San Fernando Valley State College

THE MASTICATORY APPARATUS OF FOUR

PHYLLOSTOMATOID BATS

A thesis submitted in partial satisfaction of the requirements for the degree of Master of Science in Biology

by

Dennis Robert Martin

June, 1967
The thesis of Dennis Robert Martin is approved.

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Committee Chairman

San Fernando Valley State College

June, 1967
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ABSTRACT

THE MASTICATORY APPARATUS OF FOUR PHYLLOSTOMATOID BATS

by

Dennis Robert Martin
Master of Arts in Science
June, 1967

The functional and developmental relationship of the muscles, skull, and dentition involved in mastication and feeding in four phyllostomatoid bats were studied. Dry weights of the muscles, weights of the mandibles, and skull measurements were taken. The distribution of dense bone and the development of supportive crests suggested major areas of stress arising from the masticatory musculature. Using the variations of these factors as criteria the four species of bats were classified into three categories of skull type; the breviarcuate, longarcuate, and planoarcuate. The breviarcuate and longarcuate types of skulls are adaptations to a highly specialized diet as seen in Artibeus and Desmodus. The planoarcuate type is associated with the primitive insectivorous diet in Macropastus and with the reduction of the masticatory apparatus due to the increase in importance of another mechanism in Leptonycteris, a nectar-eating bat. The mandible and masseteric muscle weights in all four bats suggest a relationship correlated with the lifting function of
the muscles compared with the weight of the mandible. The close correlation found between the weight of the pterygoid muscles and the zygomaticomandibular muscle, along with the structure of the jaw articulation, suggested lateral motion as an important function of these muscles in *Macrotus* and *Artibeus*. In *Leptonycteris* the zygomaticomandibular muscles are greatly reduced compared with the pterygoid muscles. The mechanical efficiency of the mandible as a class III lever was found to be high in *Macrotus* and *Artibeus*, corresponding to well-developed masticatory musculature, as opposed to *Leptonycteris* with low efficiency and reduced musculature. The efficiency of the apparatus in *Desmodus*, unlike *Artibeus* and *Macrotus*, is due to orientation of the temporalis. It is suggested by the articulation, muscle size and orientation, and the dentition that the action of the mandible in *Desmodus* is significantly flexible in moving anteriorly. Correlated with observations of the biting action of the vampire a possible function is discussed. Hypothetical pathways in the evolution of these bats from an early primitive insectivorous type are presented.
INTRODUCTION

Recent studies in comparative anatomy have been concerned with differences between closely related animals, where evolutionary changes are relatively recent and, thus, afford an opportunity to study mechanisms involved in their evolution. Studies done with the functional anatomy of mammals include those by Rinker (1954), Klingener (1964), and Lemire (1966) with rodents; Gaughan (1954) with insectivores; Davis (1955, 1964) and Sicher (1944a) with bears; Sicher (1944b) with the masticatory apparatus of sloths, and Schmacher (1961) with the masticatory apparatus of primates, carnivores, artiodactyls, and rodents. Surprisingly little has been done until recently with the Chiroptera, one of the most diversified orders of extant mammals. Vaughn (1959, 1966) studied the functional anatomy of the flight musculature of three species of bats; and Wille (1954) has studied the feeding apparatus in nectar-eating bats. However, the masticatory apparatus has been considered only from a descriptive standpoint and remains to be studied from a comparative and functional aspect. It is the purpose of this paper to examine the variation in the masticatory apparatus of four species of bats, with the different diets and to attempt to interpret these variations in terms of their adaptational significance and possible evolutionary relationship.

The family Phyllostomatidae exhibits a wide range of feeding habits including insectivorous, frugivorous, omnivorous, carnivorous, and neotivorous types. Three species from this family were chosen because of their availability and their obvious differences in
structure and diet. *Macrotes waterhousi californicus* (subfamily Phylllostominae) is an insect-eater and has the typical W-patterned occlusal surface on the molars. Diet and tooth pattern are considered primitive. (Allen, 1939). *Artibeus jamaicensis* (subfamily Stenoderminae) is a tropical fruit-eating bat and *Leptonycteris sborni* (subfamily Glossophaginae) a nectar-eating type. The vampire bat *Desmodus rotundus* (family Desmodontidae) was chosen because of its diet of blood and the peculiar structure of its masticatory apparatus. In addition to certain structural similarities, evidence based upon the relationship of *Desmodus* to the ectoparasitic Strebilidae (Wenzel, Tipton, and Kiewlicz, 1966) suggest a close relationship of *Desmodus* to the Phylllostominae.
ACKNOWLEDGEMENT

I am most grateful to Dr. Andrew Starrett for his advice and discussions with regard to this study and for his role in acquiring specimens for this study. I am grateful to Dr. Charles A. McLaughlin, former head curator of Mammalogy, and the Los Angeles County Museum for their co-operation in loaning the alcohol specimens and allowing me to examine their collections.

I am also grateful to Dr. George F. Fisler for his helpful comments and advise throughout this study and to Dr. Marvin Cantor, who, along with Dr. Starrett and Dr. Fisler, read this paper.

I am further indebted to Janice L. Martin for her patience and persistence in typing the first draft, and to Mrs. Janet Ives for typing the final copies.
MATERIALS AND METHODS

Materials used in this study consisted of forty-five skulls, three entire skeletons, and forty-three alcohol preserved specimens representing four species of bats. The list of specimens found at the end of this section follows the nomenclature in Hall and Kelson (1959) except for *Macrotus* (Anderson and Nelson, 1965) and *Leptonycteris* (Davis and Carter, 1962).

The preserved specimens and much of the skeletal material were obtained from the Los Angeles County Museum and are designated in this report by five digit numbers. The remainder of the material is in the San Fernando Valley State College vertebrate collection and is designated by three digit numbers.

All dissections were done with the aid of a stereo-binocular dissecting microscope using powers of 20X, 30X, and 40X. Some measurements were made with an ocular grid.

Dissections were done on the masticatory apparatus of four species of bats, *Macrotus* waterhousii, *Artibene jamaicensis*, *Leptonycteris samborni*, and *Desmodus rotundus*. Two of eight specimens of each species were dissected in detail to establish its myology. An additional six species were used to verify the original dissections.

In order to weigh the muscles each set of muscle was removed from the specimen and placed in an appropriately marked vial and dried in a 100°C oven for twenty-four hours, the vials were then corked and allowed to cool for about twelve hours. This method was used to eliminate possible effects caused by different states of preservation of the specimens. Muscles were weighed on a Mettler
analytical balance accurate to one ten-thousandth of a gram. Possible sources of error may have occurred because of loss of some muscle fibers and the inclusion of additional tissue associated with the muscles during removal. As a result, the values are not of statistical significance but are of value in relating size relationships between and among muscles.

Skull measurements were taken with a Helios dial caliper accurate to one tenth of a millimeter. In cases in Artibeus where there was a question of species identification the lengths of the forearms and skull and the percentage postorbital constriction/symph-matic breadth, as used by Starrett and de la Torre (1964), were considered as criteria.

The following cranial measurements were taken to establish relative proportions of and between skulls.

1. **Greatest Length of Skull**—From the anterior-most border of the premaxilla to the posterior-most point on the skull.

2. **Skull Depth**—From the posterior ridge of the glenoid fossa, perpendicular to the skull axis, to the top of the braincase.

3. **Zygomatic Breadth**—Greatest distance across the zygomatic arches perpendicular to the cranial axis.

4. **Palatal Width**—Greatest distance between the labial surfaces of the last large molars at the alveolar line.

5. **Least Interorbital Constriction**—Shortest distance between the orbits across the top of the skull.

6. **Length of Maxillary Tooth Row**—Distance from anterior alveolus of canine to the posterior alveolus of last molar.
7. **Mandible Length**—From anterior border of symphysis to posterior border of articular process.

8. **Coronoid Height**—From top of coronoid process to the ventral edge of mandible on a line perpendicular to the axis of the mandible.

9. **Coronoid Length**—From the anterior edge of the coronoid process at its base to the posterior border of the articular process.

10. **Molar-Dentary Height**—From lowest dorso-labial point on the crown of the last large lower molar to the ventral edge of the dentary on a line perpendicular to the axis of the mandible.

11. **Articular-Molar Length**—From posterior surface of last large lower molar to the posterior surface of the articular process.

Drawings of the skull and mandibles were made with the aid of an opaque projector. These drawings were used to determine some of the proportions and angles. They also served as a basis for the illustrations in this paper. The myology of the bats within any of the four species did not vary greatly; therefore the drawings of muscles are a synthesis of those made from the dissections.

Variation in bone density of the skull was examined and compared by shining the beam of a microscope lamp through the skull.

**Specimens**


Artibeus sp. (a small form) - skeletons: 19369, 19375, 19384, Oaxaca, Mex.

THE SKULL

The relative proportions and general appearance of the skulls of the four species of bats are illustrated in Figs. 1, 2, and 3. The cranial sutures are indistinguishable as they have been completely fused early in development. Skull measurements are given in Table 1.

From a dorsal view the cranium of Macrotes (Fig. 2a) is ovoid in shape. The rostrum tapers from the zygomatic process to the narrow premaxilla and makes up about 1/3 the length of the skull. The anterior zygomatic process is well developed but the arches are relatively thin. They run at about 30° angles postero-laterally from the axis of the skull and then curve in at about a 60° angle to the axis in the region just anterior to the auditory meatus. A sub-orbital crest is formed by the maxilla in the antero-ventral margin of the orbital fossae. This crest is a bony shelf lying almost parallel to the frontal plane of the skull, housing the roots of the last molar on its ventral surface. The internasal suture is obvious. An area of relatively dense bone is found as a line along the sagittal crest region stopping posteriorly at a point 3/4 of the way along the braincase. At this point the line of dense bone divides and runs latero-ventrally on each side to the mastoid region ending just posterior to the auditory meatus (Fig. 4a and 5a). This line corresponds to the tentorium, a sheet of ossified connective tissue which separates the cerebrum from the cerebellum. A second line of dense bone lies in an antero-ventral position on the lateral side of the brain case. Further areas of dense bone are found at the inter-orbital constriction and at the posterior region of the rostrum. The
alveolar region is composed of dense bone, especially in the canine-incisor area.

From a lateral view (Fig. 1a), the brain-case is expanded anteriorly. The slope is a gradual curve from the anterior surface of the brain-case to the end of the nasal bones. The lambdoidal crest runs postero-dorsally from the swollen mastoid region to the midline at the most posterior point of the occipital region. The zygomatic arch becomes relatively thinner posterior to the region of the anterior process. The arch curves strongly upward to the condylar region from the alveolar line. A pre-orbital ridge is distinguishable, its anterior most point is in line with the anterior edge of the second molar.

The pterygoid bones curve postero-ventrally with the hamular processes antero-medial to the glenoid fossa.

Artibeus, generally larger than Macrotus, differs in a number of characters. From a dorsal view the braincase is not as expanded proportionately anteriorly and tends to be wider in the posterior region (Fig. 2a and 2b). The zygomatic arch, from a dorsal view, is more curved than in Macrotus and the rostrum is shorter and broader. The bone density and crests are more strongly developed in Artibeus (Fig. 4b and 5b). The lines of dense bone in the braincase and the shape and position of the pterygoid bones are essentially the same as in Macrotus.

Leptonycteris has a long rostrum making up about one-half the length of the skull. From a dorsal view (Fig. 2c), the braincase is elongate narrowing gradually to the rostrum which continues to the premaxilla with little tapering. Unlike Macrotus, the zygomatic
The tear film is shown.

(a) Tear film layer
(b) Anterior tear film
(c) Tear film breakup

The tear film layer of the ocular surface appears

of dense bone (cross section) in (e) Quadricep wetted.
Table 1. Skull measurements in mm. Numbers represent the mean, range, and sample size (in parenthesis).

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<th>Arthisus jamaiicensis</th>
<th>Leptonycteris</th>
<th>Desmodus</th>
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<td>22.7 (7)</td>
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<tr>
<td></td>
<td>22.5-23.3</td>
<td>27.3-26.9</td>
<td>25.9-27.4</td>
<td>23.6-24.5</td>
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<td>12.5 (11)</td>
<td>8.4 (9)</td>
<td>11.8 (8)</td>
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<td>12.1-13.0</td>
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<td>10.7 (10)</td>
<td>12.0 (8)</td>
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<td>10.4-11.1</td>
<td>11.7-12.5</td>
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<td>4.5 (10)</td>
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<td>7.7-8.4</td>
<td>7.9-8.6</td>
<td>8.0-8.6</td>
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<td>% interorb. constriction/zygomatic breadth</td>
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<td>45.2 (10)</td>
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<td>43.8-51.8</td>
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arch, from a lateral view (Fig. 10), is very thin and lies horizontal to the skull axis. The preorbital ridges are absent and the anterior zygomatic process is weakly developed. The suborbital crest is thin and angles postero-medially to continue as the ventral edge of the pterygoid bone. The pterygoids, in general are like those of *Macrotus*, except that the hamular processes are medial to the posterior surface of the post glemoid ridge. The pattern of dense bone is much more diffuse than in *Macrotus* but the tentorial lines can be distinguished. In both *Leptonycteris* and *Macrotus* a swelling which corresponds to the position of the cerebellum (Schneider, 1957) is found on the dorso-posterior surface of the braincase. In *Leptonycteris*, *Macrotus*, *Desmodus*, and *Artibeus* this region is surrounded by dense bone (Fig. 5). In *Leptonycteris* the maxillae are expanded laterally from the rostrum in the alveolar region and the teeth do not lie directly under the lateral walls of the rostrum as they do in the other three species.

*Desmodus* has an expanded, high, arched braincase which makes up about two-thirds of the skull length. The rostrum consists of two swollen, regions of relatively dense bone lying antero-dorsal to the orbit. Bone deposition is dense in the region of the incisors and canines. From a lateral view the skull slopes continuously from the top of the braincase to the tip of the canines. The zygomatic arch is thin but not as markedly as in *Macrotus* and *Artibeus*. The anterior process starts above the cheek teeth and the arch runs postero-laterally to its posterior process at about a 100° angle to the cranial axis. The suborbital crest is absent.
The pterygoid bones have a conspicuous hamular process curving postero-ventrally at about a 60° angle from the lateral side of the antero-ventral edge of the pterygoid. The end of the hamular process lies medial to the glenoid fossa.

The distribution of dense bone on the braincase of *Desmodus* is more extensive than in the other three species being concentrated in the postero-dorsal region.

The glenoid fossa (Fig. 6 and 7) of *Macrotus* and *Artibeus* are similar. They are limited dorsally by a relatively thick, flat surface and also posteriorly by a curved post glenoid ridge. This ridge is directed ventrally and then anteriorly forming a socket for the articular process of the mandible. The glenoid fossa opens laterally allowing lateral movement of the articular processes. *Leptonycteris* has basically the same structure but differs in two significant points. First, the post glenoid ridge is curved anteriorly to a greater degree and, second, the ventral edge of the posterior zygomatic process connects with the post glenoid ridge thus blocking off the lateral end of the fossa and thereby restricting lateral movement of the mandible. *Desmodus* (Fig. 9b), in contrast, has the upper articular surface of the glenoid fossa slope antero-dorsally at an angle of about 45° to the horizontal plane. Further, the zygomatic arch blocks the lateral end of the fossa as in *Leptonycteris*, thus preventing lateral movement.

**THE MANDIBLE**

In general *Leptonycteris* has the lightest weight mandible of the four (Table 4). It is relatively straight and long (Fig. 9).
Macrotus exhibits a relatively heavier mandible which curves dorsally in the region of the vertical ramus, and the symphysial region is of denser in bone. Artibeus has the heaviest mandible. The tooth region is supported by bone to a greater degree than in the three other species of bats. Desmodus has a relatively light mandible with two major concentrations of dense bone; the canine-incisor region and the ventral edge of the dentary, which appears as distinct lateral and medial ridges.

Macrotus exhibits a relatively high vertical ramus. The anterior edge of the coronoid process rises at an angle of 90° to the axis of the mandible and gradually curves posteriorly to its tip. It is strengthened by a concentration of bone along its anterior edge. The posterior edge of the coronoid process runs from the tip postero-ventrally to the articular process. Deposition of dense bone is also seen in this area. A heavy concentration of bone extends from the articular to, and as a part of, the angular process, which is relatively long and curved. From the angular the ramus curves antero-ventrally and then runs anteriorly from a point below the last molar. On the medial side of the vertical ramus a ridge runs from the medial end of the articular to the base of the anterior edge of the ramus. The articular (Fig. 9a) is a relatively long, narrow bar angling ventro-medially. The coronoid and angular processes are deflected laterally in all four species. In Leptonysteria the ramus is longer and lower than in Macrotus due to the low coronoid process and its relatively long posterior edge. The anterior edge of the coronoid process is relatively straight and is at an angle of about 60° to the mandibular axis. The angular process extends
posteriorly and is well developed as in *Macrotrus*, but differs in
that it is a straighter process. Distribution of dense bone is
as in *Macrotrus* but is lighter throughout. *Artibeus* differs from
*Macrotrus* in having a short, round angular process, which is larger
and heavier in construction, and the coronoid process is proportion-
ately smaller in relation to the rest of the jaw.

In *Desmodus* the vertical ramus is about 1/2 the length of the
mandible. Its anterior edge is well rounded dorsally. It curves
antero-ventrally onto the lateral surface of the horizontal ramus
just below the cheek teeth. The posterior edge of the coronoid
process is almost parallel to the horizontal axis of the mandible.
The posterior edge of the vertical ramus is almost perpendicular to
the axis, ending at the angular process. From the small, pointed
angular the ramus curves at an angle of about 45° antero-ventrally
to the ventral edge of the ramus. In contrast to those of *Macrotrus*,
*Artibeus*, and *Leptonycteris* the articulation occurs above the occlusal
plane and above the insertion of the temporal muscle. In further
contrast the articular processes (Fig. 9d) of *Desmodus* are shorter
and heavier along the posterior surfaces and from a posterior view
these processes tend to be parallel to the horizontal plane.

Dorsally viewed, the dentaries (Fig. 8a) of *Macrotrus* from a V
with a small anterior region. *Leptonycteris* has a relatively wider
canine-incisor region, while that of *Artibeus* is broader and more
rounded. In *Desmodus* the alveolar line of the incisors extends higher
than the cheek teeth. The alveolar line of the canines connects the
alveolar lines of the incisors and cheek teeth.
THE DENTITION

Incisors and canines

In Macrotus the upper incisors consist of two large, shovel-shaped inner teeth and two small rounded outer teeth. The lower incisors are very small, rounded, and bifid teeth. The outer incisors are partly covered by the cingula of the lower canines (Fig. 11).

The upper canines are larger than the lower. The cingulum extends partially antero-medially from the maxilla thus extending the anterior surface of the canine forward. The posterior border is blade-like from the tip to the cingulum. The lower canines are thinner, with a flat posterior surface. The main shaft arises from the anterior portion of the cingulum, curving gradually posteriorly, the posterior portion lies lingual to the anterior edge of the first premolar.

In occlusion the lower canines are antero-medial to the upper canines and cover the labial surface of the upper outer incisors. The upper inner incisors make contact with the medial edge of the lower canines and the ventral edges of the lower incisors. The canines are not tightly interlocked until the jaws are completely closed.

In Artibeus the plan is the same except that 1) the canines are proportionately larger, 2) the inner upper incisors are small and bifid, 3) with complete closure there is a gap between the upper and lower incisors, and 4) during closure the lower canines occlude with the anterior surface of the upper canines as is evidenced by worn areas.

In both Macrotus and Artibeus the width between the mandibular tooth rows is less than that between the upper tooth rows.

In Leptonycteris the incisors are not close together but are
parastyle

paracone protocone

protoconid paraconid

Upper Molar

mesostyle metastyle metacone hypocone

trigonid talonid hypoconid entoconid metaconid

Lower Molar
spaced. The upper incisors consist of fan-shaped inner incisors and triangular outer incisors. The lower incisors are smaller and more uniform; the inner ones being the smallest. There is a noticeable gap between the inner incisors of both jaws.

The canines are relatively straight and thin teeth slanting slightly outwards from the jaw. Each upper canine has two additional cusps, one on its posterior end and one on its antero-medial edge.

When occluded the upper canines interlock with the lower canines, the inner upper incisors contact the dorsal edge of the lower inner incisors (Fig. 110), and the lateral edge of the upper outer incisor contacts the medial edge of the lower canine.

Desmodus presents an entirely different picture. The two upper incisors are very large and blade-like, and curve antero-ventrally from the premaxilla. The points are close together and the posterior edge runs back to the upper canines forming a curve. The lower incisors are relatively tall, narrow teeth which are deeply bifid. The inner incisors are separated by a median gap.

The canines are large, blade-like teeth which lie further back on the jaw relative to their position in the other bats examined.

The posterior edge of the lower canines slides against the anterior edge of the upper canines as is evidenced by flat, worn surfaces. The upper canines also come in contact with the anterior edge of the first lower premolars. The upper incisors fit into small pockets on the lingual surface of the mandible behind the incisor and symphysis.

Premeolars and Molars

In Macrotus the upper cheek teeth consist of a short, blade-like
(a) Let $O$ be the center of the circle.
(b) Let $A$ be the point of tangency.
(c) Let $P$ be the point of intersection of the tangents.
(d) Let $Q$ be the point of intersection of the secants.
(e) Let $R$ be the point of intersection of the external tangents.

**Theorem II:** Intersecting secants of the same circle.
first premolar and a large, blade-like second premolar (Figs. 1, 3 and 12). The first two molars are relatively large and squared, with the second molar being slightly larger. The crown shows the typical W-pattern opening labially and occupying the labial two-thirds of the tooth as a high ridge. The pattern is formed by commisures or ridges running between pointed cusps. The three labial cones are, beginning with the anterior one, the parastyle, mesostyle, and metastyle (Fig. 10). The two medial cones are the anterior paracone and posterior metacone. The lingual one-third of the molar is relatively flat. The protocone and the hypocone lie at the antero-lingual edge and posterolingual edge respectively.

The third molar is about one-third the length of the second molar but roughly the same width. Cusps found are a parastyle on the labial edge, a paracone on the mid-anterior edge, a reduced mesostyle posterior to the paracone, and a protocone on the antero-lingual edge.

The three lower premolars are similar in shape to the upper premolars. The first premolar is slightly broader than the other two. The second and third premolars have higher protoconids. The lower molars resemble the upper molars except the W-pattern opens lingually and the flattened lingual platform is absent. The tooth is divisible into the trigonid and the talonid. The anterior sections, the trigonid, consists of the paraconid and metaconid at the anterior and posterior lingual ends respectively, and the metaconid which lies midlabially. The commisures between these cusps form the anterior "V" of the "W". The posterior talonid consists of the entoconid on the postero-lingual end and the hypoconid on the postero-labial end of the tooth. The commisures between these cusps and between
Fig. 12. Plane of the occlusal surface of the upper
the hypoconid and metaconid complete the "W".

On occlusion the labial surfaces of the upper cheek-teeth extend over and cover the labial surfaces of the lower cheek-teeth. The paracone and metacone lie posterior to the paraconid and metaconid respectively, i.e., the lower molars interlock with the upper molars such that the lowers overlap anteriorly with the uppers. This results in a shearing action between the labial edges and surfaces of the lower cheek-teeth and the lingual surfaces and ventral edges of the upper cheek-teeth. The occlusion of the dorsal surface of the lower molars with the lingual platform of the upper molars aids in cutting or grinding food. (Fig. 13).

The first lower premolar occludes on its antero-labial edge with the antero-lingual surface of the first upper premolar and second lower premolar occludes with the postero-lingual surface of the same upper tooth. The smaller third lower premolar lies close to the antero-lingual edge of the second upper premolar but does not appear to make contact. The large second upper premolar occludes with antero-labial surface of the first lower molar. The first two lower premolars and the first upper premolar and canine apparently function in cutting up food. A space occurs between these teeth and the second upper and third lower premolar upon occlusion, separating the dentition into the anterior stabbing and cutting teeth and the posterior grinding teeth.

In comparison Artilus has proportionately larger cheek-teeth and a complete reduction of the W-pattern. All of the cheek-teeth have flattened, lingual occlusal surfaces which are smaller on the anterior teeth, and smallest on the upper canines. Although the
Commisures and styles are lost, the cones and conids are present and are well-developed. The paracone and metacone lie on the labial edges of the upper molars forming a blade-like ridge which is continued in series by the high second premolar. The lower molars are flat, except for the conids, and smaller than the upper molars.

Oclusion is the same as in Macrotus with respects to cusp orientation. The first lower premolar occludes with the lingual surface and hypocone region of the upper canine. The antero-lingual surface of the first upper premolar occludes with the posterior edge of the first lower premolar and with the anterior edge of the second lower premolar by its postero-lingual surface. The second lower premolar occludes with the hypocone region of the first upper premolar and the antero-lingual surface of the second upper premolar. The hypocone region of the second upper premolar occludes with the first lower molar. In contrast to those of Macrotus, the cheek-teeth of Artibeus have a cutting and shearing component which decreases posteriorly whereas the mashing component decreases anteriorly. Both components are found in all the cheek-teeth and even extend to the upper canines. This results in a closer integration of functional types.

In Lepontycteris the teeth are greatly reduced in size and structure and, except for the molars, they are spaced apart from each other. The laterally compressed premolars have a central protocone and an undesignated anterior and posterior cone. The first lower premolar is noticeably longer, antero-posteriorly, and lies close to the canine. The molars are relatively long, narrow teeth with all the basic cones and conids identifiable. In the upper molars the
to each other at occlusion.

Fig. 17. Outline drawing showing relation of teeth
Paracone and metacone lie near the labial side of the tooth and the protocone is at the lingual side. The cusps of the talonid and trigonid regions are arranged as in *Macrotus* but are closer together due to a lateral compression of the tooth. The commissures and styles are absent.

Upon occlusion the first lower premolar occludes with the lingual surface of the upper canine. The first upper premolar occludes by its antero-lingual surface with the postero-labial surface of the second lower premolar. The second upper premolar similarly occludes with the third lower premolar. The molar occlusions show the same basic pattern as in *Macrotus*.

*Desmodus* lacks any identifiable cusps and its cheek-teeth are greatly reduced in size and number. The dental formula, P1/2; M1/1, was taken from Miller (1907) and was also used by Hall and Kelson (1959).

The upper cheek-teeth are very small and are subquadrate in shape. The first two lower cheek-teeth are blade-like and curve back, the first upon the anterior edge of the second and the second upon the anterior edge of the third. In a cross-sectional view of the mandible the lower cheek-teeth slant dorso-laterally.

Upon closure the lingual surfaces of the upper cheek-teeth make contact with the labial surfaces of the second lower premolar and first molar. The antero-labial edge of the first lower premolar makes contact with the lingual surface of the postero-lingual surface of the upper canine beginning at the anterior edge of the premolar and proceeding posteriorly as the jaw closes, resulting in a slicing action.
The myology of bats has received little attention until recently. Earlier workers such as Cuvier (1800-1805), Kolenati (1857), Humphrey (1869), Elass (1907-1908), Maisonneuve (1878), Robin (1881), and Macalister (1872) concentrated on description. Macalister's comparative study, in which he described the myology of nineteen species of bats, *Galeopithecus* and *Pteromyx*, stood as the most complete of the early studies. More recently, Schneider (1960) described the ear musculature of *Asellus tridens* and *Eptesicus myotis*. Yoshikawa and Suzuki (1962) described the lamination of the masseteric muscles in *Rousettus aegyptius*, *Pipistrellus abramus*, and *Miniopterus schreibersi*. Park and Hall (1951) compared morphology of the tongues and stomachs of eight new world bats; Mori (1960) described the musculature of *Pteropus edulis*. Vaughn (1959, 1965) studied the form and function of the locomotor anatomy of three species of bats, representing three families, correlating anatomical studies with observations on behavior in nature and in the laboratory, and also considering the ecology in addition to structure of the organisms.

Most of the terminology employed here is from Davis (1964). Other sources will be mentioned where applicable.

The Temporalis Group (Fig. 14, 15)

In all four species this unit consisted of two major parts, the *mm. temporalis superficialis* and *temporalis profundus*. They are relatively flat, thick muscles whose fibers run in an antero-ventral direction from the braincase. In *Artibeus*, the temporal muscle is roughly five times, and in *Desmodus* about three times, the weight
Fig. 14. Lateral view of head showing the m. temporalis superficialis (ts), m. temporalis profundus (tp), and the m. suprazygomatico-mandibularis for (a) Macrotus waterhousii, (b) Artibeus jamaicensis, (c) Leptonycteris emborni, and (d) Desmodus rotundus. The zygomatic arch is not illustrated.
The second point, (c) Deformable to rigid,
(e) Macro and micro, (b) Articular, temporary, (f) Core, and the
surgical plane, (t) and the temporalis muscle.

Ref. 15. Dorrestein view of head, showing the
 temporalis.
of those of *Macrotus* and *Leptonycteris*.

1. *M. temporalis superficialis*

**Origin**

*Macrotus* - On the lateral anterior half of the *temporalis profundus* muscle, extending dorsally to the midline and anteriorly into the post orbital fossa, bordering the orbit. Attachment is fibrous to anterior border of the deep masseter.

*Artibeus* - Differs from *Macrotus* in its larger size and attachment to sagittal and temporal crests.

*Desmodus* - As in *Macrotus*, except that the area of attachment is greater.

*Leptonycteris* - On anterior portion of braincase, posterior to orbit, below midline and overlapping the *m. temporalis profundus*.

**Insertion**

Base of anterior edge of coronoid process by a tendinous sheet.

**Remarks**

In all but *Leptonycteris* the fibers of this muscle were closely associated with the deep portion along their anterior border. In *Leptonycteris* this muscle is independent of the deep part and lies further anterior than in the others.

2. *M. temporalis profundus*

**Origin**

A fleshy attachment to the braincase within the temporal fossa, bordered posteriorly by the lambdoidal crest, dorsally by the sagittal crest or midline, and anteriorly by the temporal crest. *Artibeus* is the only one with a sagittal crest. In *Leptonycteris* the muscle lies on the lateral surface of the braincase and does not reach the midline.
Insertion:

Attaches to the end of the coronoid process by a tendinous sheet. Deeper fibers attach to the dorsal surface of the medial coronoid ridge by a tendinous sheet, and to the medial surface by fleshy attachment.

Remarks:

This is the largest muscle in the masticatory group and is best developed in Artibeus, less so in Desmodus and least in Macrotus and Leptonycteris. The four sub-adult Macrotus were found to have a reduced temporal similar to that of Leptonycteris.

Action of the Temporal Group:

Applies force on coronoid in a dorso-posterior direction thus closing the jaw.

The Masseter Group (Fig. 14, and 16)

The masseteric complex was described by Yoshikawa, et al. (1961, 1962, 1965) as consisting of seven basic parts. In two microchiropterans, Miniopterus and Pipistrellus, the layers were difficult to separate because they lacked a tendinous separation found in other mammals. This suggests a unification of function being reflected in the structure. Because the purpose of the present study is to determine the relative function of these muscles, the masticatory musculature is separated into three major units based on their difference to each other in their action and fiber direction. The first is the m. masseter, whose fibers run antero-dorsally, the second is the m. zygomaticomandibularis, whose fibers run postero-dorsally, and the third is the m. suprazygomaticomandibularis, as
described by Schumacher (1961). This grouping places the components designated by Yoshikawa into major functional units which will better serve the purpose of this study.

1. **M. masseter**

   A relatively heavy, rounded unit whose fibers run antero-dorsally.

   **Origin**

   On the ventral edge and ventromedial surface of the zygomatic arch by a tendinous attachment.

   **Insertion**

   By fleshy attachment to the ventral region of the masseteric fossa on the entire lateral surface of the angular process, to the anterior limit of the fossa.

   **Remarks**

   This most superficial unit of the masseteric group entirely covers the deeper group.

   In general the areas of insertion are the same in the bats studied. *Desmodus* differs in that the area of insertion is relatively larger and extends further up on the posterior surface of the fossa corresponding to the relatively higher position of the angular process. By weight *Artibous* has the largest masseter. This muscle in *Desmodus* is about one-half and in *Macrotus* and *Leptonycteris*, about one-fifth the weight of that of *Artibous*.

   The angle of fiber direction relative to the zygomatic arch is about 25° in all but *Leptonycteris* in which it is roughly 15° as a consequence of the elongate angular process in this bat. The orientation and shape of this muscle in *Leptonycteris* gives the masseter a more elongate form.
Fig. 16. Lateral view of head showing the superficial (1) and deep (2) masseteric muscles of (a) *Macrotus waterhousi*, (b) *Artibeus jamacensis*, (c) *Leptonycteris sanborni*, and (d) *Desmodus rotundus*: m. temporalis superficialis (ts), m. temporalis profundus (tp), m. suprazygomaticomandibularis (szm), m. zygomaticomandibularis (zm), and the m. digastricus (d).
**Action**

Contraction results in force being applied on the ramus in an antero-dorsal direction thus closing the jaw.

2. *M. zygomatico-mandibularis*

This unit is Yoshikawa's (1962) *M. masseter profundus, pars posterior*. The nomenclature used here is from Schumacher (1961). The superficial portion may run dorsally and somewhat posteriorly. The deep portion runs postero-dorsally also, but angles more posteriorly.

**Origin**

Attaches to the medial surface of the zygomatic arch for its entire length by a tendonous tissue particularly in the region of the posterior zygomatic process.

**Insertion**

By a fleshly attachment to the surface of the masseteric fossa.

**Remarks**

In all four cases the insertion lies medial and ventral to the zygomatic arch. The fibers are directed toward the posterior zygomatic process. The area of insertion in *Leptonycteris* is relatively smaller than in the other three species. The weight of the *zygomatico-mandibularis* is roughly 1/2 that of the masseter in all but *Leptonycteris* in which the ratio is about 1/3. This is the deepest of the masseter complex and inserts dorsal to the masseter.

**Action**

Raises jaw by applying force in a postero-dorsal direction on the lateral surface of the ramus. Working independently, one muscle can pull the mandible laterally.

3. *M. suprazygomatico-mandibularis*
This is a small, flat muscle which lies above the zygomatic arches.

**Origin**

Attached by a thin tendinous sheet on the temporal fascia antero-dorsal to the auditory meatus.

**Insertion**

On the ventral antero-lateral border of the anterior edge of the coronoid process, by a tendinous sheet.

**Remarks**

This muscle lies in contact with the dorsal surface of the zygomatico-mandibularis muscle and curves ventrally to pass between the arch and the latter muscle. Its medial surface lies close to the temporal fascia. In Leptonycteris the muscle is comparatively smaller than in the other three species. The nomenclature is from Schumacher (1961). This muscle corresponds to the m. zygomatico-mandibularis described by Yoshikawa (1962).

**Action**

On contraction force would be applied on the region of the origin antero-ventrally. The force is directed, in part, by the delimiting position of the zygomatico-mandibularis muscle.

**The Pterygoid Group (Fig. 17)**

This consists of two separate muscles, the *pterygoides internus* and the *pterygoides externus*. These correspond to the *pterygoides medialis* and *lateralis* respectively as described by Schumacher (1961). The *pterygoides externus* is a small, round, elongate muscle whose fibers are directed antero-medially. The *pterygoides internus* is about three times larger than the *pterygoides externus*. It is a
Fig. 17. Lateral view (1) and ventral view (2) of the skull showing the pterygoideus internus (ri) and pterygoideus externus (pe) for (a) Macrotrus waterhousei, (b) Artibeus jamaicensis, (c) Lontonycteris sanborni, and (d) Desmodus rotundus. The cross hatching on the mandible represents the area of insertion. The zygomatic arch has not been illustrated in al, bl, cl, and dl. The mandible is represented as being transparent. The pterygoideus externus lies dorsal to the pterygoideus internus.
a fan-shaped muscle whose fibers are directed antero-medially on
a dorso-medial plane, relative to the axis of the skull.

1. **M. pterygoideus internus**

**Origin**

By a fleshy attachment to the postero-lateral surface of the
*os pterygoideus* anteriorly to the dorsal surface of the suborbital
crests. *Desmodus* lacks a suborbital crest and the muscle attaches
instead to the antero-medial surface of the orbital fossa.

**Insertion**

By a fleshy attachment to the medial surface of the angular
process and the adjacent surface near the mandibular foramen and
the medial ridge running between the articular process and the
anterior edge of the coronoid process.

**Remarks**

This muscle lies in contact with the *pterygoideus externus*
dorsally. The two muscles are separated by a branch of the tri-
geminal nerve which passes postero-medially from the mandibular
foramen. This muscle is relatively larger in *Artibeus* and *Desmodus*
than in *Macrotus* and *Leptonycteris*.

**Action**

The force resulting from simultaneous contraction of the
internal pterygoids would pull the mandible antero-dorsally and
medially. Contraction of a single muscle would pull the mandible
laterally.

2. **M. pterygoideus externus**

**Origin**

On the postero-lateral surface of the pterygoid bone, dorsal
to the hamular process by a fleshy attachment.

**Insertion**

On anterior surface of the medial arm of the articular process by a tendonous attachment.

**Remarks**

This muscle lies dorsal to the **m. pterygoideus internus** and ventral to the deep fibers of the **m. temporalis profundus**. In *Desmodus* it is about 1/3 the size of the **pterygoideus internus** in *Macrotus* and *Leptonysteris* and about 1/5 of that in *Artibeus*.

**Action**

Force pulls antero-medially on articular process.

**M. digastricus** (Fig. 14, 16)

This is a long, round muscle which is basically the same in all of the bats examined.

**Origin**

By a fleshy attachment to the surface of the mastoid fossa posterior to the auditory annulus.

**Insertion**

On the ventral edge of the vertical ramus.

**Remarks**

The origin is shared with the sternomastoid and clavomastoid muscles which cover the digastric laterally. Inscriptions dividing the digastric into two muscles were found in *Desmodus, Leptonysteris*, and *Macrotus* but not in *Artibeus*. In *Macrotus* the auditory annulus is relatively larger than in the other three bats and it is across this bone that the digastric lies. The inscription occurs in this region of the muscle as an epineurium of thin tendon, rather than
a raphe. In R. house a discontinuity of fibers between the anterior and posterior units of the muscle is found. A tendinous inscription is not apparent.

**Action**

Upon contraction it opens the jaw by applying force postero-dorsally at the insertion which lies well below the articulation.

**M. auriculo-mandibularis**

This is a very small, round muscle found in all the bats examined.

**Origin**

On the connective tissue of the antero-ventral region at the base of the pinna.

**Insertion**

On the dorsal edge of the angular process by a tendinous attachment.

**Remarks**

The nomenclature of this muscle is from Huber (1925). This is the m. mandibularis or styloauricularis described by Schneider (1961).
FEEDING HABITS

Based on diet the Chiroptera have been classified into six groups: the insect-eaters, fruit-eaters, flower-eaters, blood-eaters, meat-eaters, and fish-eaters (Walker, 1964). As has been pointed out by Walker (1964), and other authors, these are generalizations which are not strictly true. For example the nectar-eating bat, Glossophaga, has been found to include large quantities of insects in its diet (Carvalho, 1961; Goodwin and Greenhall, 1961; Starrett and de la Torre, 1964). The carnivorous Phyllostomus hastatus eats fruit as well (Dunn, 1933) and the fish-eating Noctilio leporinus, in some cases, has been found to feed on insects in part or even exclusively (Goodwin and Greenhall, 1961). On the other hand vampires seem to be restricted in diets, even to the point that Desmodus appears to prefer the blood of mammals whereas Diademus and Diphylla prefer the blood of fowl (Walker, 1964; Goodwin and Greenhall, 1961).

Macrotus hunts for insects among shrubs, by hovering or flying low to the ground in the pursuit of terrestrial species, picking them off leaves, or catching them in the air in flight. Stager (1943) reported finding a dead Macrotus caught in a desert shrub, Dumidiurensis. Vaughn (1959) observed these bats hovering close to the ground, possibly in pursuit of insects. Grinnell (1918) reported catching a Macrotus in a mouse trap that had been set in an open area. She suggested that the bat was after beetles which were attracted to the bait. The locomotor ability of this bat and its ability to take off from the ground has been shown by Vaughn (1959).
Husey (1925) examined the droppings at a *Macropterus* roost in Imperial Co., Calif, and was able to identify two species of grasshoppers, four species of moths, a cicada, harvest flies, beetles and one *Salix* leaf. Because some of these insects are diurnal it was suggested that they were picked off of leaves where the insects were at rest. The *Salix* leaf was probably picked up during the capture of an insect.

Vaughn (1959) found in the stomach contents of *Macropterus* a number of insects which are diurnal or do not fly. He listed orthopterans, noctuid moths and caterpillars, and scarabid and carabid beetles. He also found wings of sphinx moths, butterflies, and dragonflies. These data suggest strongly that the diet of *Macropterus* is limited to insects. However, Dobson (1878) indicated that the subspecies of *Macropterus* waterhousei in Jamaica ate such fruits as fustic berry (*Morus tinctoria*), bread fruit (*Fresnium alicastrum*), and the rose-apple (*Eugenia jambos*). Walker (1964) and Grasse (1955) also indicate that fruit is part of their diet. This suggests that the diet of *Macropterus* may not be as restricted as is indicated in the data above. An important factor may be the availability and abundance of suitable fruits.

*Artibes jamaicensis* is a strict fruit-eater although pollen or insects may be eaten accidentally. Goodwin and Greenhall (1961) listed 52 species of fruit eaten by *Artibes*. The fruit is either eaten on the tree or carried by mouth to a feeding roost or permanent roost which may be a cave, tunnel, or the heavy foliage of a shade tree. Goodwin and Greenhall (1961) reported catching four female *Artibes jamaicensis*, each with young, soaked with the yellow-green juice apparently from a mango. The manner of mastication was observed
in captive *Artibeus* by Walker (1964). The bats squeeze all but the softest fruit between their jaws to extract the juice and pulp and then expectorate the remains which bear the impressions of the teeth and palatal ridges. Starrett and de la Torre (1964) examined the stomach contents of *Artibeus* and found pulp and fibers. The esophagus of even the large *Artibeus lituratus* is small in diameter and thin-walled, an adaptation for a soft diet.

The diet of *Leptonycteris* consists of nectar, pollen, fruit, and insects (Walker, 1964). Insects and pollen may be swallowed accidentally because of their proximity to the nectar. These bats are known to visit the flowers of *Malvaviscus*, the fruit and flowers of *cactus*, and perhaps the flowers of *Datura*, the jimson weed.

Feeding is accomplished by a long extensible tongue. Nectar is lapped up from the base of the corolla. Sometimes *Leptonycteris* will lick out the juices and soft pulp from fruit (Wille, 1954). Canines may be used to tear the thin skin of cactus fruit in order to reach the juice.

*Desmodus* subsists entirely on blood. The bat will land on or near its prey and walk or climb onto it. Mann (1951) describes the locomotor adaptations as well as the feeding adaptations. These bats are surprisingly agile and can walk on an animal without eliciting a response from the victim. The site of the wound may be on the cheeks, neck, or bases of the ear of livestock or on the legs near and on the cloacal regions in chickens and turkeys (Dalquest, 1955). In addition Goodwin and Greenhall (1961) state that animals are bitten on the shoulders, flanks, at the base of the horns, tips of the ears, and around the anal region.
"Vampires bite with a swift outward thrust of the head, nip as the outward motion is completed, and quickly withdraw again. No attempt is ever made to hold or chew." (Dalquest, 1955). The wound is shallow and oval in shape. In general it is 3 to 4mm wide, 5 to 10mm long, and 1mm deep (Walker, 1964). The blood is lapped up according to some authors (Dalquest, 1955; Allen, 1939) or it is channeled in by the tongue. "The tongue is applied to the wound so as to form, with the deep groove in the lower lip, a tube through which the blood flows. This is accomplished by turning the lateral edges of the tongue downward which forms a concave lower surface" (Walker, 1964). Mann (1950, 1951) suggests that the movement of the tongue acts like a piston creating a suction which draws the blood back to the throat. Sublingual flaps on either side of the tongue run from the anterior edge of the frenulum along the lateral surface of the tongue and up to the dorsal surface to the throat. On the posterior region of the palate are two flaps which are oriented in such a way that it is possible for them to interlock with the lingual flaps thus forming a tube into the esophagus which would aid in directing the flow of blood.

The introduction of domestic animals to the New World made available an abundant and ready source of food for the vampires. They have apparently adjusted quite well to the new animals as is evidenced by the frequency of these bats where livestock is found. Their failure to successfully invade the temperate zone seems to be due to their inability to regulate body temperature. Lyman and Wimsatt (1966) showed that the vampires are evidently neither hibernators nor capable homeotherms; their temperature regulation is erratic. The only
time that it may be steady is during flight.
DISCUSSION

The adaptation of the masticatory apparatus and how it relates to various diets has been studied in many mammals (Schumacher, 1961; and others). It has been shown that these adaptations involved changes in the shape, size, and position of a basic set of muscles, the skull, and the dentition.

Studies of the developmental relationships of the neurocranium, splanchnocranium, brain, and masticatory musculature of mammals are summarized by Davis (1964). During the early development of the skull the braincase responds primarily to the growth of the brain. The facial region is genetically independent of the braincase. Cobb (1943) concluded from his studies that the development of the alveolar region of mammals is affected by tooth-size. As the masticatory musculature develops it becomes the major factor influencing the shape of the skull. The stresses originating from muscle-tooth and diet interactions may result in the development of supportive crests, ridges, increased ossification, and changes in the general architecture of the skull. Davis (1964) sums up the relationships as follows: "The mammalian skull...is a mosaic of independent morphogenetic units that are fitted into a functional unit partly by natural selection acting on their several time-tables of growth and differentiation, and partly by accommodation to extrinsic forces. The extent of the morphogenetic units may vary with time during ontogeny; the earlier in ontogeny a genetic effect is manifested, the more extensive its target is likely to be." There are two extrinsic factors which can be studied here, the dentition and masticatory musculature. It is
important to understand the relationship of these factors with the morphology of the skull in order to better interpret the evolutionary significance of the masticatory apparatus.

Dentition

The W-pattern molar is generally accepted as being the primitive in the Chiroptera and was derived from insectivore ancestors (Miller, 1907; Allen, 1940). It is the dominant form in fossil bats and is found in all extant families of bats except for the Pteropidae and Desmodontidae. The same pattern is found in fossil insectivores and in the extant families Talpidae and Soricidae. Unfortunately the chiropteran fossil record is scanty and the skeletons of forms that have been found are similar to modern day forms.

De la Torre (1961) challenged the primitiveness of the W-pattern in bats on the basis that in the mammalian fossil record the W-pattern is not the most primitive type in orders where it is found, e.g. the Insectivora. He points out the absence of intermediate forms in the chiropteran fossil record as opening up a possibility for the W-pattern being polyphyletic in bats. He states with regards to this pattern being the most primitive in bats, "As long as this view is held regarding the primitive dentition of bats, any deviation from this pattern must invariably be interpreted as a specialization. Yet, it must be granted that the Chiroptera has evolved from primitive Insectivora; it is also quite likely that it may have diverged from the main ancestral stock long before the W-pattern."

Two points should be considered, the occurrence and the versatility of the W-pattern. This pattern is found mostly in insectivorous
bats which make up the majority of bat species. The complex structure and interaction during mastication of this type of teeth, as was pointed out by de la Torre, is not primitive. It represents the most efficient type of tooth evolved for an insectivorous diet. However, its efficiency is not limited to a kind of food but to a wide range of foods, making this pattern a very stable one due to its versatility. The primitive Phyllostomines were probably insectivorous and, because of the functional advantage of the W-pattern, were able to evolve toward new diets. It seems probable that such a complex pattern originated once in the Insectivora and, because of its selective advantage, was retained by the Chiroptera. The frequency of occurrence of this pattern in the Chiroptera further attests to the stability of this character and its probable monophyletic origin.

**Macrotus** is the only one of the four bats included in this study that has the W-pattern, and, like most other bats, is insectivorous. Because of this, **Macrotus** is considered here to be the most primitive of the four species relative to the masticatory apparatus.

Both **Artibeus** and **Leptonycteris** possess the same basic cusps found in **Macrotus**, but the W-pattern has been lost due to the lateral displacement of the paracone and metacone and the loss of the styles. **Desmodus** lacks any evidence of cusps due to the great reduction undergone by the cheek teeth.

Two concepts have been significant in the development of modern theories on the evolution of eutherian teeth. In general the trend in the evolution of mammalian cheek teeth presented by Butler (1941) are based on, first, the field control concept; teeth are sequential organs in form and position during evolution, and
selection acts on the entire field rather than on individual teeth. In the evolution of modern eutherian dentition a gradient in the cheek tooth region was formed because of a reduction in number and variation in the size of the occlusal surfaces of the teeth with certain molars becoming the predominant teeth correlated with the increase in the functional significance of those teeth. This resulted in a gradient in which the predominant region may lie relatively anterior or posterior in the field depending on the position of the major functional region.

The second concept is embodied in the differential growth theory (Huxley, 1932) which states that various structures may grow at different rates relative to that of the organism.

Considering the primitive number of eutherian teeth to have been 44, (3/3I; 1/1C; 4/4P; 3/3M) the dentition of the four species of bats in this study has undergone a modification in size and form and a loss in number. In *Macrotus* (2/2I; 1/1C; 2/3P; 3/3M = 34) loss of teeth has been greatest in the premolar region, the primitive number of molars was retained. The dental gradient is greatest in the posterior portion of the molar region.

In *Artibeus* (2/2I; 1/1C; 2/2P; 2/3 or 2M = 30 or 28) loss of teeth has occurred in both premolars and molars accompanied by an increase in size of these teeth remaining and a broadening and shortening of the rostrum. As a result the gradient has been relatively shortened and shifted posteriorly. Although it is more gradual than in *Macrotus*. This difference between the gradients of the two genera corresponds to an integration of structure and
function in *Artibeus* on the one hand and division of structure and function in *Macropterus* on the other.

In *Leptonycteris* (2/2I; 1/1C; 2/1P; 2/2M = 30) there has been marked reduction of the entire cheek tooth gradient, with a loss of teeth similar to that found in *Artibeus*. The premolars and molars form an even gradient with no shift in either direction. The incisors have become reduced not only in number but in size, probably in response to the greater significance of the action of the tongue which has replaced mastication as the major feeding mechanism.

In *Desmodus* (1/2I; 1/1C; 1/1P; 1/2M = 20) the reduction and loss of cheek teeth has been extensive due to a major shift in functional significance to the canine-incisor group. There is no shift in the gradient, if it can be called a gradient, and the cheek teeth have been crowded by the anterior lengthening of the coronoid process.

**Functional Classification of Skulls**

Tucker (1954) has classified the stresses on the skull due to mastication as either circumscribed or dispersed. Circumscribed stresses are relatively strong forces limited to a small area. The magnitude of the stress depends on the limited area acted upon. Dispersed stresses are those that occur along two elongate surfaces coming together, simultaneously dispersing the force equally along a line. In those cases where dispersed stresses dominate, the skull will respond by increasing support along the major lines of stress forming a straight primary cranial arch. Areas of circumscribed stress occur at the articulation (secondary stresses) and at the major functional teeth (tertiary stresses) e.g. incisors in rodents.
or carnassials in carnivores. In cases where circumscribed stresses predominate, the primary cranial arch will be curved.

Tucker (1954) has classified functional skull types into three major groups based on the primary cranial arch: the planoarcuate, breviarcuate, and the longoarcuate. In the planoarcuate skull which is considered to be the most primitive type, the primary cranial arch runs from the glenoid fossa to the premaxilla, not forming an arch at all but a straight line, due to the predominance of dispersed stresses. This type of skull is found in artiodactyls and perissodactyls. The cheek teeth are usually the same size and shape and make up the major portion of the dental series. The masticatory musculature is usually reduced in the temporal region thus decreasing the pressure placed on the braincase. The limitation on the expansion of the braincase as a response to the growth of the brain and the effect of intrinsic factors is thereby decreased.

The second type is the breviarcuate skull which has well-developed carnassial teeth. In response to the pressure put on these teeth the anterior arm of the primary cranial arch arises from the well-developed anterior zygomatic process over the tooth and runs to the post-orbital process thus forming an anterior pre-orbital ridge, The heavy masseter results in a strong, dorsally arched zygomatic arch. The stresses produced by the large temporal muscles result in the continuation of the primary arch from the post-orbital process to the posterior zygomatic arch, thus completing a triangle. The stresses produced by the temporal muscles usually result in the formation of sagittal and lambdoidal crests.

The third type is the longoarcuate skull. Here the primary arch
runs from the glenoid fossa along the antero-ventral region of the braincase and along the curving dorsal portion of the rostrum, to the incisors. This is exemplified by the rodent skull in which the well-developed incisors perform a major function of the masticatory apparatus. As in the brevirocute skull the masticatory musculature is well-developed and exerts stresses on the braincase inhibiting further differentiation of the cranium. This results in a relatively conservative cranial form in the longirocute and brevirocute types as opposed to the greater variation in the planoracute type.

The planoracute skull is found in *Macrotus* (Fig. 18) The absence of heavy supporting ossifications (Fig. 45) a thin zygomatic arch and the light structure of the rostrum are characteristic of this type of skull. The dental series can be divided into two major functional groups: the canines and incisors which are used for catching and killing insects, and the molars, which grind up the prey. The W-pattern, by increasing the number of cutting edges, is very efficient in grinding chitin to fine bits. The function of the canines is added by the lengthening of the rostrum. This increases the speed of closure at the canine level, an adaptation found in carnivores (Davis, 1964). Because of the relatively weak force to kill and masticate insects, stresses during mastication tend to be dispersed. The closeness of the first premolars and their relatively large size suggest that they aid the canines in their function and thus, further disperse the stresses in the anterior region. The consistency of the items in the diet is reflected in the masticatory muscles which are reduced in size compared to those of *Artibius* but maintain the same relationships to
Fig. 19, Lateral views of the cranium showing primary lines of stresses during locomotion in: (a) Leptonotycteris sarah-burd, (b) Necroplus waterhousei, (c) Artibeus jamacensis, and (d) Desmodus rotundus.
each other, unlike those of *Leptonycteris*. The fact that the temporalis does not reach the crest of the skull as it does in the adults suggests that this muscle is not as important in subadults and that it is relatively weak compared to that of *Artibeus*.

In *Artibeus* there would appear to be a contradiction of Tucker's classification. The continuous row of molars would appear to place this bat's cranium in the planoarcuate type, but the skull exhibits a distinct breviarcuate primary arch. The teeth represent a specialization for the mashing of fruit, an action which requires greater force than that required for the functioning of the W-pattern. Corresponding to the molar pattern is a widening of the palate and a shortening of the rostrum. The former is in response to the increase in the size of the molars, and the latter is an adaptation for centering the force applied at the occlusal plane. The closer the molars are to the point of articulation, the greater is the force applied, thus bringing greater force to bear on a relatively large flat surface. Functionally, the entire maxillary tooth row exhibits a gradient of lingual mashing surfaces, becoming smaller anteriorly, and labial cutting surfaces, becoming smaller posteriorly. This functional unity has been emphasized by the widening of the palate and the shortening of the rostrum. The large canines are adapted for carrying and tearing open fruit.

The skull of *Leptonycteris* is unquestionably planoarcuate. The elongation of the rostrum correlates with the elongation of the tongue. The weak construction of the alveolar regions indicate the absence of strong forces acting on the dentition during mastication. Major areas of ossification developed on the anterior region of the
braincase and around the base of the rostrum thus apparently acting as support for the long rostrum.

Desmodus has a longoarcuate skull. The enlarged incisors are at the end of an arch formed by the dorsal surface of the rostrum. The area of the canines and incisors is heavily ossified.

Upon examination of the four species of bats various degrees of ossification were noted in the braincase, as were described earlier (Figs. 4, 5). Harrison (1949) showed that these areas consisted of thick porous bone containing many blood vessels. He suggested that these areas may be related to pressures which occur during flight. The effects of deceleration are probably quite severe during the fast, erratic flight of certain bats and as the nervous system may not be able to react fast enough to compensate by altering the blood pressure, compensation is made by expansion of the cranial vault when intracranial pressures are raised. He listed Macrotus and Desmodus among the fast, erratic flyers and Artibeus as closer to bats which are slower, more even flyers. My observations of the skulls of Macrotus and Desmodus indicate that Macrotus has relatively less heavily ossified areas and a thin cranium, corresponding to Harrison's classification. Desmodus, on the other hand, shows extensive patterns of bone density which become greater in older bats. It is more reasonable to explain this as a function of the temporal muscle which is involved with greater stresses than in Macrotus and thus can be expected to be more of a limiting factor in expansion of the skull. The areas of dense bone can best be interpreted as a response by the skull to the stresses set up by the m. temporalis during mastication. The lack of a wide-spread pattern of dense
in Artibeus is due to two factors. First, bone is thicker in general and second, there is the development of the sagittal and lambdoidal crests which increase the area for muscle attachment and the depth of the skull, and allow for longer fibers resulting in greater strength.

The pattern of dense bone in Leptonycteris would seem to function as support for the elongate rostrum. It may also relate to stresses set up by the temporal muscles, even though they tend to be reduced.

Masticatory Efficiency

The mandible acts as a third class lever in that the force, produced by the masticatory musculature, applied in closing the jaw lies between the fulcrum (the articular process) and the point of resistance (the dentition). The mechanical efficiency of the mandibular lever is an adaptation of the masticatory apparatus. In the Chiroptera, as in other mammals, the coronoid process may extend higher than the articular process (Macrotus, Artibeus), only slightly above the articular process (Leptonycteris) or may be on a level parallel to or below the articular process (Desmodus). The coronoid process acts as an extension of the lever arm at whose end the major force of the temporalis (Fig. 19, Table 2) is applied. Ostrow (1966) points out that the mandible functions primarily in the transmission of force, generated by contraction of the m. temporalis, to the site of dental occlusion, as efficiently as possible without interfering with other capacities. Relative efficiency can be determined by calculating the moment arm or torque of the vertical ramus. The moment arm is defined as the perpendicular distance between the line of
the applied force (the \textit{m. temporalis}) and the fulcrum (the glenoid fossa). Thus, the force applied anywhere along the dentition is a function of the moment arm as well as the magnitude of the applied force. This is expressed in the formula

\[ m = \sin (\theta - \delta) d \]

Where \( m \) is the length of the moment arm of the applied force, \( \theta \) is the angle between the applied force and the lever axis, and \( \delta \) is the angle between the diagonal distance, \( d \), from the top of the coronoid process to the center of the articular process and the lever axis (see Fig. 19). The moment arm gives comparisons of the magnitude involved in the lever, but for a more realistic comparison the percent of the moment relative to the length of the mandible is used. This eliminates much of the discrepancy due to differences in absolute size and gives a better quantification of efficiency.

Estimation of the direction of the force of the \textit{m. temporalis} introduces a possible error because the temporalis fibers radiate from the coronoid process and contraction is probably variable in magnitude relative to the position of the mandible. Also, this formula does not consider friction and assumes that the \textit{m. temporalis} is the only muscle involved. It signifies the efficiency of the skeletal elements and the direction of the major force being applied.

Using the above formula to consider mechanical efficiency (Table 2) \textit{Artibeus} is found to be relatively more efficient than \textit{Macrotus}, with both having the same basic apparatus. The greater efficiency in \textit{Artibeus} can be correlated with the relatively greater force required for mashing fruit. The efficiency of the W-pattern
Fig. 19: a) Measurements taken for determining the mandibular efficiency. \( A \) is the distance from the top of the coronoid process to the axis of the mandible, \( B \) is the distance from the center of articulation to the line of the principal axis, \( C \) is the distance from the center of articulation to a line perpendicular to the axis of the mandible, \( D \) is the distance from the center of articulation to the center of the occlusal surface of the last molar, \( E \) is the distance from the line of articulation to the line of forces, \( F \) is the projection of the line of forces on the vertical plane, \( G \) is the distance from the center of the occlusal surface of the last molar to the line of articulation, \( H \) is the angle between the posterior line and the line of articulation, \( I \) is the angle formed by the line of forces and the line of articulation, and \( J \) is the distance from the center of the occlusal surface of the last molar to the posterior line.
Table 2. Measurements of the mandibular lever used in determining the mechanical efficiency of the mandible. An explanation of the symbols are found in the text (p.) and in Figure 19.

<table>
<thead>
<tr>
<th></th>
<th>Macrotus</th>
<th>Artibeus</th>
<th>Leptonycteris</th>
<th>Desmodus</th>
</tr>
</thead>
<tbody>
<tr>
<td>h(mm)</td>
<td>4.0</td>
<td>7.0</td>
<td>2.0</td>
<td>0.5</td>
</tr>
<tr>
<td>a(mm)</td>
<td>5.0</td>
<td>9.0</td>
<td>7.5</td>
<td>9.0</td>
</tr>
<tr>
<td>d(mm)</td>
<td>6.5</td>
<td>11.5</td>
<td>7.5</td>
<td>9.0</td>
</tr>
<tr>
<td>θ</td>
<td>35°</td>
<td>38°</td>
<td>35°</td>
<td>50°</td>
</tr>
<tr>
<td>δ</td>
<td>38°</td>
<td>38°</td>
<td>15°</td>
<td>5°</td>
</tr>
<tr>
<td>(θ+δ)</td>
<td>73°</td>
<td>76°</td>
<td>50°</td>
<td>53°</td>
</tr>
<tr>
<td>sin(θ+δ)</td>
<td>0.9563</td>
<td>0.9703</td>
<td>0.7660</td>
<td>0.7986</td>
</tr>
<tr>
<td>m</td>
<td>6.22</td>
<td>11.2</td>
<td>5.74</td>
<td>7.2</td>
</tr>
<tr>
<td>%m(l)</td>
<td>44.0</td>
<td>53.1</td>
<td>31.9</td>
<td>51.3</td>
</tr>
<tr>
<td>l</td>
<td>14.9</td>
<td>19.1</td>
<td>17.9</td>
<td>14.9</td>
</tr>
</tbody>
</table>
molars in *Macroctus* compensates for the difference in mechanical efficiency. The masticatory efficiency of *Desmodus* is relatively high. This bat has compensated for the low coronoid process, which decreases efficiency, by increasing the angle of the temporalis to the axis of the occlusal plane thus applying the closing force more directly to the horizontal ramus.

In *Leptonycteris* masticatory efficiency is low and can be attributed to the decrease in the selective value of the lever mechanism because of the increase in the role of the tongue. It must be kept in mind that efficiency, as used here, refers only to a third class lever and does not consider the efficiency of other systems that may exist with these structures.

**Lateral Jaw Motion**

The possibility of lateral movement of the jaw is indicated in *Artibenes* and *Macroctus* by the open, lateral end of the glenoid fossa (Fig. 6) and the cylindrical articular processes. The canines are limiting only when near complete occlusion. The zygomatico-mandibular and pterygoid muscles are roughly equal in weight. Contraction of the left zygomatico-mandibularis and the right pterygoideus muscles would result in the jaw moving to the left. Contraction of the opposite set of muscles pulls the jaw to the right. A further possible adaptation to grinding is the dorso-lateral slant of the articular processes which allow for lateral rocking motion. The surface area of the glenoid fossa also indicates that slight antero-posterior movement may occur.

*Desmodus* and *Leptonycteris* are limited in lateral jaw movement
compared to the other three species, in its antero-posterior movement and thus the jaw may not function as a class III lever. In contrast the upper surface of the glenoid fossa extends anteriorly well beyond the diameter of the articular process suggesting the probable forward movement of this process. Further, the surface of contact on the articular process is greatest on its posterior surface and the post glenoid ridge is not strongly developed. This suggests that, unlike the condition where the post-glenoid ridge is well-developed to support the force against it during mastication, significantly less force is applied at that point in Desmodus. The articular process, therefore, is experiencing its greatest pressure when in contact with the upper surface of the glenoid fossa and not when it is in its most posterior position.
Table 3. Measurements used to determine the displacement of the occlusal surface of the teeth relative to the structure of the mandible. An explanation of the symbols are found in the text and in Figure 19.

<table>
<thead>
<tr>
<th></th>
<th>Macrotus</th>
<th>Artibeus</th>
<th>Leptonycteris</th>
<th>Desmodus</th>
</tr>
</thead>
<tbody>
<tr>
<td>a(mm)</td>
<td>5.6</td>
<td>11.6</td>
<td>9.0</td>
<td>8.7</td>
</tr>
<tr>
<td>b(mm)</td>
<td>1.2</td>
<td>1.6</td>
<td>2.0</td>
<td>3.6</td>
</tr>
<tr>
<td>c(mm)</td>
<td>5.5</td>
<td>11.5</td>
<td>6.8</td>
<td>8.0</td>
</tr>
<tr>
<td>λ</td>
<td>12°</td>
<td>8°</td>
<td>13°</td>
<td>24°</td>
</tr>
<tr>
<td>α</td>
<td>45°</td>
<td>45°</td>
<td>45°</td>
<td>45°</td>
</tr>
<tr>
<td>(λ + α)</td>
<td>57°</td>
<td>53°</td>
<td>58°</td>
<td>69°</td>
</tr>
<tr>
<td>cos(λ + α)</td>
<td>0.5446</td>
<td>0.6018</td>
<td>0.5299</td>
<td>0.3584</td>
</tr>
<tr>
<td>cos λ</td>
<td>0.9781</td>
<td>0.9903</td>
<td>0.9744</td>
<td>0.9135</td>
</tr>
<tr>
<td>cos λ-(λ + α)</td>
<td>0.4335</td>
<td>0.3885</td>
<td>0.4445</td>
<td>0.5551</td>
</tr>
<tr>
<td>x(mm)</td>
<td>2.4</td>
<td>4.5</td>
<td>4.0</td>
<td>4.8</td>
</tr>
<tr>
<td>%(x/c)</td>
<td>43.6</td>
<td>39.1</td>
<td>45.44</td>
<td>60.0</td>
</tr>
</tbody>
</table>
Masticatory Musculature (Table 4, 5)

1. *M. temporalis*

The more efficient lever in *Macrotus* and *Artibeus* allows for relatively smaller muscles. The difference in efficiency between them can be attributed to the greater selective pressure for efficiency in the fruit-eating habit of *Artibeus*. *Macrotus* compensates for this by the efficiency of the w-pattern molars. The lower efficiency seen in *Leptonycteris* is due to the loss in importance of the apparatus for mastication. In this bat the *M. temporalis* has responded to the reduction of the masticatory function by the division of the superficial and deep parts into relatively independent units. The superficial muscle lies significantly anterior to the deep muscle and applies lifting force directly to the horizontal ramus whereas the deep temporal muscle applies force at the tip of the coronoid process. These muscles probably function only in closing the jaw or in maintaining it partially open during feeding and probably are not concerned with the application of force for mastication. *Desmodus* has high mechanical efficiency, but a significantly large temporalis in contradiction to the condition in *Macrotus* and *Artibeus*. Upon closer examination it is found that the apparatus does not function as in the *Macrotus* type but appears to be a different system, a specialization to a sanguinivorous diet. It must be kept in mind that "efficiency" as used here refers to a third class lever and does not consider other mechanisms. The mandible and muscles of *Macrotus*, *Artibeus*, and *Leptonycteris* represent the third class lever in structure and function. In *Desmodus* the mandible is structurally a third class lever but the function, as indicated
Table 4. Relative weights of the masticatory muscles and the mandible expressed as percentages. m-wt=mandible weight, mas.=masseter, zyg=zygomatocomandibularis, pteryg.=pterygoideus internus and externus, digas.=digastricus, and temp.=temporalis.

<table>
<thead>
<tr>
<th></th>
<th>Macrotus</th>
<th>Artibene</th>
<th>Leptonycteris</th>
<th>Desmodus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mandible weight (m-wt) in grams</td>
<td>0.069 (5)</td>
<td>0.345 (2)</td>
<td>0.049 (5)</td>
<td>0.103 (2)</td>
</tr>
<tr>
<td>Mas./m-wt</td>
<td>15.7</td>
<td>8.2</td>
<td>17.9</td>
<td>14.0</td>
</tr>
<tr>
<td>Zyg./m-wt</td>
<td>9.0</td>
<td>4.9</td>
<td>56.6</td>
<td>8.4</td>
</tr>
<tr>
<td>Mas.+zyg./m-wt</td>
<td>24.7</td>
<td>13.1</td>
<td>23.4</td>
<td>22.4</td>
</tr>
<tr>
<td>Temp./m-wt</td>
<td>74.0</td>
<td>73.6</td>
<td>116.0</td>
<td>139.0</td>
</tr>
<tr>
<td>Pteryg./m-wt</td>
<td>9.7</td>
<td>5.3</td>
<td>13.6</td>
<td>11.3</td>
</tr>
<tr>
<td>Digas./m-wt</td>
<td>10.5</td>
<td>7.3</td>
<td>17.5</td>
<td>14.9</td>
</tr>
</tbody>
</table>
Table 5. Dry weights, in grams, of masticatory musculature. The numbers represent the mean, range, and the sample size (in parenthesis). The last three rows are ratios.

<table>
<thead>
<tr>
<th>Musculature</th>
<th>Macrotus (adult)</th>
<th>Macrotus (subadult)</th>
<th>Artibeus</th>
<th>Leptonycteris</th>
<th>Desmodus</th>
</tr>
</thead>
<tbody>
<tr>
<td>M. temporalis</td>
<td>0.051 (4)</td>
<td>0.014 (4)</td>
<td>0.254 (7)</td>
<td>0.057 (8)</td>
<td>0.142 (8)</td>
</tr>
<tr>
<td></td>
<td>0.049-0.052</td>
<td>0.011-0.017</td>
<td>0.195-0.338</td>
<td>0.050-0.069</td>
<td>0.107-0.172</td>
</tr>
<tr>
<td>M. masseter</td>
<td>0.011 (4)</td>
<td>0.004 (4)</td>
<td>0.028 (7)</td>
<td>0.009 (7)</td>
<td>0.014 (8)</td>
</tr>
<tr>
<td></td>
<td>0.010-0.013</td>
<td>0.003-0.005</td>
<td>0.021-0.033</td>
<td>0.007-0.011</td>
<td>0.010-0.019</td>
</tr>
<tr>
<td>M. zygomatico-mandibularis</td>
<td>0.006 (4)</td>
<td>0.002 (4)</td>
<td>0.017 (7)</td>
<td>0.002 (6)</td>
<td>0.009 (8)</td>
</tr>
<tr>
<td></td>
<td>0.006-0.007</td>
<td>0.001-0.003</td>
<td>0.010-0.025</td>
<td>0.002-.003</td>
<td>0.006-0.012</td>
</tr>
<tr>
<td>M. Pterygoideus internus</td>
<td>0.005 (4)</td>
<td>0.003 (4)</td>
<td>0.015 (7)</td>
<td>0.005 (8)</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>0.004-0.007</td>
<td>0.002-0.003</td>
<td>0.010-0.020</td>
<td>0.004-0.006</td>
<td>--</td>
</tr>
<tr>
<td>M. Pterygoideus externus</td>
<td>0.002 (4)</td>
<td>0.001 (4)</td>
<td>0.003 (7)</td>
<td>0.002 (8)</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>0.001-0.005</td>
<td>0.001-0.001</td>
<td>0.002-0.004</td>
<td>0.001-0.002</td>
<td>--</td>
</tr>
<tr>
<td>M. digastricus</td>
<td>0.007 (4)</td>
<td>0.004 (4)</td>
<td>0.025 (7)</td>
<td>0.009 (8)</td>
<td>0.015 (8)</td>
</tr>
<tr>
<td></td>
<td>0.007-0.008</td>
<td>0.004-0.004</td>
<td>0.020-0.030</td>
<td>0.008-0.010</td>
<td>0.008-0.022</td>
</tr>
<tr>
<td>M. masseter/m.</td>
<td>1.74 (4)</td>
<td>1.84 (4)</td>
<td>1.62 (7)</td>
<td>3.14 (7)</td>
<td>1.67 (8)</td>
</tr>
<tr>
<td>zygomaticomandibularis</td>
<td>1.66-1.79</td>
<td>1.16-2.43</td>
<td>1.27-2.91</td>
<td>2.09-4.83</td>
<td>1.35-2.28</td>
</tr>
<tr>
<td>M. ptterygoideus internus/m.</td>
<td>3.40 (4)</td>
<td>3.20 (4)</td>
<td>4.56 (7)</td>
<td>3.03 (8)</td>
<td>--</td>
</tr>
<tr>
<td>ptery-gus externus</td>
<td>1.38-4.44</td>
<td>2.74-6.38</td>
<td>2.17-3.91</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>M. temporalis/mm.</td>
<td>3.02</td>
<td>2.18</td>
<td>5.60</td>
<td>4.95</td>
<td>6.21</td>
</tr>
<tr>
<td>masseter and</td>
<td>2.64-3.33</td>
<td>2.00-2.26</td>
<td>5.11-6.28</td>
<td>4.02-5.84</td>
<td>5.52-7.07</td>
</tr>
<tr>
<td>zygomaticomandibularis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
previously, does not conform.

2. Masseteric muscles

Here we find a strong correlation between the weight of the masseter and zygomaticomandibularis and the weight of the mandible. The action of this group of muscles on the mandible is to pull upward thus countering the weight of the mandible. The lifting function is further emphasized in that the two components of the masseteric muscles vary in ratio to each other but, as a whole, maintain a relatively constant ratio to the mandible. The lower ratios in *Artibius* for all muscles except the *M. temporalis* may be a consequence of the larger size of *Artibius* resulting in an increase in strength to some power greater than the square of each linear dimension. The strength of a muscle is increased in three ways; an increase in fiber number, lengthening of fibers, and an increase in cross-section of the muscle. All three occurred in *Artibius*, relative to *Macropterus*. However, an increase in length means a decrease in speed. The masseteric muscles contribute more to the speed in closing the jaws, whereas the temporalis contributes mainly to the force applied in crushing the material between the teeth. Power more than speed, is adaptively more important to *Artibius* with its frugivorous diet.

The masseter is twice the size of the *M. zygomaticomandibularis* in *Macropterus*, *Artibius*, and *Desmodus* but three times the size in *Leptonycteris*. This variation in size may be due to the greater reduction of *zygomaticomandibularis* muscle in relation to the change in diet. The zygomatic arch is well developed in *Macropterus*, *Artibius*,
and Desmodus, but is reduced in *Leptonycteris*. The zygomatico-
mandibularis inserts along most of the medial surface of the arch
and the decrease in its size correlates with the decrease in size
of the zygomaticomandibularis. This can be attributed to the
mechanical inhibition of lateral movement of the mandible. A
further peculiarity of *Leptonycteris* is the small angle of the
masseter relative to the axis of the cranium. This can be attributed
to the need to counteract the action of the tongue which
travels parallel to the axis of the skull. The masseter has become
relatively longer due to the lengthening of the coronoid. This
eelongation tends to increase the strength at the expense of speed
of the masseter muscles. In *Leptonycteris* the temporal muscles
conform more to the masseters, relative to the situation in the
other three species, in speed and strength. The primary function
probably is to maintain the position of the jaw and counteract the
action of the tongue with the aid of the pterygoids. The absence
of strong stresses arising due to mastication are, at least in
part, responsible for the relatively light construction of the
mandible.

3. *Pterygoid muscles*

In relation to mandibular weight the pterygoid muscles appear
to be stronger in *Leptonycteris* probably as a compensation for the
reduced zygomaticomandibularis. They probably function primarily
in supporting the mandible.

Interaction of the pterygoid and zygomaticomandibular muscles
result in lateral movement as suggested by their almost equal weights
and opposing positions as seen in *Macrotus* and *Artibeus*. 
4. *M. digastricus*

The variation in the ratio of this muscle to that of the mandible suggests that there is no relation to mandible weight. The values for the ratio correlate with those of the *m. temporalis*, which fact suggests that the digastric and the temporal muscles work in opposition to each other in controlling the opening and closing of the jaws.

**Biting Mechanism in Desmodus**

From what has been stated above, the masticatory apparatus in all the Desmodus function basically in the same manner. Lateral motion of the mandible is accomplished to some degree in *Artibeus* and *Macrotus* whereas *Leptonycteris* and *Desmodus* are limited to movement along a dorso-ventral plane. The well-developed post-glenoid ridges aid in limiting the jaw to scissor-like motions in *Leptonycteris*. In *Desmodus* the large canines and the lateral border of the glenoid fossa limit lateral motion, yet the pterygoids and the zygomaticomandibularis are well developed. Also, the surface of the glenoid fossa slants about 45° antero-dorally extending for about twice the distance of the width of the articular process. The only observed function of the masticatory apparatus of *Desmodus* has been in making a quick, precise bite in order to remove a piece of skin without disturbing the host, yet deep enough to cause blood to flow. Using the information gathered the following hypothesis for the mechanisms of the bite of the vampire bat is presented.

Walker (1964) states that the wound made is 5 to 10mm long which would require the mouth of *Desmodus* to be open at the not unreasonable angle of about 30°. The depth of the wound varies from 1 to 5mm, the
width is 3 to 4 mm. This width is greater than the lmm between the tips of the upper incisors.

The posteriorly flattened articular process and the well-developed pterygoid and masseter muscles would interact in moving the articular forward in the fossa as the jaw is opened. This has the effect of moving the lower incisors forward, relative to the skull and slanting the ends of the incisors toward the target. The incisors act as hooks, aided by their deeply bifid ends, when contact is made with the integument of the host. Contraction of the temporalis and zygomaticomandibularis pulls the jaw closed dorso-posteriorly. During this time the lower incisors pull upward causing the skin of the victim to fold out toward the mouth of the bat.

With the closing of the jaws the upper incisors cut through, whereas the lateral edges of these teeth enlarge the wound by slicing off adjacent tissue. As the jaw slides back to its initial position, the canines occlude, thus limiting posterior movement of the jaw and directing the action of the upper incisors. The peculiar action of the articulation results in the incisors performing a scooping motion.

This hypothesis requires further studies with living specimens both in the laboratory and in the field. It is important to remember that in considering the action of muscles, contraction may not occur throughout the entire bundle but may vary with time and position of the mandible. Thus, in attempting to describe the function of a system, the differential nature of muscle action as well as the significance of skull and tooth structure and function should be considered.
Evolution of the Masticatory Apparatus

The majority of chiropteran species are found in the tropical areas where an abundance of food presumably exists year around and the physical environment is significantly less of a limiting factor than are biotic factors, a situation which is reversed in the temperate zone. The abundance of niches offers the opportunity for extensive adaptive radiation resulting in the relatively high degree of variation of fauna found in the tropics today (Dobzhansky, 1950; Klopfer, 1962). The analysis of the feeding habits and functional morphology of the masticatory apparatus suggests possible relationships in the evolution of Artibeus, Leptonycteris, and Desmodus to the Phyllostominae represented here by Macrotrix.

The masticatory apparatus in Macrotrix represents the primitive chiropteran condition; the canines are well developed for catching insects; the jaw functions as a third class lever and with the structure of the coronoid process, produces a relatively high degree of efficiency during mastication. The efficiency of the W-pattern tooth compensates for the need for large, powerful temporal muscles. As a consequence the masticatory musculature does not greatly inhibit the evolutionary plasticity of the cranium. This condition (the planarcurate skull) can lead to greater diversification along several lines. In relation to the W-pattern, specialization of diet has occurred with little change in the pattern, as demonstrated in Phyllostomus hastatus, an omnivorous bat, Phyllostomus discolor, a frugivorous bat, and Noctilio leporinus, a piscivorous
bat. On the other hand, as with *Artibeus*, *Leptonycteris*, and 
*Pomppus*, specialization in diet has led to modifications in the 
molar pattern.

*Artibeus* probably evolved from an insectivorous bat which 
captured insects found predominantly on fruit. Occasional pieces of 
fruit could have been eaten by accident in pursuit of an insect. 
From this situation evolution toward a diet of fruit pulp and juice 
ocurred. Among the adaptations of the teeth to this diet included 
a greatly reduced W-pattern, an increase in size of and a flattening 
of the molars. The canines have become larger, relative to the 
primitive condition, as an adaptation for tearing open large fruit 
and for carrying fruit while in flight. The trend was to apply the 
greatest amount of force over the whole cheek-tooth row as an 
adaptation to mashing fruit. This was accomplished by increasing 
the size, and thus the power, of the masticatory musculature. The 
shortening and broadening of the rostrum compressed the cheek-
tooth region and thus unified the forces directed to the dentition 
to a greater degree than found in *Hipposideros*. The relative increase 
in stress on the skull by the musculature resulted in the 
development of supportive ridges and the deposition of dense bone 
in the braincase and rostrum. As a consequence, a breviarqueate 
skull has developed, which is limited in further evolutionary mod-
difications as a consequence of the stress factors mentioned above. 
The effect of these forces are seen in the various species of 
*Artibeus* which exhibit the same general cranial structure and form 
a gradient in size from the smallest (*A. nanus*) to the largest 
(*A. lituratus*).
Leptonycteris may have evolved from a bat which fed on insects frequenting flowers. As a consequence of catching insects in the corolla of the flower, parts of the flower would have been eaten, and after a period of time, flowers became part of the diet. Development of an elongate rostrum probably evolved as an adaptation for reaching into the corolla of the flower. The tongue became the primary feeding mechanism and a consequence the masticatory apparatus has become reduced. The rostrum and dentition have been modified with the greater development of the tongue as the primary feeding mechanism. In general the cheek-teeth have become laterally compressed. They have been reduced and deflected laterally and are apparently limited to tearing the thin skin of fruit. The incisors have become reduced and in several members of the Glossophaginae the lower incisors have been lost (Cheironycteris, Amura, Lichonycteris). The mandible still functions as a class III lever, as it does in Macrotus and Artibeus, but it has become reduced in mechanical efficiency. The musculature has also become greatly reduced. The function of the temporal muscles is probably maintenance of the relatively light mandible at an open position in support of the tongue action. The structural limitations placed on lateral jaw movement have resulted in the reduction of the m. zygomaticomandibularis. This reduction in the musculature has decreased many of the stresses on the skull and, as a consequence, a primitive type of planoarcuate skull has evolved. Many of the glossophagines still include insects in their diet but, when considering the type of masticatory apparatus involved, probably only as a supplement to their main diet.

The feeding habits of Desmodus may have evolved as proto-
cooperation between the bat and individuals of some of the larger mammals. Proto-cooperation, (Allee, 1958) as used here, refers to the interrelations between organisms which are more beneficial than harmful for the individuals of the species involved. The vampire ancestor may have specialized in feeding on the ectoparasites of larger mammals and, by way of the blood-sucking parasites, incorporated blood into its diet. The ability to make a quick and precise bite would be advantageous for removing ectoparasites with a minimum of disturbance to the host. One of the most pronounced adaptations is the increase in the size of the upper middle incisors. Enlarged upper middle incisors are characteristic in most species of the Phyllostominae, e.g. Macrotus, Micronycteris, Tonatia, Trachops, and Phyllostomus. These teeth may be an adaptation for picking insects off of leaves while hovering, as was suggested for Macrotus earlier. Corresponding to the increased importance of the upper incisors in Desmodus, the canines lose their major function of piercing and tearing and now function as guides, controlling the distance between upper and lower incisors, resulting in greater precision during the bite. The direction of the force exerted by the masticatory apparatus toward the incisors is expressed as a longoarctuate skull, supporting major stresses at the incisors. The mechanism of the mandible, its articulation, and the masticatory musculature have diverged from the basic class III lever found in the primitive insectivorous bat. The new system involves a relatively complex series of actions in which the mandible has some freedom of forward movement. The well-developed masticatory muscles supply the power and speed required for this biting function.
SUMMARY

A comparative study was made of the structure and function of the masticatory apparatus in four Phyllostomateid bats, *Macropterus waterhousei californicus*, *Artibeus jamaicensis*, *Leptonycteris sborni*, and *Desmodus rotundus*. The masticatory myology, skull and dentition were described. Remarks concerning their action, diet and feeding habits were made.

All four bats differ in diet. The relation of this factor to the function of the masticatory apparatus was considered.

Of the four, *Macropterus* was considered to be the most primitive, exhibiting the W-pattern molar, planocarnate skull, and an insectivorous diet. The mechanics of the jaw and associated muscles were of a class III lever type, exhibiting a relatively high degree of efficiency, second only to *Artibeus*. *Artibeus* was shown to have a brevisarcuate type of skull, heavy masticatory musculature, and large teeth as adaptations for a frugivorous diet. The ratio of the weight of the *m. temporalis* to the weight of the mandible suggests that a general decrease in muscle size occurred corresponding to an increase in efficiency of the lever. This relation is also found in *Macropterus* and *Leptonycteris*. *Leptonycteris* is a specialized nectivorous bat. It has the more primitive form of planocarnate skull which is probably secondarily derived from an insectivorous planocarnate type. Adaptations include the reduced masticatory musculature, reduced pattern and size of teeth and an elongate skull. The weight of the *m. temporalis* is relatively large compared to the weight of the mandible, corresponding to the lower
efficiency of the lever.

Desmodus, a sanguinivorous bat, exhibits a distinct long-arculate skull, reduced cheek-teeth, loss of cusps, and an increase in size and modification in shape of the incisors and canines. The mechanical efficiency of the lever is high but, in contrast to Macrotus and Artibeus, Desmodus has a proportionately larger m. temporalis compared to the weight of the mandible. Consideration of the mechanics and architecture of the osteology, myology and known feeding habits suggests that a different mechanism is used by Desmodus. Possible pathways in the evolution of the various types of masticatory apparatus from an insectivorous type are discussed.
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