VARIATIONS IN THE BASIHYAL IN SELECTED GENERA

OF THE CHIROPTERAN FAMILY PHYLLOSTOMIDAE


by

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## APPROVAL BY THESIS DIRECTOR

This thesis has been approved on the date shown below:

_____
Dr. William J. McCauley
Professor of Zoology

_____
Date  *August 17, 1967*

## ACKNOWLEDGMENTS

I wish to express my appreciation to Dr. William J. McCauley for suggesting this study and for his guidance. I would like to thank Dr. Russell Davis for his help in obtaining supplies and editing, Dr. Edward Joy for his help in editing this thesis, and Dr. E. Lendell Cockrum for the use of the material in the University of Arizona mammal collection.

## TABLE OF CONTENTS

# LIST OF TABLES

LIST OF ILLUSTRATIONS

# ABSTRACT

In an attempt to determine whether or not variations in the shape of the basihyal could be related to feeding habits and to determine possible taxonomic and evolutionary significance, the basihyal bones in certain genera of the chiropteran Family Phyllostomidae were examined.

The phyllostomids studied were placed into nine groups based on the shape of the basihyal:

Group A. This group consists of only one species, Desmodus rotundus, which is sanguivorous.

Group B. This group includes the insectivorous species Macrotus waterhousi, Chilonycteris psilotis, and Pteronotus davyi.

Group C. This group contains only one species, Carollia prespicillati, which is frugivorous.

Group D. This group includes the nectivorous bats Leptonycteris sanborni and Glossophaga soricina.

Group E. This group contains one species, Choeronycteris mexicana, which is nectivorous.

Group F. This group contains the frugivorous species Phyllostomus discolor, Artibeus nanus, Artibeus lituratus, and Artibeus jamaicensis.

Group G. This group contains only one species, Anoura geoffroyi, which is nectivorous.

Group H. Group H contains the frugivorous species Sturnira lilium.

Group I.  This group contains the frugivorous species
*Centurio senex*.

When the feeding habits of these species are compared, it is apparent that there is only one feeding habit within each group.  However, some of the groups have the same feeding habits.  There is no single basihyal shape which can be specifically correlated with a specific feeding habit.

# INTRODUCTION

All of the previous work concerning the mammalian
hyoid apparatus has been primarily concerned with the
musculature of this region, and secondarily with the entire
hyoid apparatus. Sprague (1943) has done a detailed
study of the musculature and hyoid apparatus of placental
mammals with special consideration of the Order Chiroptera.
His findings are discussed later on in the introduction.
Dobson (1881) observed a relationship between the structure
of the hyoid and food habits of Epomops franqueti. He
was concerned with the attachment of the entire hyoid
apparatus and made no special reference to the basihyal.
Pocock (1916) found a functional relationship between the
structure of the hyoid and the voice in many species of
Felidae. He found that in roaring cats the anterior
cornua of the hyoid were ligamentous and allowed the
larynx and tongue considerable movement. In the cats
which purr but never roar, the anterior cornua were com-
pletely bony and restricted the movement of the hyoid
apparatus.

The study of the hyoid apparatus of passerine
birds by George (1958, 1961) proved to be helpful in the
clarification of a difficult area of taxonomy. It was in

1

the hope that a similar study might be helpful in the interpretation of the phyllostomid bats, that these studies were undertaken. The object of this thesis was the investigation of the basihyal bones in some of the genera of the chiropteran Family Phyllostomidae in an attempt to determine whether or not variations in the shape of the basihyal could be related to feeding habits. The possible taxonomic and evolutionary significance of these various shapes has also been considered.

The hyoid region of vertebrates consists of a set of skeletal elements derived from the second and third visceral arches. The morphological position is in the ventral branchial region. The evolution of this region is functionally closely associated with the development and changes of the mechanisms of breathing, swallowing, and phonation, and with the development of the tongue.

The hyoid apparatus of mammals results from the fusion of the hyoid arch and the third visceral arch. A typical bat hyoid apparatus (Phyllostomus discolor) is pictured in Fig. 1. There is a median ventral piece called the body or basihyal from which extend two anterior cornua and two posterior cornua. The posterior cornua or thyrohyals project dorsally from the lateral border of the body. The thyrohyals are sometimes fused to the body and are usually articulated by means of the thyrohyal
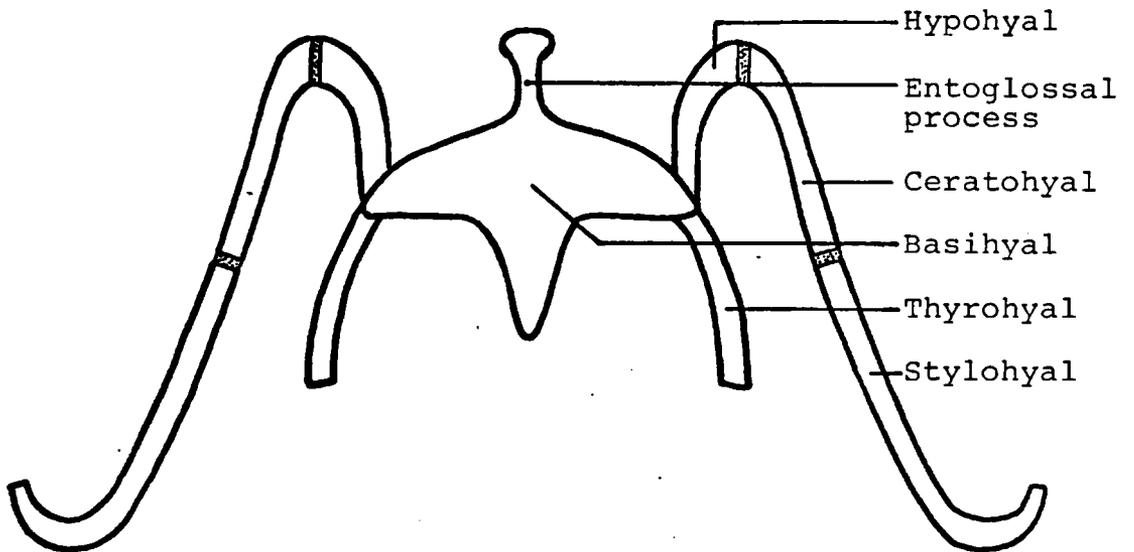
Figure 1.  The hyoid apparatus of a typical phyllostomid
bat (Phyllostomus discolor). 15X

ligament with the anterior horns of the thyroid cartilage of the larynx (Sprague, 1943).

The anterior cornua of bats extend from the basihyal to the auditory bulla. The anterior cornua are segmented and consist of four portions (Sprague, 1943): hypohyals, ceratohyals, stylohyals, and tympanohyals. Willie (1954) considers three segments and calls these ceratohyals, epihyals, and stylohyals. He does not consider the tympanohyal since it is so small.

Variations in the shapes of the basihyal may be due to functional modifications in the throat musculature. Sprague (1943) has done a great deal of work on the hyoid region of placental mammals and the following description of the hyoid musculature comes from his work. Sprague states that it is unlikely that any change in the hyoid musculature would affect the tympanohyal, since normally this element is small and has no muscles attached to it. Developmental changes in the auditory region would seem most likely responsible. The other segments of the anterior cornua usually have a development closely associated with the adjacent musculature.

The stylohyoideus, styloglossus, and stylopharyngeus muscles are characteristically attached to the stylohyal. Willie (1954) notes that the stylohyoideus is absent in most of the genera of the Microchiroptera.

The hypohyal is usually small and unimportant as a point for muscular attachment. The ceratohyoideus muscle is characteristically inserted into the ceratohyal, and the constrictor pharyngis medius muscle commonly takes part of its origin from it.

The thyrohyals, as a rule connected to the basihyal, have a number of muscle attachments. The ceratohyoideus and medial constrictor muscles originate from its entire anterior border. The thyrohyoideus muscle inserts into the posterior border of the thyrohyal.

Although the sternohyoideus and omohyoideus muscles commonly insert into the basihyal, they may insert partially, or wholly, in the case of the omohyoideus, into the thyrohyal. In addition to the sternohyoideus and omohyoideus muscles, the geniohyoideus, genioglossus, hyoglossus, mylohyoideus, digastricus, and hyoepiglotticus muscles may find attachment on the basihyal.

The reduction, of one or more elements in the anterior cornua, resulting in a ligament or even complete loss of the element, has been correlated with the shifting of the formerly attached muscles to other areas or to the reduction or loss of the muscles themselves.

Willie (1954) made a general survey of bats representing different food habits. He found that only the nectar-eating bats of the subfamily Glossophaginae had a

highly modified musculature of the throat. Some of these modifications are easily correlated with the specialized food habits of these bats. The most striking adaptations of the musculature are the new origin and insertion of the sternohyoideus, and a highly modified geniohyoideus. The sternohyoideus muscle does not insert on the basihyal as usual, but instead inserts on the tongue. This has solved the problem of retracting the long tongue of the nectar-eating bats.

The Family Phyllostomidae, American leaf-nosed bats, have the following diagnostic characteristics: skull without postorbital processes; premaxillae complete, fused to each other and to the maxillae, the palatal branches isolating two lateral palatal foramina; teeth variable according to genus; tragus present but variable; nose leaf usually present; humerus with well-developed trochiter, but smaller than the trochin, capitellum distinctly offset from the axis of the shaft; second digit of the manus with well-developed metacarpal and small phalanx; third finger with three complete bony phalanges; seventh cervical vertebra free from the anterior thoracic vertebra; fibula present, cartilaginous proximally; pelvis normal; and the sacrum forming a flattened narrow urostyle posteriorly (Hall and Kelson, 1959).

The present classification, based on Miller (1907), consists of seven subfamilies: Chilonycteriinae, Phyllostominae, Glossophaginae, Carollinae (Hemiderminae), Sturnirinae, Stenoderminae, and Phyllonycterinae.

The Family Phyllostomidae is almost entirely neotropical. The number of species of this group decreases on the border of the sub-tropical areas. Northwards the distribution barely extends within the borders of the United States, some species being reported from the most southern parts of California, Arizona, Texas, and Florida (Key Islands) respectively (Olof Ryberg, 1947).

The phylogeny of bats is not well known. Fossil chiropterans are found scattered throughout the Tertiary, but it is only rarely that much except teeth and jaws are found of these small and delicate forms. They are common as fossils only in Pleistocene cave deposits. Flying adaptations must have developed in the Paleocene, or at least by earliest Eocene, because Middle Eocene deposits in both Europe and North America have yielded skeletons of Microchiropterans with well-developed wings (Romer, 1966).

It is possible that bats, essentially insectivorous in their beginnings, have been derived from an arboreal insectivorous group, for in such features as are not connected with flight the bats might well be included in the Order Insectivora. The primitive insectivore

basihyal is considered by Sprague (1943) to be a bar-shaped structure with no entoglossal process. Flower (1885) also mentioned that the basihyal of insectivores was a transversely extended (bar-shaped) structure. Neurotrichus gibbsi is the insectivorous shrew-mole which was used to illustrate this primitive condition (Fig. 2).

Within the Family Phyllostomidae there are various nutritional and biological groups. The majority are insectivorous, but there are also some nectivorous, frugivorous, sanguivorous, and carnivorous types. The lack of these types of food in winter prevents the constant appearance of these bats in temperate zones. This would perhaps be possible if hibernation occurred, but there is no record of hibernation within this group.

Included in this study are the vampire bats (Desmodontidae) since karyotypic data have indicated that these bats show basic relationships to the Family Phyllostomidae (Baker, 1967). The vampires are neotropical bats and have a diet which consists exclusively of blood. These and the subfamilies of the Family Phyllostomidae will be considered in more detail below.
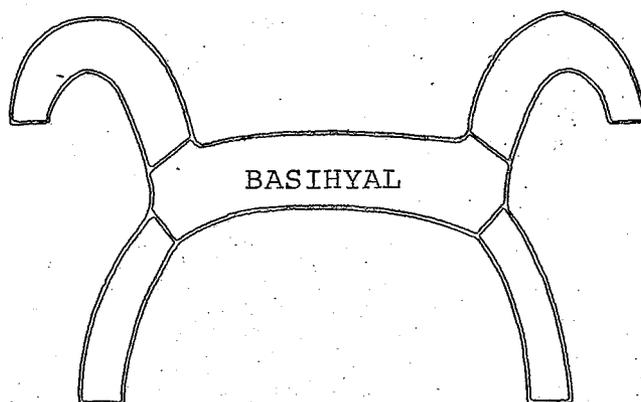
Figure 2.   The basihyal of the shrew-mole _Neurotrichus gibbsi_.   Used here to represent a "theoretical generalized" insectivore hyoid.   15X

# METHODS AND MATERIALS

The materials used in this study were obtained primarily from the mammal collections of the University of Arizona, and were of two types: (1) skeletal material which had been cleaned by the use of dermestid beetle larvae and later bleached, and (2) alcoholic specimens. In a few cases, freshly killed specimens were also dissected. Dissection of both freshly killed and alcohol-preserved specimens verified that the delicate hyoid elements of the skeletal material had not been harmed by the cleaning process.

Due to the small size of the hyoid bone, all dissection was done under a binocular dissecting microscope. In the case of the freshly killed specimens, dermestid beetle larvae were allowed to clear away some of the superficial tissue and then the remaining portion was dissected.

X-ray photographs of the hyoid bones of alcohol preserved, formaldehyde preserved, and freshly killed specimens were also tried, but this proved fruitless. Since only some of the structures were visible, this technique was not considered valid.

In some cases specimens were cleared in potassium hydroxide, stained with alizarin red, and further cleared in increasing concentrations of glycerin. This method yielded some suitable specimens and made it easier to dissect out the small basihyal.

The drawings of the basihyals were done with a camera lucida and appear at a magnification of 15X. These drawings were made from specimens which were considered to be typical of the respective genera. The proportions between the processes were kept constant so that the specimen which was drawn would not vary from the other specimens examined. Within a species there were minor differences in roundness and degree of tapering at the extreme tips of proceses, but these minor variations were not considered in this study. The general shape drawn in the figures is constant within a genus.

There was no sexual dimorphism found within a species. The sample size was variable, but only in three cases did it drop below fifteen of each species examined. Due to the number of specimens available there were only three specimens of Centurio, Carollia, and Anoura examined.

RESULTS

Subfamily Chilonycteriinae. The members of the
subfamily Chilonycteriinae (mustache bats) have the following
diagnostic characteristics: teeth normal; humerus without
secondary articulation with the scapula, the tubercles
are short, rising scarcely above the level of the head,
epitrochlea small, large spinous process; muzzle without
nose leaf; and a lower lip with plate-like outgrowths.
Bats in this subfamily are found in tropical America,
north to Cuba, and the southern border of the United
States (Miller, 1907).

The two species which were studied in this subfamily
were Pteronotus davyi and Chilonycteris psilotis. Both
of these species are insectivores. The general shape of
the basihyal is very similar (Fig. 4). There are no
hypohyals present in either species. The attachment of
the ceratohyals to the basihyal is from an anterior
direction to the ventral margin of the lateral processes
of the basihyal. Pteronotus has a basihyal which was
larger in mass and was concave posteriorly. Pteronotus
also had an entoglossal process that had a sharper point
than Chilonycteris.

Subfamily Phyllostminae.  The members of the sub-
family Phyllostominae (big-eared or leaf-nosed bats)
have the following diagnostic characteristics:  teeth
essentially normal, though in some genera there is a
reduced condition of the mesostyle and commissures of
$m^1$ and $m^2$, and of the paraconid and metaconid of $m_1$ and
$m_2$; humerus with a definite secondary articulation with
the scapula, epitrochlea large, with slightly developed
spinous process; muzzle with nose leaf; and the lower
lip is without plate-like outgrowths., Members of this
subfamily are found in the warmer parts of America, north
to the Bahamas and southern California (Miller, 1907).

The two species which were studied were Phyllostomus
discolor and Macrotus waterhousi.  Both of these species
are insectivorous and frugivorous.  Macrotus feeding
mostly on insects and Phyllostomus feeding mostly on
fruit.  They both had a different shape to the basihyal
(Figs. 4 and 8).  Macrotus had a shape similar to Artibeus.
There was no distinct subspecific variation in the shape
of the basihyal between Macrotus waterhousi californicus
and Macrotus waterhousi mexicanus.  The hypohyals attach
to the outer ventral margin of the lateral processes of
the basihyal in both Macrotus and Phyllostomus.

Subfamily Glossophaginae.  The members of the sub-
family Glossophaginae (long-nosed bats) have the following
diagnostic characteristics:  teeth slightly abnormal, upper

molars with the styles reduced in size and closely approx-
imated to the paracone and metacone, this in connection with
the obsolescence of the commissures nearly obliterating the
W-pattern; lower molars have the five typical cusps present,
but reduced in height, particularly the paraconid, the com-
missures very rudimentary; all the cheek teeth are elongated;
the rostrum is elongated; the tongue is long and highly
extensible, its surface armed with conspicuous bristle-
like papillae; and the nose-leaf is present and well de-
veloped, though never very large. These bats are found in
the warmer parts of America, north on the mainland to south-
ern Arizona and in the West Indies to Cuba (Miller, 1907).

The species studied were: Glossophaga soricina,
Leptonycteris sanborni, Choeronycteris mexicana, and Anoura
geoffroyi. The shape of the basihyal was similar in Glosso-
phaga and Leptonycteris, but Anoura and Choeronycteris each
had shapes that differed from the other members of this sub-
family (Figs. 6, 7, and 9). Glossophaga and Leptonycteris
each had a basihyal which appeared squatty, there were no
tapering processes, but instead the processes appeared to
have square, blunt ends. Choeronycteris and Anoura each
had tapering processes. Choeronycteris had a shorter ento-
glossal process by comparison with the others. All the
species had the hypohyals attaching to the basihyal from an
anterior direction. This point of attachment was on the
ventral inner margin of the basihyal.

Subfamily Carollinae (Hemiderminae). The members
of the subfamily Carollinae (common short-tailed bats)
have the following diagnostic characteristics: teeth
abnormal, first and second upper molars with the protocone
greatly reduced or obsolete, occupying the entire very
narrow inner edge of the tooth; paracone and metacone are
large and trenchent, parastyle and metastyle are present,
though small; neostyle absent, an angular concave commissure
that is nearly in line with the main axis of the toothrow
connects the outer cones and styles, but no trace of a
W-pattern is present; they have lower molars with the
protoconid well developed and forming with its commissures
a median longitudinal cutting ridge, close to the corner
of which the rather small metaconid may be situated; the
paraconid and entoconid are small or absent; and the
rostrum, tongue, and nose-leaf are normal. The members
of this subfamily are found in the warmer parts of America,
north to southern Mexico and in the West Indies to Jamaica
(Miller, 1907).

The only species studied in this subfamily was
Carollia prespicillati. The diet of this bat consists of
fruit. The shape of the basihyal is unique in having
reduced dorsal and ventral processes. These processes
are round and small (Fig. 5). The entire basihyal is
concave in a posterior direction. The hypohyals attach

to the outer ventral margin of the basihyal. There was

no other basihyal which resembled Carollia and consequently

Carollia was placed in a group by itself.

Subfamily Sturnirinae. The members of the sub-

family Sturnirinae (yellow-shouldered bats) have the

following diagnostic characteristics: teeth highly ab-

normal, upper molars with a distinct protocone, paracone,

and metacone situated at extreme edges of the crown, the

space between occupied by a conspicuous longitudinal

groove, continuous from one tooth to the next, the lower

molars are similarly grooved, the five typical cusps

present at the margins of the crown, those on the outer

side are lower and indistinct, but the metaconid and

entoconid are well developed; and the tongue, rostrum,

and noseleaf are normal. Members of this subfamily are

found in tropical America, north to Jamaica and southern

Mexico (Miller, 1907).

The only member of this subfamily studied was

Sturnira lilium. This species had a basihyal which was

oblong in shape and had a reduced entoglossal process as

compared with other subfamilies studied (Fig. 10). This

shape was unique and very slightly resembled Centurio

senex (in that Centurio was also oblong) but Centurio

lacks an entoglossal process. Sturnira lilium had no

hypohyals and the ceratohyals attached to the ventral

outer margin of the basihyal from an anterior direction. Both Sturnira and Centurio are frugivorous, but neither of these had a basihyal which resembled any of the other frugivorous species studied.

Subfamily Stenoderminae. The members of the subfamily Stenoderminae (short-faced bats) have the following diagnostic characteristics: teeth highly abnormal, upper molars with crowns elongated across the main axis of the toothrow, paracone and usually the metacone are well developed at the extreme outer margin of the tooth, the two cusps together with their commissures forming a cutting edge, which is often ringed by two cingula, an outer and an inner, the lower molars have the main portion of the crown nearly flat, on the outer edge are two low broad cusps, the protoconid and the hypoconid, between which a mesostyle is sometimes present; the tongue is normal; the rostrum is usually broadened and shortened; and the noseleaf is usually present, though sometimes rudimentary or absent. Members of this subfamily are found in the warmer parts of America, north to Cuba, southern Florida, and central Mexico (Miller, 1907).

The species studied in this subfamily were: Artibeus nanus, Artibeus jamaicensis, Artibeus lituratus, and Centurio senex. As mentioned before, Centurio senex had a basihyal which was oblong in shape and lacked an entoglossal process. The thyrohyals seemed to be fused

to the basihyal but there were not enough specimens available to verify this. The basihyal of Centurio resembled that of Sturnira only in that it had an oblong shape. Centurio lacked hypohyals. The ceratohyals attached to the outer ventral margin of the basihyal from an anterior direction (Fig. 11).

Only slight differences between the species of Artibeus were found. Artibeus lituratus had a longer dorsal process on the basihyal than the other species examined. Exclusive of this one difference, the species of Artibeus were fairly uniform in shape. All of the species had a basihyal which was concave in a posterior direction. Hypohyals were present and attached to the outer ventral margin of the basihyal from an anterior direction (Fig. 8). In the general shape of the basihyal, Artibeus nanus, Artibeus jamaicensis, and Artibeus lituratus resemble Phyllostomus discolor. Each specimen of Artibeus sp. and Phyllostomus discolor had a small ball-like tip on the entoglossal process. Both Phyllostomus discolor and Artibeus sp. are frugivorous.

Desmodontidae. The Desmodontidae (vampire bats) have the following distinguishing characteristics: they are similar to typical members of the Family Phyllostomidae in respect to the wing, pectoral girdle, and pelvis, except that the tuberosities of the humerus are more nearly

equal in size, and both tuberosities more distinctly exceed the head; the fibula is large, extending to the head of the tibia; the tibia, fibula, and femur are deeply grooved for accommodation of muscles; the teeth are highly specialized for cutting, all traces of a crushing surface are absent, the cheek teeth are so reduced that the length of the entire upper row is less than that of the canine along the alveolus; and the nostrils are surrounded by dermal outgrowths that form a very rudimentary noseleaf. These bats are found in the warmer parts of America, north to southern Mexico (Miller, 1907).

The basihyal of _Desmodus rotundus_ is unique in having an entoglossal process which is long and widens at the tip instead of tapering as in the typical phyllostomids examined (Fig. 3). The basihyal is concave posteriorly. There are no hypohyals present and the ceratohyals attach to the outer ventral margin of the lateral processes of the basihyal. _Desmodus rotundus_ is the only sanguivorous species which was studied. The shape of the basihyal is unlike any of the other species examined and therefore _Desmodus rotundus_ was placed in its own group (Table 4).
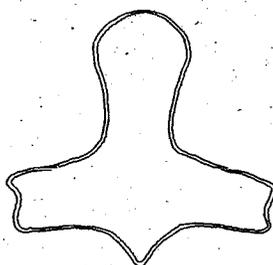
Figure 3.   Group A.   Basihyal shape of <u>Desmodus rotundus</u>.
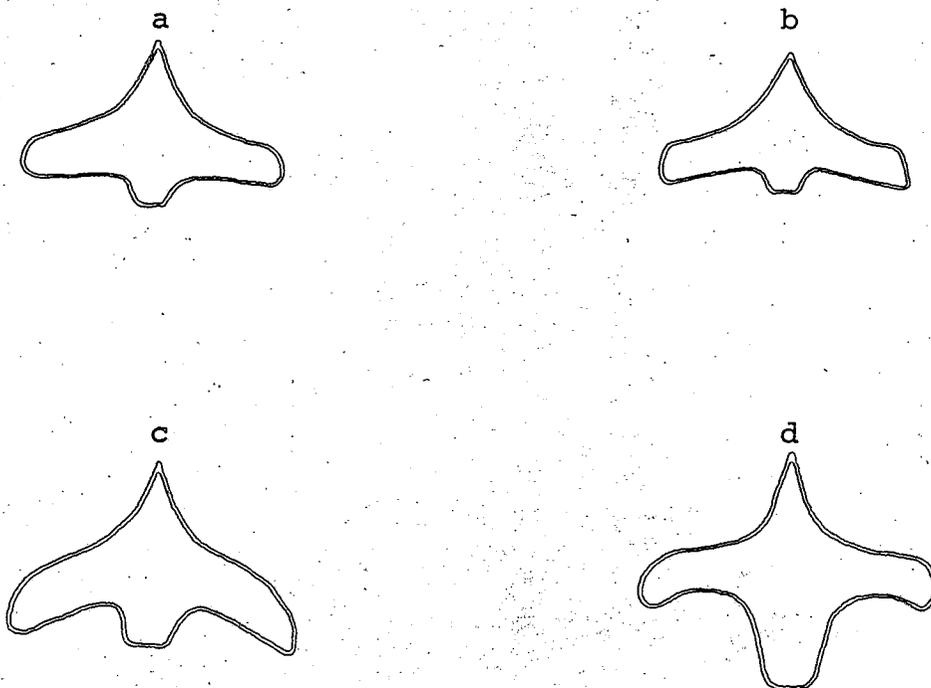


Figure 4.   Group B.   Basihyal shapes of (a) <u>Macrotus waterhousi californicus</u>, (b) <u>Macrotus waterhousi mexicanus</u>, (c) <u>Chilonycteris psilotis</u>, and (d) <u>Pteronotus davyi</u>.

Figure 5.  Group C.  Basihyal shape of Carollia prespicillati.
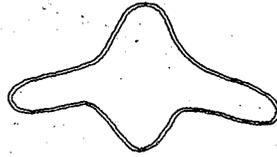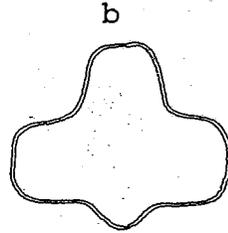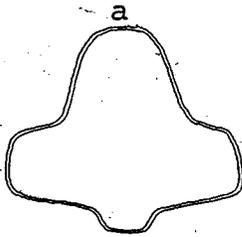


Figure 6.  Group D.  Basihyal shapes of Leptonycteris sanborni and Glossophage soricina (a and b, respectively).
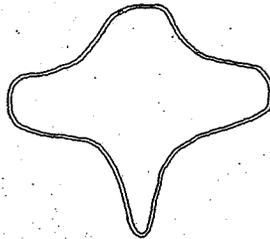


Figure 7.  Group E.  Basihyal shape of Choeronycteris mexicana.
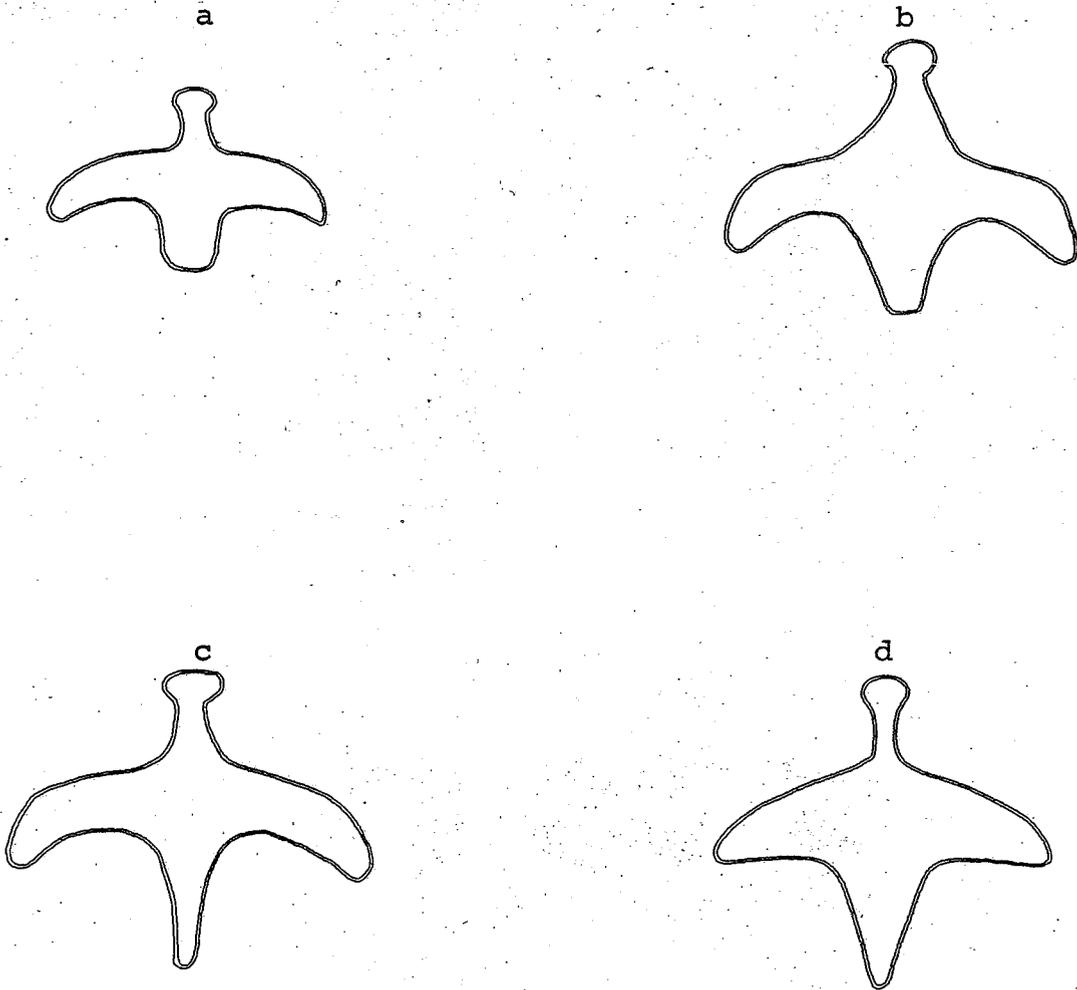
Figure 8. Group F. Shapes of the basihyal of (a) <u>Artibeus</u> <u>nanus</u>, (b) <u>Artibeus jamaicensis</u>, (c) <u>Artibeus</u> <u>lituratus</u>, and (d) <u>Phyllostomus discolor</u>.

Figure 9.   Group G.   Basihyal of <u>Anoura</u> <u>geoffroyi</u>.
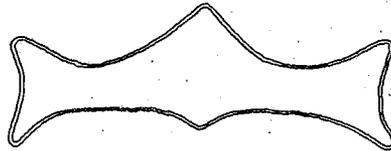


Figure 10.   Group H.   Basihyal of <u>Sturnira</u> <u>lilium</u>.
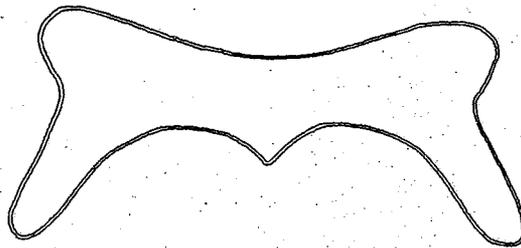


Figure 11.   Group I.   Basihyal of <u>Centurio</u> <u>senex</u>.

Table 1. Species, subfamily and food habits of the bats examined. Food habits based on Cockrum (1962) and Ross (1967). Classification based on Miller (1907).

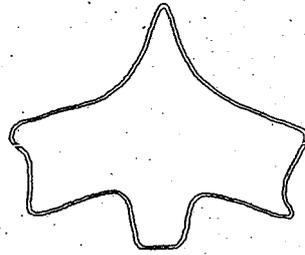| Species Examined | Subfamily | Food Habits |
|---|---|---|
| Anoura geoffroyi | Glossophaginae | Nectivorous |
| Artibeus jamaicensis | Stenoderminae | Frugivorous |
| Artibeus lituratus | Stenoderminae | Frugivorous |
| Artibeus nanus | Stenoderminae | Frugivorous |
| Carollia prespicillati | Carollinae | Frugivorous |
| Centurio senex | Stenoderminae | Frugivorous |
| Chilonycteris psilotis | Chilonycteriinae | Insectivorous |
| Choeronycteris mexicana | Glossophaginae | Nectivorous |
| Desmodus rotundus | (Desmodontidae) | Sanguivorous |
| Glossophaga soricina | Glossophaginae | Nectivorous |
| Leptonycteris sanborni | Glossophaginae | Nectivorous |
| Macrotus waterhousi californicus | Phyllostominae | Insectivorous Frugivorous |
| Macrotus waterhousi mexicanus | Phyllostominae | Insectivorous Frugivorous |
| Phyllostomus discolor | Phyllostominae | Frugivorous Insectivorous |
| Pteronotus davyi | Chilonycteriinae | Insectivorous |
| Sturnira lilium | Sturnirinae | Frugivorous |

# DISCUSSION

The traditional classification of bats makes use of morphological structures. Miller's classification (1907) uses teeth, pectoral girdle, wing structure and attachment, tuberosities on the humerus and other long bones, tragus, interfemoral membrane, tongue, and other structures. This method is subject to problems resulting from the occurence of convergence due to environmental adaptations to a given way of life.

Baker (1967) makes use of karyotypes (chromosome morphology) of the phyllostomid bats in order to group them. He justifies this on the theoretical basis that the karyotype of an individual would not be adaptive to a given way of life. By using this method he has grouped the bats according to their assumed common ancestry (Table 3).

The use of the shape of the basihyal as a class-ificational technique is a method that also involves morphology, but has not been previously considered as a method of grouping bats.

A study of the hyoid apparatus of insectivore mammals from the literature and from skeletal material in the University of Arizona mammal collection would lead one

to believe that the primitive condition of the basihyal
was a bar-shaped structure which lacked an entoglossal
process or any other processes. The mammalian hyoid that
is drawn in Figure 2 is that of the insectivore shrew-
mole Neurotrichus gibbsi. It is used to represent the
"theoretical generalized" insectivore hyoid.

When the shapes of the basihyals of phyllostomid
bats were compared to this "generalized" insectivore
type, only Sturnira lilium and Centurio senex showed close
resemblance. Both of these species are frugivorous.
Centurio senex has no entoglossal process, but Sturnira
lilium does have one. Both of these species lack hypohyals.
All of the other species of phyllostomids studied varied
greatly from this bar-shaped structure, and had entoglossal
processes (Figs. 4 thru 11).

There are three general categories into which the
various phyllostomid basihyals fall: (1) the lateral
processes longer than the dorsal or ventral processes,
(2) the lateral processes nearly equal in length to the
dorsal and ventral processes, and (3) the lateral processes
shorter than the dorsal and ventral processes. The
basihyals can also be further grouped on the basis of the
shapes of the respective processes. The methods used in
this thesis to group the basihyals are a combination of
these methods, since in some cases the dorsal process may
be shorter or longer than the ventral process.

The species examined have been grouped in Table 4 according to the general shape of the basihyal. This classification fits Baker's karyotypic classification (1967) in some ways (Table 3), and Miller's morphological classification (1907) in others (Table 2). In Miller's classification Desmodus rotundus is placed in a separate family. Baker suggests that Desmodus has close affinities to members of the Family Phyllostomidae. A classification based on the shape of the basihyal would suggest that Desmodus rotundus is specialized, but its basihyal does not seem to be as divergent from the "typical" phyllostomid-type as are those of certain other accepted members of the Family Phyllostomidae (Centurio senex, for example). In Desmodus rotundus, however, the basihyal is unique. The long entoglossal process widens at its tip instead of tapering as in the other species examined, and the shape is distinctive (Fig. 3).

Baker placed Chilonycteris and Pteronotus in the same group. Miller groups Chilonycteris and Pteronotus in the same subfamily. A method of classification based on the shape of the basihyal shows agreement with Baker and Miller since by this method Chilonycteris and Pteronotus are placed in the same group, but Macrotus waterhousi is also added. Pteronotus could be placed by itself due to the larger dorsal process, and sharply tapering entoglossal

process, but the general shape is close to those of <u>Macrotus</u>
and <u>Chilonycteris</u>. <u>Macrotus</u>, <u>Chilonycteris</u>, and <u>Pteronotus</u>
are all insectivorous.

The shape of the basihyal of <u>Carollia</u> <u>prespicillati</u>
places it in a group by itself. In <u>Carollia</u> the dorsal
and ventral processes are short and round (Fig. 5). Baker
places <u>Carollia</u> in the same group with <u>Choeronycteris</u>,
whereas Miller places <u>Carollia</u> in a separate subfamily
(Tables 2 and 3). <u>Carollia</u> is frugivorous.

<u>Leptonycteris</u> <u>sanborni</u> and <u>Glossophaga</u> <u>soricina</u>
can be placed in the same group on the basis of the similar
shape of the basihyal. Baker agrees with this but also
adds the genera of <u>Phyllostomus</u> and <u>Macrotus</u> (Table 2).
Miller includes these but also adds the genera of <u>Anoura</u>
and <u>Cheoronycteris</u> (Table 3). <u>Leptonycteris</u> and <u>Glossophaga</u>
are both nectivorous.

The shape of the basihyal of <u>Choeronycteris</u> <u>mexicana</u>
is unique and places it in a group by itself. The short
entoglossal process and the long dorsal process require
this separate grouping. Baker places this genus in the
same group as <u>Carollia</u> and Miller places it with <u>Glossophaga</u>,
<u>Leptonycteris</u>, and <u>Anoura</u> (Tables 2 and 3). <u>Choeronycteris</u>
is a nectar feeder.

<u>Anoura</u> <u>geoffroyi</u> is placed in a group by itself
according to the shape of the basihyal. Baker agrees with
this in his karyotypic study. Miller groups <u>Anoura</u> with

Leptonycteris, Glossophaga, and Choeronycteris (Tables 2 and 3). The basihyal of Anoura is close in shape to those of Glossophaga and Leptonycteris, but the entoglossal process of Anoura is slightly longer and tapers to a point, whereas the others have a blunt-ending entoglossal process. The dorsal process in Anoura is comparably longer than in the other two genera and also tapers to a point, whereas Leptonycteris and Glossophaga have more rounded dorsal processes (Fig. 6). Anoura is a nectar feeder.

Centurio senex and Sturnira lilium are each placed in a separate group based on their basihyals. Centurio lacks the entoglossal process and is more massive then Sturnira (Figs. 10 and 11). These were the only basihyals which resembled the bar-shaped type and could be grouped for this reason, but the absence of the entoglossal process on Centurio is considered primitive and places it in a group by itself. Baker places both Sturnira and Centurio in the same group, whereas Miller places Centurio and Sturnira in separate subfamilies (Tables 2 and 3). Both of these genera are frugivorous.

According to the shape of the basihyal, Phyllostomus discolor, Artibeus nanus, Artibeus jamaicensis, and Artibeus lituratus can be placed in the same group. All of these species have knob-like structures on the tips of the entoglossal processes (Fig. 8). Baker and Miller both

place Artibeus and Phyllostomus in separate groups. Baker

places Phyllostomus in the same group with Leptonycteris

and Glossophaga (Table 3). Baker also places Artibeus

with Sturnira and Centurio. Miller places Phyllostomus

and Macrotus in one subfamily and Artibeus in the same

subfamily as Centurio (Table 2). Phyllostomus and Artibeus

are both frugivorous.

Some slight species variation was found within the

genus Artibeus (Fig. 3). The differences were slight

between Artibeus nanus and Artibeus jamaicensis, but in

Artibeus lituratus the dorsal process was considerably

longer than in the other two species. There was no dif-

ference in the shape of the basihyal between the sub-

species Macrotus waterhousi californicus and Macrotus

waterhousi mexicana. Previous to 1965 these two subspecies

were considered to be separate species. Anderson and

Nelson (1965) combined these into the respective sub-

species. As one might expect, while there typically may

be only slight difference in the shape of the basihyal

within a species, greater differences can be expected (at

least in the case of Artibeus) between different species.

On the basis of the shape of the basihyal, there

is no one type that can be given as the general shape for

any specific food habits. The species can be grouped

with respect to the shape of the basihyal, and will fall

into distinct groups, but there will be more than one

group with the same food habits (Table 4). There is only one feeding habit found in each group, but there are some species that feed on both insects and fruit. In these cases the predominant food type seems to fit the present basihyal groupings. Macrotus has been observed feeding primarily on insects (Vaughan, 1959) and also secondarily on plant material (Ross, 1959). In captivity some species eat food which would ordinarily be ignored in their natural habitat, as long as the usual food source was available.

The primitive form of bat basihyal is considered to be derived from a bar-shaped Insectivora type (Sprague, 1943). Assuming that bats which feed on insects represent the more primitive ancestral stock within the family, the basihyal of the insectivorous genera Macrotus, Chilonycteris, and Pteronotus should be of this bar shape. But instead, all three have basihyals which have definite dorsal and ventral processes (Fig. 4).

On this basis, the value of the basihyal in tracing evolutionary trends appears to be limited. Apparently, adaptations and specializations for particular nutritional mechanisms have occurred, and the resulting convergence has served to obscure certain evolutionary relationships. The capture of all insects (terrestrial, flying, and aquatic) does not require the same apparatus. Therefore, one might expect considerable variation in the anatomy of various insectivorous mammals.

However, a comparison between individuals with short squatty basihyals and those having basihyals with long slender processes may be of some value and may provide supplementary evidence for taxonomic studies. The basihyal may also give assistance in determining the possible food habits of little known species; but in order to establish a conclusive food habit/shape correlation, a complete survey of all the genera in the Family Phyllostomidae would be required. This would allow a determination of all possible variations in shape of the basihyal and more substantial conclusions could then be drawn.

Table 2. Classification based on Miller (1907).

Subfamily Chilonycteriinae

*Chilonycteris psilotis*

*Pteronotus davyi*

Subfamily Phyllostominae

*Macrotus waterhousi mexicanus*

*Macrotus waterhousi californicus*

*Phyllostomus discolor*

Subfamily Glossophaga

*Anoura geoffroyi*

*Choeronycteris mexicana*

*Glossophaga soricina*

*Leptonycteris sanborni*

Subfamily Carollinae (Hemiderminae)

*Carollia prespicillati*

Subfamily Sturnirinae

*Sturnira lilium*

Subfamily Stenoderminae

*Artibeus jamaicensis*

*Artibeus lituratus*

*Artibeus nanus*

Family Desmodontidae

*Desmodus rotundus*

Table 3. Classification based on Baker (1967).

Group A

Pteronotus

Group B

Choeronycteris

Carollia

Group C

Anoura

Group D

Leptonycteris

Glossophaga

Phyllostomus

Macrotus

Group E

Micronycteris

Group F

Uroderma

Group G

Sturnira

Artibeus

Centurio

Group H

Desmodus

Table 4. Groups based on the shape of the basihyal.

Group A - Sanguivorous

Desmodus rotundus

Group B - Insectivorous

Macrotus waterhousi
Chilonycteris psilotis
Pteronotus davyi

Group C - Frugivorous

Carollia prespicillati

Group D - Nectivorous

Leptonycteris sanborni
Glossophaga soricina

Group E - Nectivorous

Choeronycteris mexicana

Group F - Frugivorous

Phyllostomus discolor
Artibeus nanus
Artibeus jamaicensis
Artibeus lituratus

Group G - Nectivorous

Anoura geoffroyi

Group H - Frugivorous

Sturnira lilium

Group I - Frugivorous

Centurio senex

## SUMMARY AND CONCLUSIONS

The basihyal bones in certain genera of the chiropteran Family Phyllostomidae were examined in an attempt to determine whether or not variations in the shape of the basihyal could be related to food habits. The possible taxonomic and evolutionary significance of these various shapes has also been considered.

There are three general categories into which the various phyllostomid basihyals fall: (1) the lateral processes longer than the dorsal and ventral processes, (2) the lateral processes nearly equal in length to the dorsal and ventral processes, and (3) the lateral processes shorter than the dorsal and ventral processes. The basihyals were also grouped on the basis of the shapes of the respective processes.

The phyllostomids studied have been placed into nine groups based on the general shape of their basihyals. Group A consists of _Desmodus rotundus,_ which is sanguivorous. Group B includes _Macrotus waterhousi, Chilonycteris psilotis,_ and _Pteronotus davyi._ All of these species are insectivorous. Group C has only one species, _Carollia prespicillati,_ which is frugivorous. Group D includes _Leptonycteris sanborni_ and _Glossophaga soricina,_ both are

nectivorous.  Group E contains only one species,
_Choeronycteris mexicana_, which is nectivorous.  Group
F includes _Phyllostomus discolor_, _Artibeus nanus_, _Artibeus
jamaicensis_, and _Artibeus lituratus_, all of which are
frugivorous.  Group G contains only _Anoura geoffroyi_,
which is nectivorous.  Group H contains one species,
_Sturnira lilium_, which is frugivorous.  Group I contains
one species, _Centurio senex_, which is frugivorous.

Species within any one group based on the shape
of the basihyal all share the same feeding habit, but a
given feeding habit occurs in more than one group in some
cases.  Thus there is no single shape of basihyal which
can be specifically correlated with a specific feeding
habit.

Since the primitive form of bat basihyal is
considered to be derived from a bar-shaped Insectivora
type, Group B (insect feeders) should include this
primitive shape.  However, group B is made up of basihyals
which have definite dorsal and ventral processes (Fig. 4).
On this basis, the value of the basihyal in tracing ev-
olutionary trends is limited.  Apparently, adaptations
and specializations for particular nutritional mechanisms
have occurred, and the resulting convergence has served
to obscure certain evolutionary relationships.

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