF THE
PELVIC AND PECTORAL GIRDLES
OF THE PHYLLOSTOMATIDAE
(CHIROPTERA; MAMMALIA)

By

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Comparative Osteology of the Pelvic and Pectoral Girdles of the Phyllostomatidae (Chiroptera; Mammalia)

BY DAN W. WALTON AND GLORIA M. WALTON
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ABSTRACT

The Chilonycterinae are the most primitive of the subfamilies of the Phyllostomatidae. Two basic groups comprise this subfamily: the first includes the genera *Pteronotus* and *Chilonycteris*; the second, the genus *Mormoops*. This grouping is based principally upon the characteristics of the humerus and the innominate.

Within the subfamily Phyllostomatinae two types are recognized. The *Macrotus*-type is considered the more primitive, because of its resemblance to the chilonycterines, and the *Phyllostomus*-type the more advanced. From these two phyllostomatine groups are derived the more advanced lines of the Phyllostomatidae. The phyllonycterine line appears to be derived from the *Macrotus*-type. The sturnirine-glossophagine line and the stenodermine line are derived from the *Phyllostomus*-type. The *Vampyrops*-type of stenodermine shows affinities with the glossophagines and is considered the more primitive stenodermine. The *Artibeus*-type stenodermine is considered the more advanced. The carolline group shows relationships to the *Macrotus*-type of phyllostomatine and also shows affinities with the sturnirines. A more thorough study of the genera involved is needed to determine this relationship.

The family Phyllostomatidae has its closest affinities with the Desmodontidae, and post-cranial evidence offers little reason to consider these as separate families. Other close relationships of the Phyllostomatidae appear to exist with the Noctilionidae and possibly with the Emballonuridae.

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INTRODUCTION

The purpose of this study is to investigate the relationships among the sub-families of the family Phyllostomatidae. The investigation is centered on a comparative study of the three elements of the pectoral girdle (the humerus, scapula and the sternum) and of the two elements of the pelvic girdle (sacrum and innominate). The use of comparative morphology as a method of investigating relationships among organisms is generally considered to be a reliable and basic technique by students of evolution. The assets and limitations of this approach are discussed in detail by Davis (1964).

Bats of the family Phyllostomatidae are limited in geographic distribution to the New World (Simpson, 1945). Early Oligocene fossils from Egypt were described as phyllostomatid bats (*Provampyrus orientalis* Schlosser, 1911) and were accepted as such by Walker (1964), but this allocation was not accepted by Allen (1939), Simpson (1945), Ryberg (1947) and Savage (1951). The position or correct identification of these fossils was not discussed by Viret (1955) and Dechaseaux (1958) in reviews of fossil bats. A fossil phyllostomatid from the Oligocene of Nevada reported by Hall (1930) was later shown to be an insectivore by Patterson and McGrew (1937). The earliest record of a phyllostomatid is from the Miocene of Colombia (Savage, 1951). *Notonycteris magdalensis* Savage, 1951 was named and described from parts of three individuals. This record is not considered by Viret (1955) and is not included by Dechaseaux (1958) in discussions of Miocene Chiroptera. Pleistocene and Recent Phyllostomatidae are numerous mainly from the Antilles (Anthony, H. E., 1917, 1918, 1926; Jones, 1958; Koopman, 1951; Koopman and Ruibal, 1955; Koopman and Williams, 1951; Reynolds, Koopman and Williams, 1953; Williams, 1952).

The most recent comprehensive study of the relationships between the bats of the family Phyllostomatidae is that of Miller (1907) who presented the early nomenclatorial history and synonymy. Previously Dobson (1875, 1878) had suggested two subfamilial groups and established generic groups. Miller (1907) drew heavily from these studies of Dobson and organized the generic groups as seven sub-families. Dobson (1875, 1878) included the desmodontids in the Phyllostomatidae while Miller (1907) recognized Desmodontidae Gill, 1884. Simpson (1945) extended the superfamily Phyllostomato-

dea Weber, 1928, to include the Phyllostomatidae and Desmodontidae. Bourlière (1955) grouped with this same superfamily the Phyllostomatidae and Noctilionidae and he treated the desmodontids as a subfamily of the Phyllostomatidae. Brosset (1966) followed the arrangement presented by Bourlière (1955).

The subfamily Chilonycterinae of the Phyllostomatidae was considered a distinct family (Mormopidae and Lobostomidae, respectively) by Gill (1872, 1886) and H. Allen (1892). Dobson (1875, 1878) suggested the genus *Noctilio* (which he considered a member of the family Emballonuridae) as the connection between the Emballonuridae and Phyllostomatidae. Winge (1941) included *Noctilio* with the Mormopini (= Chilonycterinae). Simpson (1945) followed Miller (1907) and included the Noctilionidae in the superfamily Emballonuroidea and placed the superfamily Rhinolophoidea between the Emballonuroidea and the Phyllostomatoidea.

Bell (1836) and Flower and Lydekker (1891) discussed the general anatomic features of the Chiroptera. Koopman and Cockrum (1967) reviewed general anatomy for each of the seventeen families of bats. Few authors discussed pelvic characters. Flower (1885) described the pelvis of the genus *Phyllorhina* (= *Hipposideros*) which he placed in the family Rhinolophidae. Dobson (1875) included the Rhinolophinae and Phyllorhininae (= *Hipposideridae*) in the family Rhinolophidae on the basis of innominate characters. Miller (1907), Simpson (1945), and Bourlière (1955) recognized two separate families, *Hipposideridae* and Rhinolophidae, on the basis of the same innominate characters. Hall (1934) reported on the pelvis of selected genera of the Vespertilionidae.

H. Allen (1881) reported on the ethmoid bone in bats and (1889) on the wing membrane and associated phalanges of the Pteropidae, Rhinolophidae, *Hipposideridae*, Nycteridae, Vespertilionidae, Molossidae, Emballonuridae, Rhinopomatidae, Noctilionidae, Phyllostomatidae, Desmodontidae, Natalidae and Thyropteridae. Thomas (1904) reported on the osteology of *Myzopoda* (*Myzopodidae*). The general adaptations for flight in the Chiroptera were discussed by R. Anthony (1912) and anatomical aspects of the wing, associated digits and the feet of the Microchiroptera were presented by R. Anthony and Vallois (1913). Sanborn (1943) reported on the external characters of the subfamily Glossophaginae (Phyllostomatidae) and Wille (1954) dis-

cussed the muscular adaptations for nectar feeding in this subfamily. Grassé (1955) presented a general discussion of chiropteran anatomy. Vaughan (1959) reported on the comparative morphology of three bats: *Eumops* (Molossidae), *Myotis* (Vespertilionidae) and *Macrotus* (Phyllostomatidae), and (1966) reported further on the morphology of the Molossidae. Barbu (1960) studied the osteology of *Miniopterus* (Vespertilionidae). Romankowowa (1963) reported on the hyoid apparatus of bats of the families Rhinolophidae and Vespertilionidae. Wassif and Madkour (1963) reported on the osteology of *Rhinopoma* (Rhinopomatidae). Studies of chiropteran morphology by Macalister (1872), Robin (1881) and Shrivastava (1962) considered musculature and internal organs. Gupta (1967) reported on the musculature of the plagiopatagium with special emphasis on the families Desmodontidae, Molossidae and Pteropidae. The comprehensive study of the families and genera of bats by Miller (1907) covered various aspects of chiropteran anatomy, but dwelt heavily on dentition.

Baker (1967) was able to group most of the phyllostomatid genera in seven groups according to a karyotype analysis. The groups were as follows: (A) *Pteronotus*; (B) *Choeronycteris*, *Choeroniscus*, and *Carollia*; (C) *Leptonycteris*, *Glossophaga*, *Phyllostomus*, *Trachops* and *Macrotus*; (D) *Micronycteris*; (E) *Anoura*; (F) *Artibeus*, *Sturnira*, *Vampyrops*, *Chiroderma*, *Enchisthenes* and *Centurio*; and (G) *Uroderma*.

The seven subfamilies of the family Phyllostomatidae were distinguished by diversity in dental characters (Miller, 1907). Illustrations and a discussion of the evolution of the second upper molar in the Phyllostomatidae were presented by Grassé (1955). The diversity in dental characters falls into two general categories: variation in tooth number and modifications of the basic W or dilambdodont pattern of the crown of the cheek teeth. The classification of Miller (1907) was based largely on diversity of the crown pattern of the molars, and a detailed description of the variation accompanied his classification.

Dental characters are widely used and accepted in studies of mammalian evolution. A detailed description and discussion of the dentition of the Chiroptera was presented by Miller (1907). More general descriptions and discussions of chiropteran dentition were cov-

ered by Allen (1939), Grassé (1955) and Dechaseaux (1958). It is not the purpose of this study to test the validity of the classification of the Phyllostomatidae based on dentition as proposed by Miller (1907) nor to test the usefulness of dental characters in the study of mammalian evolution, but to investigate relationships between the recognized subfamilies as reflected by characters other than dentition.

MATERIALS AND METHODS

Genera used for comparative purposes in this study are considered typical of the particular subfamily or family in which they are placed by Simpson (1945). Simpson (1945) serves as a nomenclatorial guide and terminology used in reference to skeletal elements follows Miller (1907) and Vaughan (1959).

Skeletal elements selected for study and comparison are the following: scapula, sternum, humerus, innominate and sacrum. Observations were made of the general and specific configurations of these elements. Generalized illustrations of these elements are presented in Figures 1, 3, 4 and 5. Figures 6, 7 and 8 are pelvic views of *Desmodus rotundus*. This genus was chosen as the model due to the presence of pelvic characters found in most of the subfamilies of the Phyllostomatidae as well as in most other chiropteran families. Both male and female specimens were examined where possible.

The genera listed below were selected for study and comparison.

FAMILY: PHYLLOSTOMATIDAE

SUBFAMILY	GENUS
Chilonycterinae	<i>Chilonycteris</i> , <i>Mormoops</i>
Phyllostomatinae	<i>Macrotus</i> , <i>Phyllostomus</i>
Glossophaginae	<i>Glossophaga</i> , <i>Lonchophylla</i> , <i>Choeronycteris</i>
Carollinae	<i>Carollia</i> , <i>Rhinophylla</i>
Sturnirinae	<i>Sturnira</i>
Stenoderminae	<i>Vampyroops</i> , <i>Artibeus</i> , <i>Vampyrodes</i>
Phyllonycterinae	<i>Phyllonycteris</i>

Because of the association noted above of the desmodontids and noctilionids to the phyllostomatids, *Desmodus* (Desmodontidae) and *Noctilio* (Noctilionidae) are included in the study. To obtain a perspective of the variation throughout the order, genera and families

other than Phyllostomatidae, Desmodontidae and Noctilionidae were examined and are listed below.

FAMILY	GENUS
Pteropidae	<i>Cynopterus</i> , <i>Pteropus</i> , <i>Rousettus</i> , <i>Epomophorus</i> <i>Macroglossus</i>
Rhinopomatidae	<i>Rhinopoma</i>
Emballonuridae	<i>Saccopteryx</i> , <i>Peropteryx</i>
Nycteridae	<i>Nycteris</i>
Megadermatidae	<i>Megaderma</i>
Rhinolophidae	<i>Rhinolophus</i>
Hipposideridae	<i>Hipposideros</i>
Natalidae	<i>Natalus</i>
Furipteridae	<i>Furipterus</i>
Thyropteridae	<i>Thyroptera</i>
Vespertilionidae	<i>Myotis</i> , <i>Plecotus</i> , <i>Euderma</i> , <i>Eptesicus</i> , <i>Pipistrellus</i> , <i>Lasiurus</i> , <i>Histiotis</i> <i>Antrozous</i>
Mystacinidae	<i>Mystacops</i>
Molossidae	<i>Tadarida</i> , <i>Molossus</i>

The terms width and length used in reference to the skeletal elements refer to greatest width and greatest length. No volumetric measurements were made.

RESULTS AND DISCUSSION

Miller (1907) pointed out that certain skeletal elements of the Chiroptera, especially those associated with flight, were of taxonomic importance and was able to demonstrate that particular characteristics of the elements associated with flight were peculiar to certain families, subfamilies and genera. Vaughan (1959, 1966) demonstrated that peculiarities in both osteology and myology are of functional significance. The choice of skeletal elements in this study was based on the findings and suggestions of Miller (1907) and Vaughan (1959). No representative of the family Myzopodidae was available for study and any reference to that family in the following discussion is based on Thomas (1904) and Miller (1907).

THE SCAPULA

Scapula of the Phyllostomatidae: General Description. The general outline of the scapula is that of an oval, the length about twice the width. The posterior tip, the small end of the oval, is blunt and a cartilaginous extension is present. The greatest width of the scapula occurs at the level of the base of the acromial process. The spine is dis-

tinct, straight in most, but deflected toward the posterior tip in others. The supraspinous fossa is one-third to one-half the size of the infraspinous fossa. The axillary border is thickened and depressed anteromedially immediately posterior to the glenoid fossa. The vertebral and coracoid borders are much less thickened and the latter is deeply notched. A ventrally directed flange from the coracoid border is usually absent.

The acromial process extends laterally beyond the glenoid fossa and hooks medially toward the dorsal base of the coracoid process. The distal portion is flattened on the medial surface. The glenoid fossa faces anterolaterad and there is a facet for articulation with the trochiter of the humerus.

The infraspinous fossa has a deep trough and a ridge which passes from the axillary border of the glenoid fossa to the posterior tip of the scapula. The trough appears as a prominent ridge in the subscapular fossa. Three distinct facets are formed in the infraspinous fossa and four in the subscapular fossa (Fig. 1).

The coracoid process is large, tapers little and extends at least to the

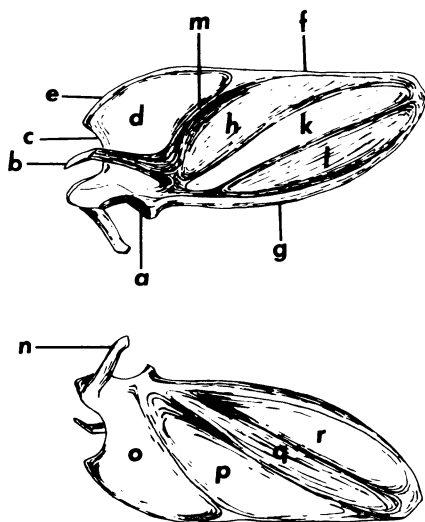


Fig. 1. Generalized phyllostomatid scapula; dorsal and ventral aspects. Parts or areas indicated by letters are as follows: a. glenoid fossa; b. acromial process; c. notch of coracoid border; d. supraspinous fossa; e. coracoid border; f. vertebral border; g. axillary border; h. anteromedial facet of 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.

level of the axillary border. The tip is variable in configuration.

Discussion of the Phyllostomatid Scapula.—The scapulae of the Phyllostomatidae are remarkably homogeneous. The greatest divergence from the general pattern is in the Chilonycterinae in which there is no secondary articulation with the humerus and a small ventrally directed flange is present on the coracoid border. The ridge in the infraspinous fossa is clearly evident in all the subfamilies but in the Phyllonycterinae is raised into a low secondary spine.

The tip of the coracoid process is the most variable character of the phyllostomatid scapula. The tip is simple in the Chilonycterinae, some of the Phyllostomatinae (*Macrotus*), and Stenoderminae (*Artibeus*), the Carolliinae and the Phyllonycterinae. In others, the variation extends from the weak equally bifid condition seen in the Phyllostomatinae (*Phyllostomus*) to the unequally bifid condition seen in some of the Stenoderminae (*Vampyrops*). Detailed illustrations of the tips of the coracoid process are presented in Figure 2.

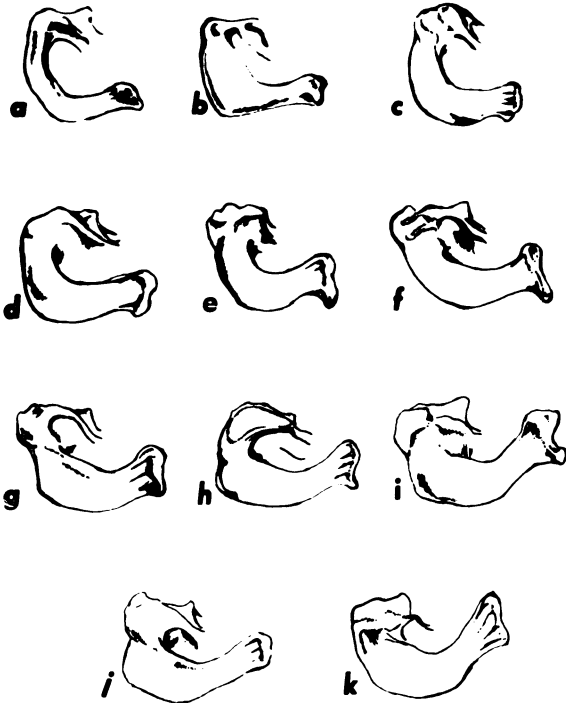


Fig. 2. Coracoid processes of the Phyllostomatidae. a. *Chilonycteris*. b. *Mormoops*. c. *Macrotus*. d. *Phyllostomus*. e. *Glossophaga*. f. *Choeronycteris*. g. *Sturnira*. h. *Carollia*. i. *Vampyrops*. j. *Artibeus*. k. *Phyllonycteris*.

Except for the peculiarities of the scapula of the Chilonycterinae and the Phyllonycterinae, the scapulae of the Phyllostomatidae may be divided into two basic groups on the basis of the tip of the coracoid process. Group 1 comprises those having a simple tip: the Chilonycterinae, some of the Phyllostomatinae (*Macrotus*), the Caroliinae, some of the Stenoderminae (*Artibeus*) and the Phyllonycterinae. Group 2 comprises those having a complex tip: some of the Phyllostomatinae (*Phyllostomus*), Glossophaginae, Sturnirinae and some of the Stenoderminae (*Vampyrops*). The greatest divergence from the general plan of the phyllostomatid scapula is the lack of secondary articulation with the humerus in the Chilonycterinae.

Comparison and Discussion of the Seventeen Families.—The notch in the coracoid border is deep in the Emballonuridae, Noctilionidae, Nycteridae, Megadermatidae, Rhinolophidae, Hipposideridae, Phyllostomatidae, Desmodontidae, Natalidae, Vespertilionidae and Molossidae; it is shallow in the Pteropidae, Rhinopomatidae, Furipteridae, Thyropteridae and Myzopodidae, and very shallow in the Mystacinidae. 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, and absent in the Rhinopomatidae, Desmodontidae, Furipteridae, Thyropteridae and Mystacinidae.

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

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

A notch in the axillary border is present in the Pteropidae, Noctilionidae, Nycteridae, Megadermatidae, Rhinolophidae and Hipposideridae. It is either present or absent in the Phyllostomatidae and Vespertilionidae, and absent in all other families.

The anterior portion of the axillary border is rounded in the Noctilionidae, Megadermatidae, Rhinolophidae, Hipposideridae, Mystacinidae and Molossidae. It is rounded or flattened in the Vespertilionidae, and flattened 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. It is lacking in the Megadermatidae, Rhinolophidae, Hipposideridae, Desmodontidae, Vespertilionidae and Molossidae.

The coracoid process is untapered except in the Pteropidae, Natalidae, Furipteridae and Molossidae. Generally, the coracoid process is large and conspicuous, the length may be as great as one-half the length of the scapula. Relative to the size of the scapula, the smallest coracoid process is found in the Mystacinidae.

The distal tip of the coracoid process is complex in the Phyllostomatidae, Desmodontidae and Vespertilionidae. It is simple in all other families. The tip is generally directed laterally, but in the Vespertilionidae and the Molossidae the distal tip is directed posterolaterally to posteriorly. For a comprehensive discussion of the functional significance of the direction of the coracoid process, see Vaughan (1959; 1966).

The acromial process is normally recurved anteroventrally. In the Furipteridae, however, it is recurved dorsomedially. It does not 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 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 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. 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 molossid scapula is here considered the most primitive of the seventeen families of the Chiroptera. It has a posteriorly directed acromion with a lateral projection that resembles a metacromion; the acromion is in line with the spine and the general outline of the scapula of the Molossidae is similar to mammals other than bats. This is not to imply that the molossid scapula does not show modifications

peculiar to that family (see Vaughan, 1959; 1966) or that the molossids represent the most primitive family. The retention of a primitive scapular form is probably related to the importance of terrestrial quadrupedal locomotion in this family (Vaughan, 1966). Vaughan (1966) also suggested that certain characteristics of the molossids indicate that the group may have diverged early from the other families of the Chiroptera. The scapula of the molossids and the mystacinids are the most distinctive among all of the families of bats.

THE STERNUM

The Sternum of the Phyllostomatidae: General Description.—The lateral processes of the manubrium or presternum are directed antero-laterad or laterad and may bear a distinct notch on the posterior border or be pierced by a foramen. The vertical process is higher than the keel of the mesosternum and in profile resembles the blade of a hatchet. The vertical process is directed posteroventrad.

The median ridge of the mesosternum is well developed and usually raised into a distinct ventral keel. The greatest height of the keel varies in position, but occurs between ribs 3-7. The ventral margin of the keel is serrate or smooth. There is no clear boundary between the mesosternum and xiphisternum; the posterior tip of the xiphisternum is laterally expanded and always possesses a large cartilaginous extension. In the discussion that follows, the combined mesosternum and xiphisternum will be referred to as the body of the sternum. A generalized phyllostomatid sternum is presented in Figure 3.

Discussion of the Phyllostomatid Sternum.—The lateral processes of the manubrium are directed laterally in the Chilonycterinae and anterolaterally in all other phyllostomatid subfamilies. There is a distinct notch on the posterior margin in *Glossophaga* (Glossophaginae), *Carollia* and *Rhinophylla* (Carolliinae), *Sturnira* (Sturnirinae), *Vampyrops* (Stenoderminae) and *Phyllonycteris* (Phyllonycterinae). In *Choeronycteris* (Glossophaginae) and *Artibeus* (Stenoderminae) the lateral processes are pierced by a foramen near the junction with the base of the manubrium.

The ventral margin of the vertical process is greater in length than the length of the presternum of the Chilonycterinae. The length of the ventral margin of the vertical process is highly variable in the other members of the family, but the length never exceeds that of

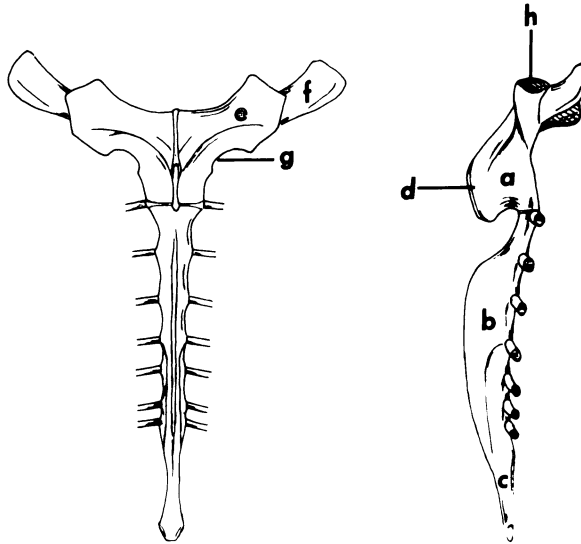


Fig. 3. Generalized phyllostomatid sternum; ventral and profile views. Parts and areas indicated by letters are as follows: a. presternum or manubrium; b. mesosternum with keel; c. xiphoid portion; d. vertical process of the manubrium; e. lateral process of the manubrium; f. expanded costal cartilage of the first rib; g. notch in posterior margin of the lateral process of the manubrium; h. point of articulation with the clavicle.

the base of the presternum. The variation is such that no clear patterns or relationships can be seen.

The ventral margin of the keel of the body of the sternum is distinctly serrate in *Phyllostomus* (Phyllostomatinae), *Glossophaga* (Glossophaginae) and *Vampyrops* (Stenoderminae), less so in *Choeronycteris* (Glossophaginae), *Carollia* (Carolliinae) and *Artibeus* (Stenoderminae). It is smooth in the Chilonycterinae, *Macrotus* (Phyllostomatinae), Sturnirinae and Phyllonycterinae. The height and development of the keel appear to be related to size.

Miller (1907) comments on the general pattern of the sternum of the Phyllostomatidae in relation to the other families of the Microchiroptera and Vaughan (1959) considers the sternum of *Macrotus* in detail.

Comparison and Discussion of the Seventeen Families.—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. In the Nycteridae there is a large ventrally directed lobe

and a small anterior lobe which is directed anteroventrally. Both lobes in the Pteropidae are directed ventrally. In the Furipteridae the single vertical lobe is forked and appears in the form of a "Y".

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

A single foramen pierces the lateral lobes of the presternum of some of the Phyllostomatidae. In the Rhinolophidae and Hipposideridae two foramina pierce the lateral lobes (Miller, 1907). 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. For a description of the fusion of the presternum, ribs and vertebrae peculiar to the Rhinolophidae and Hipposideridae, see Grassé (1955).

A distinct notch in the posterior margin of the lateral lobes is seen in some of the Vespertilionidae and some of the Phyllostomatidae.

A secondary lateral process from the lateral lobes of the presternum is present in the Megadermatidae, Rhinolophidae and Hipposideridae. In the Natalidae and Furipteridae there is a secondary lateral projection from the ventral terminus of the first costal cartilage.

The median ridge is generally present and sometimes raised into a distinct keel (Miller, 1907). In the Furipteridae the mesosternum 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 of the body of the sternum is highly variable. With only one exception, the greatest height always occurs on the mesosternum. This exception occurs in the Furipteridae where the greatest height is found on the xiphoid portion.

THE HUMERUS

The Humerus of the Phyllostomatidae: General Description.—The head of the humerus projects medially from the long axis of the shaft and varies from elliptical to oval in shape (long axis of the head is from anterior to posterior). The position of the head is always distal to at least one tuberosity and usually to both. The lesser tuberosity, or trochin, is less than half the size of the head. The greater tuberosity, or trochiter, is half or greater the size of the head and articulates

with the scapula (see discussion of the scapula). The pectoral and deltoid ridges are dorsoventrally compressed. The anterior margin of the proximal end of the humerus is, therefore, raised into a prominent flange. The flange reaches its greatest height at the level of, and opposite the proximal base of the head, extends distally for the proximal fourth of the length of the shaft and either tapers sharply or ends abruptly.

There is a shallow to deep pit in the proximal end of the shaft bounded by the head, the two tuberosities and the base of the proximal end of the pectoral-deltoid flange. The point of insertion of the *teres major* and the *latissimus dorsi* is conspicuous on the distal base of the lesser tuberosity and the bicipital groove is well defined.

The shaft of the humerus is slightly sigmoid in shape. In cross section the shaft varies from circular at the proximal end to elliptical at the distal end.

The distal articular surfaces are rotated anteriorly and both lateral and medial epicondyles are widely displaced from the long axis of the shaft. There is usually a small, distally directed spinous process from the distal face of the medial epicondyle. The medial epicondyle is separated from the trochlea by a rounded depression. The dorsal rim of the trochlea is greatly enlarged and may persist as a low ridge on the posterior surface of the distal end of the shaft.

A generalized phyllostomatid humerus is shown in Figure 4.

Discussion of the Phyllostomatid Humerus.—The head of the humerus is dorsoventrally compressed and is elliptical in outline in the Chilonycterinae; it is oval in the Phyllostomatinae and Glossophaginae, and more circular in the other subfamilies.

The greater tuberosity projects only slightly above the level of the head and the lesser tuberosity in the Chilonycterinae and the lesser tuberosity is the larger. There is no articulation with the scapula by the greater tuberosity in the Chilonycterinae. In all the other subfamilies, the greater tuberosity projects well above the level of the head and lesser tuberosity and is the larger. In the Sturnirinae, the lesser tuberosity approaches the size of the greater tuberosity.

In *Chilonycteris* (Chilonycterinae) the lesser tuberosity forms a high ridge distally which rivals the pectoral-deltoid flange in height above the shaft. A similar situation exists in *Macrotus* and to a lesser degree in *Phyllostomus* of the Phyllostomatinae. In the Carollinae the

development of the ridge is as in *Chilonycteris* and *Macrotus*. In all others the ridge is not conspicuous.

The pit in the proximal end of the humerus is deep in all sub-families and the bicipital groove is conspicuous. In *Mormoops* (Chilonycterinae), however, the pit is displaced into the medial base of the lesser tuberosity.

The pectoral-deltoid flange takes two general patterns in the family. In the Chilonycterinae, *Macrotus* (Phyllostomatinae) and Caroliinae the pectoral-deltoid flange maintains its greatest height over its entire length. In *Mormoops* the anterior rim of the flange curls dorsally over its entire length. In the other members of the family the pectoral-deltoid flange reaches its greatest height opposite the head, then tapers to the level of the shaft.

The shaft of the humerus is generally sigmoid in shape, although the humeri of the Chilonycterinae, *Macrotus* (Phyllostomatinae) and Phyllonycterinae tend to be straight.

The Chilonycterinae are distinguished by the long spinous process

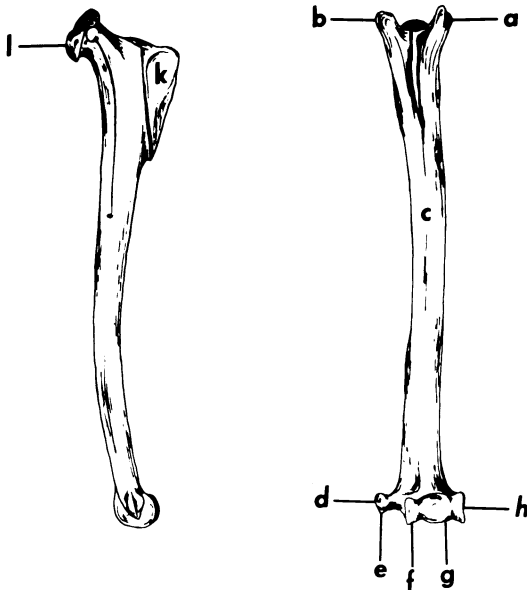


Fig. 4. Generalized phyllostomatid humerus; anterior and dorsal aspects. Parts and areas indicated by letters are as follows: a. greater tuberosity; b. lesser tuberosity; c. shaft; d. medial epicondyle; e. spinous process of the medial epicondyle; f. trochlea; g. capitulum; h. lateral epicondyle; k. pectoral-deltoid flange; l. head.

of the medial epicondyle; it extends beyond the distal extremities of the trochlea and capitulum. In *Mormoops* the capitulum and trochlea are separated by a deep notch. The dorsal rim of the trochlea does not persist as a ridge, although a well developed ridge arises on the posterior face of the distal end of the shaft. The spinous process is displaced posteromedially to appear continuous with the dorsal rim of the trochlea. The spine extends well beyond the distal end of the humerus and no gap exists between the trochlea and medial epicondyle. The spinous process is present in the Phyllostomatinae, Glossophaginae and Carolliinae. The spinous process may become so rounded, however, in the Carolliinae as to appear absent. A distinct gap between the medial epicondyle and the trochlea exists in all except *Mormoops*. In the Sturnirinae and Phyllonycterinae the distal portion of the rim of the trochlea is rounded and the posterior portion is elevated. The medial epicondyle in the Phyllonycterinae is more nearly in line with the shaft than in other subfamilies. The dorsal rim of the trochlea is greatly elevated and persists on the posterior surface of the shaft as a low ridge in the Glossophaginae and in *Artibeus* (Stenoderminae).

Three features appear significant in the development of the phyllostomatid humerus: (1) there is a definite elaboration of the proximal extension of the greater tuberosity for secondary articulation with the scapula; (2) the pectoral-deltoid ridges are compressed to form a prominent anteriorly directed flange from the proximal quarter of the shaft; (3) there is a suppression of the spinous process of the medial epicondyle. The form of the humerus of *Mormoops*, however, is so unique that it bears little similarity to the other members of the family.

Comparison and Discussion of the Seventeen Families.—Humeri of the Nycteridae and Myzopodidae were not available and only the proximal end of the humerus of the Furipteridae. The discussion below does not, therefore, include these families.

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 oval; it is elliptical in the Megadermatidae and Mystacinidae, and variable in the Phyllostomatidae.

With the exception of the Pteropidae, the greater tuberosity al-

ways 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; 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 quite low in the Desmodontidae. The humeri of the Pteropidae and Desmodontidae are superficially quite similar.

The ridge on the distal base of the lesser tuberosity seen in some of the Phyllostomatidae is present 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 epicondyle is consistent throughout the Chiroptera. Only in the Phyllostomatidae is the process completely lost.

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

Miller (1907) considered the humeri of the Rhinopomatidae and Emballonuridae the least specialized among the Microchiroptera and the humerus of Noctilionidae only a slight modification of the pattern seen in the Rhinopomatidae and Emballonuridae. In his discussion of the Old World leaf-nosed bats, Miller made the statement (p. 16) that the greater tuberosity of Rhinolophidae and Hipposideridae forms, "a definite secondary articulation with the scapula by a surface about half as large as the glenoid fossa". This is affirmed in the description of the Rhinolophidae (p. 107), but no mention of secondary articulation with the scapula is present in the description of the Hipposideridae (pp. 109-110). In the description of the Phyllostomatidae (which follows that of the Rhinolophidae and Hipposideridae) Miller makes the following statement (p. 117): "This is the first family in which the humerus has a definite double articulation with the scapula". The distinction between what constitutes a secondary or double articulation is not clear. If there is no distinction between the two terms, the impression is conveyed by Miller that the Phyllostomatidae are the "first" to have articulation between the

greater tuberosity of the humerus and the scapula.

The humeri of the Nycteridae, Megadermatidae, Rhinolophidae and Hipposideridae are considered by Miller as somewhat more advanced than those of the Rhinopomatidae, Emballonuridae and Noctilionidae. Also similarities in the shoulder joints between the Rhinolophidae and Hipposideridae and the Phyllostomatidae and Desmodontidae are said to exist, but details of the similarities are not clear.

The Natalidae, Furipteridae, Thyropteridae and Myzopodidae are thought to agree in form of the humerus and Miller points to similarities and differences in these four families to the Phyllostomatidae. Miller considers the transition of the humeral form of the phyllostomatids to the Vespertilionidae, Mystacinidae and Molossidae as rather abrupt. The humerus of the Pteropidae (Megachiroptera) shows several differences from the microchiropteran humerus, particularly in development and arrangement of the proximal end of the bone. Detailed description of the pteropid humerus is presented by Miller (1907) and the basic differences have been covered above.

THE PELVIS

The Pelvis of the Phyllostomatidae: General Description.—The dorsoventrally compressed pelvis is narrow across ischial borders. The bones are normal except for the narrow ascending ischial ramus. The innominate is set level on the sacrum, and sacroiliac and sacroischial joints are present. Neither joint is ankylosed.

The ilium is rotated slightly dorsomedial so that the shallow gluteal fossa faces dorsomedial. Immediately anterior to the acetabulum the ilium is elliptical in cross section. Its anterior end is triangular. An iliac fossa is present, and the iliac crest is slightly expanded dorsoventrally. The ventral surface is smooth.

A broad, ossified symphysis pubis is found in males (see Fig. 5). A narrow, well developed pubic spine extends cephalad to a level opposite the middle of the ilium (Fig. 6). The spine tapers to the tip. Dorsal and ventral ischial tuberosities are present.

The acetabulum faces dorsolaterad and slightly caudad, and embedded in the anterolateral cartilaginous rim is a small sesamoid bone. The oval obturator foramen is three to four times larger than the acetabulum. The caudal rim of the obturator foramen angles posteroventrally to the pubis, and the puboischial angle formed is approximately 45° .

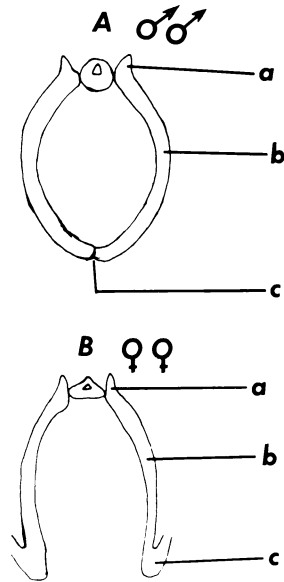


Fig. 5. Diagrammatic representation of the caudal view of male and female pelvises. Parts or areas indicated by letters are as follows: A. a. dorsal ischial tuberosity; b. ascending ramus of the ischium; c. symphysis pubis. B. a. dorsal ischial tuberosity; b. ascending ramus of the ischium; c. ventral ischial tuberosity.

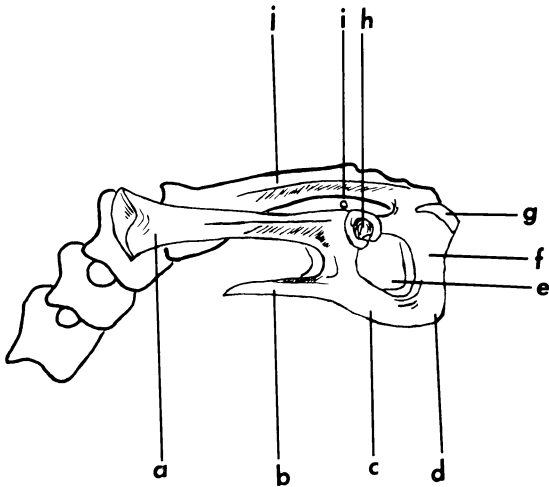


Fig. 6. Diagrammatic representation of the lateral view of the pelvis of *Desmodus rotundus*. Parts or areas indicated by letters are as follows: a. ilium; b. pubic spine; c. pubis; d. ventral ischial tuberosity; e. obturator foramen; f. ischium; g. dorsal ischial tuberosity; h. acetabulum; i. sesamoid bone; j. sacrum.

Just posterior to the first sacral vertebra, the centra of the sacrum are dorsoventrally compressed. Lateral boundaries are effaced, and a transversely flattened urostyle is formed. This formation occurs early in life (Miller, 1907). The number of vertebrae cannot be determined due to the complete fusion of the sacral elements (Fig. 6).

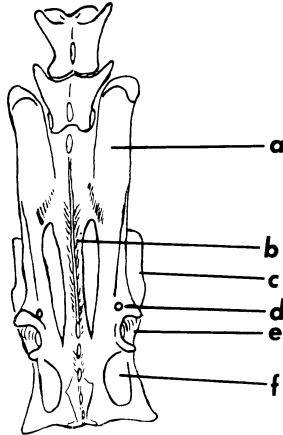


Fig. 7. Diagrammatic representation of the dorsal view of the pelvis of *Desmodus rotundus*. Parts or areas indicated by letters are as follows: a. ilium; b. sacrum; c. pubic spine; d. sesamoid bone; e. acetabulum; f. obturator foramen.

Discussion of the Phyllostomatid Pelvis. The pelvis of the Chilonycterinae, Phyllostomatinae and Stenoderminae are sturdy in construction; it is lightly built in the other subfamilies. Strong ridges and tuberosities seem to be apparent only in the Chilonycterinae. A very narrow ascending ischial ramus is found in the Phyllostomatinae, Carollinae and Phyllyonycterinae, and the ilium is elongated in the Phyllyonycterinae and Stenoderminae. All the bones of the sturnirine pelvis are very narrow.

The innominate is set at an angle to the sacrum only in the Glossophaginae, Chilonycterinae and Phyllostomatinae. Ankylosis of the sacroiliac joint may be seen in *Phyllostomus* (Phyllostomatinae) and Chilonycterinae. The sacroischial joint is present only in the Phyllostomatinae, Chilonycterinae and Stenoderminae. In the latter subfamily, ankylosis of the joint occurs in *Vampyrops*.

In cross section, the ilium is elliptical in the Glossophaginae, *Carollia* (Carollinae) and Stenoderminae, round in the Sturnirinae, Phyl-

lonycterinae and *Rhinophylla* (Carolliinae), and triangular in the Chilonycterinae and Phyllostomatinae. In the Carolliinae, the anterior end of the ilium becomes more triangular in shape. The ilium is rotated dorsomedial in the Phyllostomatinae, Glossophaginae, Carolliinae and Stenoderminae. Gluteal and iliac fossae are completely obliterated in *Rhinophylla* (Carolliinae), Sturnirinae and Phyllonycterinae. The gluteal fossa, when present, is shallow and faces dorsad in the unrotated ilium and dorsomedial in the rotated ilium. This fossa is most deeply concave in the Chilonycterinae. The ventral surface of the ilium is generally smooth, but in the Chilonycterinae a shallow ventral fossa is present.

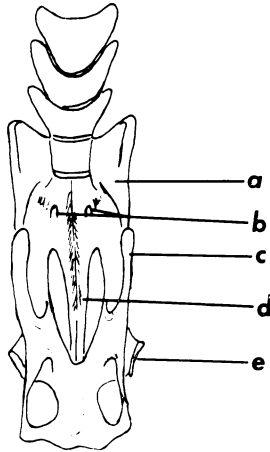


Fig. 8. Diagrammatic representation of the ventral view of the pelvis of *Desmodus rotundus*. Parts or areas indicated by letters are as follows: a. ilium; b. intervertebral foramina; c. pubic spine; d. sacrum; e. acetabulum.

The symphysis pubis, present in all males, is generally broad and ossified. In *Macrotus* (Phyllostomatinae) and Glossophaginae the symphysis is narrow; in the sturnirines and the Phyllonycterinae it is ligamentous. The pubic spine is well developed and narrow in all groups. It is generally directed cephalad to a level opposite the middle of the ilium. The Carolliinae have the shortest spine and the Glossophaginae the longest. In the Stenoderminae the spine is directed dorsad as well as cephalad, a character peculiar to this subfamily. A large, well developed ventral ischial tuberosity is present in all subfamilies except the Phyllostomatinae and Stenoderminae. The dorsal ischial tuberosity is completely effaced in the glossophagines, *Glossophaga*

and *Choeronycteris*, and in the Carolliinae. It is present in all other subfamilies.

Mormoops (Chilonycterinae) is unique in that the ventral ischial tuberosity and ascending ischial ramus of each innominate appear as separate units fused ventrolaterally to the base of the pubis and connected dorsally to the remainder of the ischium by a small ligament.

The acetabulum faces dorsolaterad and caudad and shows slight variation among subfamilies. The sesamoid bone is situated anterolaterally in the anterior cartilaginous rim of the acetabulum. The obturator foramen is generally three to four times the size of the acetabulum. It is round in the Glossophaginae and Phylloonycterinae, oval in the Chilonycterinae, Phyllostomatinae, Carolliinae and *Artibeus* (Stenoderminae), and triangular in the remaining subfamilies. The caudal rim of the foramen is always directed ventrally to the pubis. In the Carolliinae, Glossophaginae, Sturnirinae and *Macrotus* (Phyllostomatinae) it is also angled caudally.

The phyllostomatid sacrum is fused into a transversely flattened urostyle with lateral boundaries almost or completely effaced and dorsal boundaries reduced and fused together. The degree and extent of reduction and fusion of these elements differs in the family. The urostyles of *Chilonycteris* (Chilonycterinae), *Phyllostomus* (Phyllostomatinae), *Vampyroops* (Stenoderminae) and *Sturnira* (Sturnirinae) are well-developed, distinct structures. The sacral urostyles of the other genera are less distinct. There are five sacral vertebrae in *Macrotus* (Phyllostomatinae) as noted by Vaughan (1959), five in *Glossophaga* (Glossophaginae) and three to five in *Rhinophylla* (Carolliinae). Fusion of the sacral elements prevents counting of the vertebrae in the other subfamilies. Generally, the first two vertebrae enter into the sacroiliac joint.

Comparison and Discussion of the Seventeen Families.—In general, the pelvis is small and narrow. Sturdier construction in the Pteropidae, Rhinolophidae, Rhinopomatidae, Noctilionidae, Hipposideridae, Desmodontidae, Mystacinidae and Molossidae is characterized by strong ridges and tuberosities.

Innominate elements (ilium, pubis and ischium) vary slightly among the families. The ilium is elongated in the Pteropidae, Rhinopomatidae, Megadermatidae, Desmodontidae and Mystacinidae whereas it is compressed anteroposteriorly in the Rhinolophidae and Hipposideridae. The ischium is consistently narrower than the pubis in all

families except the Rhinopomatidae. In this family the ventral pubic element is narrower than the ischium. Reduction in the ventral pubic and ischial elements is noted in the Natalidae, Rhinolophidae and Hipposideridae by Miller (1907). There is a similar reduction in the ventral elements of the Nycteridae. The reduction causes the dorsal and ventral margins of the innominate to appear parallel.

The innominate is set evenly on the sacrum in the Pteropidae, Emballonuridae, Rhinopomatidae and Desmodontidae. It is angled to the sacrum in all other families and is most sharply angled in the Hipposideridae, Megadermatidae and Molossidae. A single anterior fusion, termed the sacroiliac joint, is generally the only connection between the innominate and sacrum. Ankylosis of this joint is seen only in the Pteropidae, Noctilionidae, Desmodontidae and Molossidae. There are anterior (sacroiliac joint) and posterior (sacroischial joint) connections between sacrum and innominate only in the Pteropidae, Rhinopomatidae, Emballonuridae, Noctilionidae, Phyllostomatidae, Desmodontidae and Furipteridae. The sacroischial fusion is given additional rigidity in the Pteropidae, Noctilionidae and Desmodontidae by the fusion of the two dorsal ischial tuberosities directly beneath the sacroischial joint.

The ilium is generally compressed dorsoventrally and is broader and thicker at the anterior end. In cross section anterior to the acetabulum, the ilium is round in the Pteropidae and Desmodontidae, elliptical in the Emballonuridae, Megadermatidae, Phyllostomatidae, Furipteridae, Thyropteridae and Vespertilionidae, and triangular in all other families. Anteriorly, the ilium of the Desmodontidae and Pteropidae becomes laterally compressed. The gluteal and iliac fossae which lie in the dorsal and lateral iliac surfaces, respectively, are completely absent only in the Desmodontidae and Pteropidae. The gluteal fossa is generally shallow. It is most deeply concave in the Rhinolophidae, Hipposideridae, Natalidae and Molossidae. The ventral iliac surface is concave only in the Nycteridae, Rhinolophidae, Hipposideridae and Natalidae.

Two general patterns in the chiropteran ilium seem clear: (1) dorsoventral and anteroposterior compression of the bone with a more deeply concave gluteal fossa and a fossa along the ventral iliac surface; (2) anteroposterior expansion of the ilium with reduction or loss of the gluteal and iliac fossae as the bone becomes more rounded in cross section.

All male specimens examined in this study were found to have a symphysis pubis. Miller (1907), however, noted a symphysis present only in males of the families Myzopodidae, Noctilionidae, Thyropteridae and Vespertilionidae. Wassif and Madkour (1963) describe the absence of the symphysis in males of the genus *Rhinopoma* (Rhinopomatidae). This is contradictory to the findings of Bell (1836), Flower (1885), Flower and Lydekker (1891) and this study. The symphysis is usually quite narrow, ossified and placed in a ventro-caudal position. The symphysis in the Rhinopomatidae and Thyropteridae is moved anteriorly and in the Rhinolophidae more dorsally. Ossification of the symphysis is lacking in some genera, but there is no information on the relationship of age to completeness of fusion. Winge (1941) notes the relative looseness of the symphysis pubis in comparison to other mammals. This he ascribes to the lateral rotation of the hind leg.

A pubic spine, which is a continuous ossification of the ascending pubic ramus (Barbu, 1960; Wassif and Madkour, 1963), is present. It is poorly developed or reduced in the Myzopodidae, Pteropidae, Vespertilionidae, Mystacinidae and Thyropteridae. It is quite short and narrow in the Rhinolophidae, Desmodontidae, Megadermatidae, Furipteridae, Noctilionidae and Molossidae. In all other families there is a moderately well developed spine.

The Hipposideridae are unique in the possession of a preacetabular foramen (Dobson, 1875). This foramen is formed by a supplemental bridge of bone which connects the anterior tip of the pubic spine with the anterolateral end of the ilium. In two other families, there is a ligamentous connection between the iliac crest and the spine. This is seen in *Molossus* (Molossidae) and *Rhinopoma* (Rhinopomatidae).

Ventral and dorsal ischial tuberosities are not present in the Hipposideridae. The Noctilionidae and Mystacinidae are missing the ventral tuberosity only and the Emballonuridae, Nycteridae and Rhinolophidae the dorsal tuberosity only. Both tuberosities are present in all other families.

The acetabulum generally faces dorsolaterad and caudad. The acetabulum of the Rhinopomatidae and Noctilionidae is situated caudad to the usual position. There is a small sesamoid bone embedded anterolaterally in the cartilaginous rim of the acetabulum in the Emballonuridae, Noctilionidae, Hipposideridae, Phyllostomatidae, Desmodontidae and Molossidae. This bone may be present in other fam-

ilies, but due to small size it may be lost in skeletal preparations.

The shape of the obturator foramen is variable. It is round in Molossidae, Hipposideridae, Thyropteridae, Emballonuridae and Rhinopomatidae, elliptical in Nycteridae and Rhinolophidae, triangular in Emballonuridae and Megadermatidae and oval in all other families. The obturator foramen generally exceeds the size of the acetabulum by three to four times. Relative to the size of the innominate, the obturator foramen in the Myzopodidae, Rhinopomatidae, Rhinolophidae, Hipposideridae and Thyropteridae is no more than twice the size of the acetabulum. The caudal rim of the foramen is directed ventrally to the pubis in all families except the Pteropidae, Nycteridae, Megadermatidae, Phyllostomatidae and Vespertilionidae where it is directed posteroventrally to the pubis and in the Rhinopomatidae and Thyropteridae where it is directed anteroventrally to the pubis.

The sacrum is a solidly fused bone. The centra beyond the first one are always compressed dorsoventrally, but fusion of the vertebrae varies among the families. The sacral boundaries are clearly indicated in the Rhinopomatidae, Natalidae, Mystacinidae and Molossidae, whereas they are obliterated in the Megadermatidae. The sacrum appears dorsoventrally compressed in the Nycteridae, Hipposideridae, Rhinolophidae, Furipteridae, Thyropteridae and Vespertilionidae due to the reduction or obliteration of the dorsal boundaries and retention and fusion of the lateral boundaries. A urostyle structure is found in the Pteropidae, Emballonuridae, Noctilionidae, Desmodontidae and Phyllostomatidae. The urostyle arches above the mid-line in the Pteropidae, Noctilionidae and Desmodontidae only. The number of sacral vertebrae varies among families. Bell (1836) noted one vertebra for the Pteropidae. This study finds that instead of one vertebra the Pteropidae have five coalesced vertebrae. The Desmodontidae and Thyropteridae seem to have from three to five vertebrae. The Pteropidae, Rhinopomatidae, Emballonuridae, Nycteridae, Rhinolophidae, Hipposideridae, Natalidae, Vespertilionidae and Molossidae all have five sacral vertebrae. The Mystacinidae have seven. Due to the degree of fusion of the elements, the number of vertebrae in the other families is difficult to ascertain. According to Flower (1885), the Megadermatidae have three, the Vespertilionidae three, the Molossidae four and the Hipposideridae three to four.

The Rhinopomatidae and Emballonuridae share pelvic characters with many of the families. This is not to imply that these two families

are ancestral, but that they exhibit many primitive characters of the order.

Comparison of the Families on Other Osteological Features.—Eight osteological characters were selected for comparison: two cranial characters and six post-cranial characters. The information for this portion is taken from Miller (1907), Grassé (1955) and Bourlière (1955) and has been rechecked on material used in this study where possible. These characters are considered by Miller (1907) to be of taxonomic significance in the Chiroptera.

1. Premaxillaries are complete in the Noctilionidae, Phyllostomidae, Desmodontidae, Natalidae, Furipteridae, Thyropteridae, Myzopodidae, Mystacinidae and may be complete in the Molossidae. They are completely absent in the Megadermatidae and lack either the nasal or palatine portion in the other families.

2. A post-orbital process is present in only five families. It is most highly developed in the Pteropidae and the post-orbital bar is complete in two genera. It is well developed in the Emballonuridae, indistinct in the Noctilionidae and obscured by the supraorbital ridges in the Nycteridae and Megadermatidae. There is no trace of the post-orbital process in the other families.

3. The seventh cervical and first thoracic vertebrae are fused in the Nycteridae, Megadermatidae, Molossidae and some of the Vespertilionidae. In the Rhinolophidae the seventh cervical and the first thoracic are fused with the first rib, presternum and ventral half of the second rib. The condition in the Hipposideridae is similar to that in the Rhinolophidae except the fusion includes the second thoracic, entire presternum and second rib. The fusion in the Thyropteridae is between the first two thoracics and does not include the seventh cervical. No fusion in this region occurs in other families.

4. In the Hipposideridae the lumbar vertebrae are solidly fused, the boundaries obliterated and zygapophyses are absent. The fifth and sixth lumbar vertebrae of the Rhinolophidae have a distinct bifid or double hypophysis. In the Natalidae and Furipteridae the last thoracic and all the lumbar vertebrae are fused, the boundaries obliterated and laterally compressed. The third lumbar has two minute ventral processes in the Mystacinidae. No fusion in this region occurs in other families.

5. The fibula is entirely lacking in the Nycteridae. The proximal

half is lacking in the Thyropteridae. In the Desmodontidae, Mystacinidae and Molossidae the fibula is large and complete. All other families have a thin fibula and the proximal end may not be ossified.

6. In the Emballonuridae, Nycteridae, Rhinolophidae, Hipposideridae, Natalidae, Furipteridae and Thyropteridae, the second manal digit has a metacarpal but lacks phalanges. The phalanges are represented by a single, short cartilaginous rod in the Myzopodidae. The Rhinopomatidae and Noctilionidae have the metacarpal and two phalanges and the Pteropidae have the metacarpal and three phalanges. In all other families the digit has a metacarpal and one phalanx.

7. The third manal digit of the Phyllostomatidae, Desmodontidae, Thyropteridae, Myzopodidae, Vespertilionidae, Mystacinidae and Molossidae has a metacarpal and three phalanges. In all other families the digit has a metacarpal and two phalanges.

8. In the Hipposideridae, Thyropteridae and Myzopodidae there are two phalanges in each digit of the foot. In the Rhinolophidae only the hallux has two phalanges and all other digits have three; the third and fourth toes are fused to the base of the phalanges.

RELATIONSHIPS AMONG THE SUBFAMILIES OF THE PHYLLOSTOMATIDAE

Dobson (1875) recognized two subfamilies of the Phyllostomatidae: Lobostominae and Phyllostominae. The former included three genera (*Chilonycteris*, *Pteronotus* and *Mormoops*) and is equal to the Chilonycterinae of Miller (1907). The Phyllostominae of Dobson (1875) included all the other known genera of the family. This subfamily was, however, divided into four groups: the Vampyri (including such genera as *Macrotus*, *Lonchorbina*, *Phyllostomus*, *Carollia* and *Rhinophylla*), the Glossophagae (included genera such as *Glossophaga*, *Phyllonycteris* and *Lonchoglossa*), the Stenodermata (*Artibeus*, *Vampyroptus*, *Stenoderma* and *Sturnira*) and the Desmodes (only *Desmodus* and *Diphylla*). *Rhinophylla* was considered the connecting link between the Vampyri and Glossophagae. *Brachyphylla* (Stenodermata) was considered a connection with the Desmodes.

Although Dobson (1875) placed *Noctilio* as a possible connection between the Lobostominae and Emballonuridae, he felt that a satisfactory connection between the Lobostominae and Phyllostominae was lacking. H. Allen (1889) suggested that *Mormoops*, because of peculiarities of the wing membrane and terminal phalanges of the

digits, may be more closely allied to the Emballonuridae than to the Phyllostomatidae.

Miller (1907) did not comment on the relationships among the subfamilies, but it is apparent from the placement in the text and descriptions that the Chilonycterinae were considered the most primitive. The Phyllostomatinae were considered the basal group from which the remaining subfamilies radiated. The desmodontids were not included in the Phyllostomatidae and the Noctilionidae were placed close to the Emballonuridae. Placement of the Nycteridae, Megadermatidae, Rhinolophidae and Hipposideridae between the Noctilionidae and the Phyllostomatidae implies closer affinities between the Rhinolophidae and Phyllostomatidae than between the Phyllostomatidae and Noctilionidae. Carvalho (1961) suggested that the Phyllostomatidae may have their origin in the Rhinolophidae.

Winge (1941) presented a different view of the phyllostomatid phylogeny. Three basic lines were recognized: Mormopini (*Chilonycteris*, *Mormoops* and *Noctilio*), Desmodes and the Phyllostomatini. The Phyllostomatini were further divided into two groups of genera: Phyllostomata (including the Glossophagae) and Stenodermata (including *Sturnira*). The Phyllostomatidae were considered more closely related to and derived from the Rhinolophidae. This opinion was shared by Carvalho (1961) and Bourlière (1955).

Bourlière (1955) considered the Chilonycterinae (Lobostominae of Dobson (1875) and Mormopini of Winge (1941) the most primitive of the Phyllostomatidae, but did not include *Noctilio* in this subfamily as did Winge (1941). *Noctilio* is retained in the family Noctilionidae, but is allied with the Phyllostomatidae under the superfamily Phyllostomatoidea. The vampire bats (desmodontids) were included in the Phyllostomatidae as the subfamily Desmodinae rather than retaining the familial status accorded them by Miller (1907) and Simpson (1945). Bourlière (1955), following the view of Winge (1941), considered *Macrotus* the most primitive of the Phyllostomatinae, *Vampyrum* somewhat more evolved and *Phyllostomus* the most highly evolved.

The fossil phyllostomatid described by Savage (1951) from the Miocene of Colombia showed affinities with the Phyllostomatinae, particularly to *Chrotopterus* and *Vampyrum*. In comparing the fossil material to recent genera, Savage (1951) recognized at least two groups within the Phyllostomatinae: the *Notonycteris-Chrotopterus-*

Vampyrum group and another group typified by *Phyllostomus*.

The findings of this study also suggest that the Chilonycterinae are the most primitive of the subfamilies of the Phyllostomatidae. Within this subfamily, however, the genus *Mormoops* deviates from the general pattern of the humerus and innominate so greatly that it is hardly recognizable as a phyllostomatid humerus and innominate. Within the family Phyllostomatidae, however, the closest alliance of the chilonycterines appears to be with the *Macrotus*-type of phyllostomatine.

Within the Phyllostomatinae two basic types appeared. These two types are referred to as the *Macrotus*-type and the *Phyllostomus*-type. From the information presented by Savage (1951), the *Macrotus*-type recognized here is equivalent to his *Notonycteris-Chrotopterus-Vampyrum* group. The *Macrotus*-type is considered to represent the more primitive form of the "true" phyllostomatid (those having secondary articulation between the scapula and the humerus).

From the two lines or types of phyllostomatines are derived the other members of the family. Figure 9 is a diagrammatic presentation of the possible phylogeny of the family.

The phyllonycterines show the closest affinities to the *Macrotus*-type of phyllostomatine. Miller (1907) felt that their closest alli-

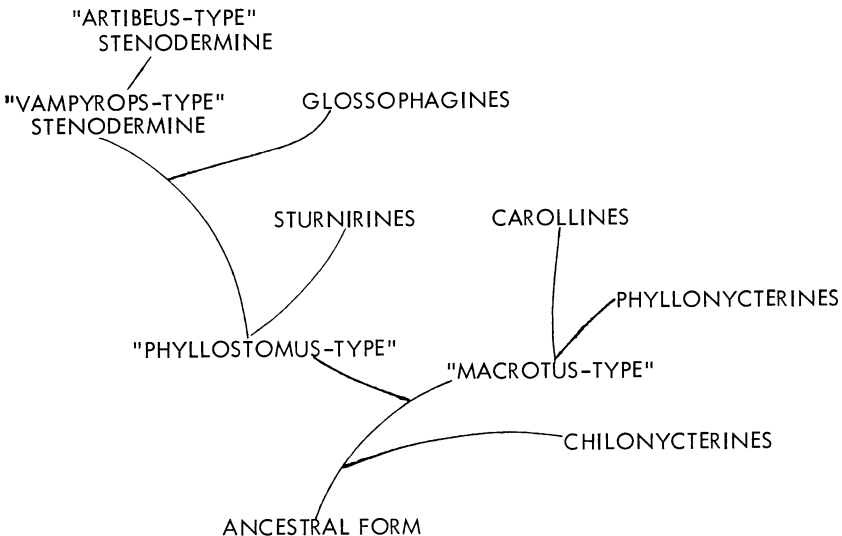


Fig. 9. Diagrammatic presentation of the possible phylogeny of the Phyllostomatidae.

ance was to the stenodermines, but the findings presented herein suggest otherwise.

Figure 9 shows the carollines as having their origin from this same line. The placement of the carollines next to the sturnirines is intended to imply that there is some question as to the exact position and relationship between these two groups. As was shown previously in this study, there are similarities as well as differences between these two groups and, although the sturnirines appear to have their closest affinities to the glossophagines, the genera which make up these two groups may represent a single group with *Carollia* as the most primitive member.

From the *Phyllostomus*-type are derived two basic groups which are referred to here as the glossophagine-sturnirine complex and the stenodermine group. Of the stenodermine group, *Vampyrops* appears to represent the more primitive type and *Artibeus* the more advanced. The stenodermine *Vampyrops* and the glossophagine *Glossophaga* have sufficient similarities to indicate that these two genera are not far removed from the characteristics of a common ancestral form.

Myologically, the Phyllostomatidae is a remarkably homogeneous family (Walton, 1967). Osteologically, differences were seen in the elaboration of the keel on the body of the sternum, the distal tip of the coracoid process of the scapula, the elaboration of various parts of the distal and proximal ends of the humerus, in primary and secondary articulations of the innominate with the sacrum and consequent ankylosis of these joints, the extent of development of the urostyle-like sacrum, and size and shape of the innominate. Although the study of phyllostomatid dentition by Miller (1907) was comprehensive, more genera have been recognized since his study and it would be most interesting to reevaluate dental characters, especially the cusp patterns of the molars, following the techniques used by Savage (1951).

The basic areas of disagreement with the classification and relationships proposed by Miller (1907) are summarized below as follows.

1. The lack of secondary articulation between the humerus and scapula in the Chilonycterinae constitutes a major deviation from the general pattern of the rest of the family and the configuration of the humerus of *Mormoops* is radically different from anything else seen in the family. Whether such deviations, as well as differences not in

the scope of this study, warrant subfamilial or familial status for this group certainly deserves consideration. It is the opinion of the writers that if the Chilonycterinae are retained in the Phyllostomatidae as a subfamily, two groups should be recognized within the subfamily: the *Chilonycteris-Pteronotus* complex and the *Mormoops* group.

2. The subfamily Phyllostomatinae is not a homogeneous group, but contains at least two major groups: the *Macrotus*-type and the *Phyllostomus*-type. The brief analysis of dental characters by Savage (1951) supports this idea. Indeed, if the fossil phyllostomatid described by Savage (1951) possessed double rooted premolars as the evidence suggested, then the possibility of a third extinct group cannot be overlooked. On the basis of karyotype analysis (Baker, 1967), *Phyllostomus* and *Macrotus* are placed in the same group with no significant difference between them.

3. The association between the Sturnirinae and Carollinae is not clear and a detailed study of the involved genera could perhaps reveal that only one group should be recognized.

4. The subfamilies Glossophaginae and Stenoderminae are much more closely related than extreme genera of each family would indicate. By extreme genera is meant *Choeronycteris* and *Artibeus* as opposed to more centric genera such as *Glossophaga* and *Vampyrolops*.

5. The subfamily Phyllonycterinae appears to have its affinities with the *Macrotus*-type of Phyllostomatinae, not with the Stenoderminae as Miller (1907) suggested.

RELATIONSHIPS OF THE PHYLLOSTOMATIDAE TO THE OTHER FAMILIES

The desmodontids have often been considered phyllostomatids, most recently by Bourlière (1955). Myologically (Walton, 1967) and osteologically they are very close to the phyllostomatids. The radical departure from the basic dental pattern of the Phyllostomatidae led Miller (1907) to consider the desmodontids a separate family. Differences such as the form of the humerus, ilium and sacrum noted previously further distinguish them from the phyllostomatids. If the Chilonycterinae are to be considered a subfamily of the Phyllostomatidae, such divergent humeral patterns as *Mormoops* vs. *Artibeus*, varied dental patterns and configurations such as *Choeronycteris* vs. *Phyllostomus* and varied innominate construction such as *Mormoops* vs. *Sturnira* are considered sufficiently uniform to be included in the

same family, there seems no logical reason to exclude the Desmodontidae. Doubtless, the divergence in dental, humeral and pelvic configurations reflect considerable temporal isolation for the group. Dobson (1875), Winge (1941) and Bourlière (1955) seem to have, however, sufficient justification for considering the desmodontids as a subfamily of the Phyllostomatidae.

The Noctilionidae appear remarkably similar to the Chilonycterinae. Whether they form the connecting link, as Dobson (1875) suggested, between the Phyllostomatidae and the Emballonuridae, is doubtful. Differences do exist between these three families and these have been noted previously in this study. These authors are, however, in agreement with Dobson (1875, 1878), Winge (1941) and Bourlière (1955) that the Noctilionidae are closely related to the Phyllostomatidae.

The Emballonuridae and Noctilionidae are considered related families by Miller (1907) and Simpson (1945). The problem in evaluating any relationship between the Noctilionidae, Emballonuridae and the Phyllostomatidae (including the desmodontids) is complicated by occurrence of emballonurids in both the Old and New Worlds. Only New World representatives were available for this study. The impression gained from observations on this material, however, is that the possibility does exist that the three families are closely related. Rather than the view held by Dobson (1875) of the Emballonuridae as ancestral to the Phyllostomatidae via the Noctilionidae, the similarities and differences among these families seem best explained by postulating a common ancestral group.

The relationship between the Rhinolophidae and the Phyllostomatidae suggested by Miller (1907), Simpson (1945), Bourlière (1955) and Carvalho (1961) seems, at best, an extremely remote one. The loss of portions of premaxillary, fusion of the vertebrae with ribs and sternum and loss of phalanges differs so drastically from the pattern seen in the Phyllostomatidae, it is difficult to suppose any close relationship of these two families. The presence of foliaceous appendages on the rostrum of the Rhinolophoidea (Nycteridae, Megadermatidae, Rhinolophidae and Hipposideridae) and Phyllostomatidae is not a reliable criterion of relationship for there are no studies which indicate that these structures are homologous.

In summary, the evidence seems to indicate that there is little reason for separating the desmodontids and phyllostomatids at the fam-

ily level and that there is justification for relating the Noctilionidae and Phyllostomatidae. The position of the Emballonuridae in relation to the Noctilionidae and Phyllostomatidae is not clear, but the possibility does exist that the three families are related through a common ancestral group. Furthermore, the relationship of the Phyllostomatidae to the Rhinolophoidea seems remote and much less probable than a relationship between the emballonurids and the phyllostomatids.

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