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The Dentition of Glossophagine Bats: Development, Morphological Characteristics, Variation, Pathology, and Evolution

By

Carleton J. Phillips

UNIVERSITY OF KANSAS
LAWRENCE 1971

September 24, 1971

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Development, Morphological Characteristics,
Variation, Pathology, and Evolution

By

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INTRODUCTION

Mammalogists, vertebrate paleontologists, and medical scientists long have been interested in mammalian dentition. To a great extent this interest has resulted from 1) an abundance of fossil remains consisting in many cases only of teeth and associated bone, 2) the realization that teeth are especially useful in mammalian taxonomy, and 3) the high incidence of oral and dental disease in man. Although the dentitions of many kinds of mammals have been studied intensively with regard to evolution, development, structural characteristics, variation, relationships to oral diseases, use as taxonomic characters, and as indicators of age, literally hundreds of problems relating to mammalian teeth remain to be solved and, perhaps more importantly, hundreds of questions remain to be asked. In the past few years, emphasis in dental research has been placed on interdisciplinary studies (for examples see Person, 1968, and Levy, 1966); accordingly, in the investigation reported here the major objective was to analyze, from the broadest base possible, the dentitions of all of the nominal genera of one subfamily of free-living mammals. Thus, I have tried to consider the dentitions of bats of 13 genera of the Neotropical subfamily Glossophaginae (Phyllostomatidae) from the point of view of a systematist as well as from that of a pathologist and an embryologist.

This study is an outgrowth of research on dentition of North American bats, begun in 1967 by J. Knox Jones, Jr. and me with financial aid from The University of Kansas General Research Fund. Three previous reports resulting from the project have been published (Phillips and Jones, 1969, 1970; Phillips *et al.*, 1969). Late in 1967 it became apparent that the so-called fruit- and nectar-feeding bats of the subfamily Glossophaginae were of special interest because of 1) the differential degree of modification of the dentition at the generic level; 2) an interesting amount of

variation in the morphological configurations of the teeth; 3) a relatively high incidence of dental abnormalities possibly having a genetic basis; and 4) the occurrence of several pathological conditions including a previously unstudied kind of periodontal disorder. All four of these matters are covered in varying detail in this report.

Chiropteran dentitions have not been studied in the same detail as in most other orders of mammals, although Slaughter (1970) recently has discussed the evolutionary trends in this group. This results mostly from the extremely incomplete nature of the fossil record (Romer, 1966:212-213; Jones and Genoways, 1970). The best available descriptions of the dentition of many of the recent microchiropteran genera are by Miller (1907), whereas Andersen's (1912) descriptions of the teeth of most of the Megachiroptera still are about the best available. Some authors more recently have given dental characteristics special attention in generic reviews (for example, Handley, 1959, and Davis, 1969). Variations and abnormalities in chiropteran teeth have been studied rarely or mentioned incidentally. Colyer (1936) wrote extensively on variations and diseases in the teeth of mammals but included no mention of the Chiroptera, although he studied the dentitions of representatives of nine orders. A few papers dealing specifically with abnormalities and variations in chiropteran dentition have been published (for example, Stager, 1943; Frum, 1946; Glass, 1953; Mumford, 1963; Phillips and Jones, 1969, 1970), but remarks on variation in teeth of bats often have been made in reports dealing with faunas (see Allen, 1922; Goodwin, 1942; Hershkovitz, 1949; Hoffmeister and Goodpaster, 1954; de la Torre, 1955; Baker, 1956; Phillips, 1968), and in taxonomic reviews (see Allen, 1916; Miller and Allen, 1928; Sanborn, 1932, 1933, 1937; Handley, 1959; Findley and Jones, 1967; Phillips, 1966;

Andersen, 1912). Included in the above citations are two of special interest here (HersHKovitz, 1949; Hoffmeister and Goodpaster, 1954) because dental variations in two glossophagine genera (*Glossophaga* and *Leptonycteris*) are discussed briefly.

The subfamily Glossophaginae is comprised of 13 nominal genera; one genus (*Monophyllus*) is endemic to the Antilles, three (*Choeronycteris*, *Musonycteris*, *Hylonycteris*) are known only from North America, two (*Scleronycteris*, *Platalina*) only from South America, and the remaining seven (*Glossophaga*, *Leptonycteris*, *Lonchophylla*, *Anoura*, *Choeroniscus*, *Lichonycteris*, and *Lionycteris*) from both North and South America and, in some cases, the Antilles as well. As a rule, glossophagine bats are of small or medium size and are delicate in build. The nose is noticeably elongate in all genera, although more dramatically so in some than in others. The overall reduction in dentition, elongation of the nose, and the presence of an extremely long, extensible tongue, are adaptations thought to indicate fruit- and nectar-feeding by the glossophagines, but some (*Glossophaga*, for example) are known to include insects and other meats in their diets. Park and Hall (1951) studied the gross anatomy of the tongues and stomachs of *Leptonycteris*, *Glossophaga*, and *Choeronycteris*, and Wille (1954) reported on muscular adaptations increasing the effectiveness of the tongue. John R. Winkelmann of Gettysburg College, currently is doing a comparative study of structure of the tongues of several kinds of glossophagines. The continuing interest in the specialized feeding habits of glossophagines is reflected in the histological and histochemical studies of Rouk (1968) and Forman (1971) on the stomachs of species of two genera (*Leptonycteris* and *Glossophaga*). Eisentraut (1950) discussed the dentition of the glossophagines in relation to feeding habits and nutrition.

Taxonomically, the glossophagines

are relatively poorly known. The species comprising several genera are in need of revisionary study or review. One genus (*Glossophaga*) is now being studied by J. Knox Jones, Jr. and James Dale Smith, whereas several other genera (*Choeroniscus*, *Monophyllus*, *Leptonycteris*, and *Hylonycteris*) have been studied recently (Handley, 1966a; Schwartz and Jones, 1967; Davis and Carter, 1962; Phillips and Jones, 1971). Two factors explain the inadequate documentation of the relationships of many glossophagines—lack of adequate series of specimens, and the apparently common occurrence of sibling species that can be distinguished only by extremely subtle differences. Nearly all aspects of the investigation reported here deal only with genera because glossophagine species are poorly defined in more than half of the genera and, furthermore, in the better known taxa the dental differences between species are minimal.

METHODS AND MATERIALS

More than 2400 specimens of bats of the subfamily Glossophaginae were examined. Some of the nominal glossophagine genera (*Glossophaga*, *Anoura*, and *Leptonycteris*) are fairly well represented in museum collections, but others (for example, *Musonycteris*, *Hylonycteris*, *Scleronycteris*, and *Platalina*) are rare, accounting for disparity in the completeness of the following generic accounts.

In the initial stage of this study, specimens of glossophagine bats deposited in several institutions were examined and data were recorded on a standardized form. Specimens having abnormal conditions, such as 1) instances in which teeth never were present in life as an apparent result of dental agenesis, 2) supernumerary teeth, and 3) pathological conditions evidenced by lesions and loss of dental tissue, were recorded and described on a separate form for ease of analysis. In this survey, only materials stored as dried museum skins

with skulls, skeletons, or skulls alone, were studied because specimens stored in alcohol are more difficult to handle; the mouths of such specimens frequently are closed tightly and cannot be opened without damage. The term "supernumerary teeth," as used herein, refers to extra permanent teeth that have resulted from one of three causes: 1) double initiation; 2) partial or complete dichotomy in the stage of morpho-differentiation; and 3) atavism. Extra premolars found between the upper canine and P3, were considered to be atavistic if they had but a single root, and if they clearly were not deciduous premolars that had been retained. Furthermore, these extra premolars are preceded by the deciduous P2 that normally is not replaced, at least in the genera that have been studied. These criteria eliminate both supernumerary teeth resulting from double initiation, because such teeth would be morphological duplicates of the P3, and supernumerary teeth resulting from partial or complete dichotomy, because such teeth are morphologically abnormal to the extent that they no longer resemble any normal coronal configuration (Fig. 1). Most kinds of dental abnormalities (supernumerary teeth, lesions resulting from acute diseases, and missing teeth) are easily recognized in skulls cleaned of flesh. Indeed, overall dental variation is more easily studied on cleaned skulls. Specimens missing one or more teeth do, however, present a problem that can be solved only through subjective selection. I was conservative in my determination of whether a tooth or teeth were congenitally lacking or instead had been lost in life—as a result of disease, structural deficiencies, or mechanical damage—as opposed to instances in which teeth had been lost in preparation or as a result of the collecting technique employed. Among specimens lacking teeth from other than the last two causes, teeth were considered to have been lost in life if their former presence was indicated by a modified alveolus or by root fragments. Because supporting bone is

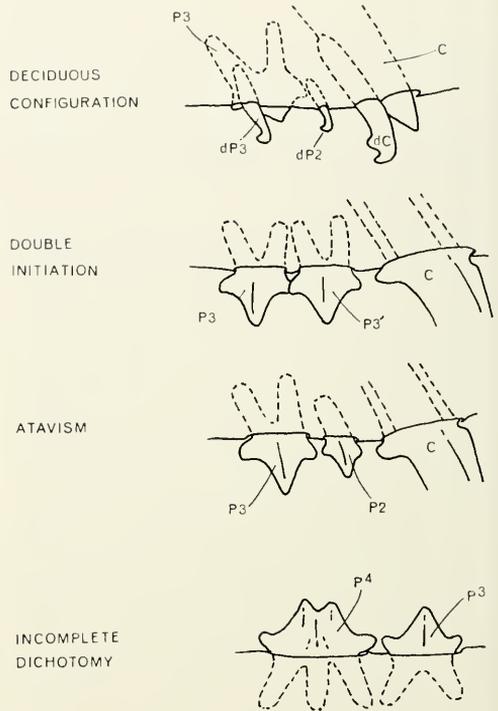


FIG. 1.—The apparently typical deciduous configuration in glossophagine genera lacking a permanent upper P2 is shown (top) along with examples of causes of supernumerary teeth.

relatively thin in the small-sized glossophagine bats, transillumination with a bright light source revealed whether a socket or root fragments were lacking. If lacking, the indication would be that a permanent tooth never had been present, probably as a result of dental agenesis. The recognition of agenesis is important because of the possible relationship of a high incidence to an evolutionary trend toward loss of a given tooth. Here again I was conservative and consequently it is more likely that the incidences of agenesis given in the generic accounts are lower, rather than higher, than the actual incidences in nature.

All of the specimens examined by me are deposited in the collections of the nine institutions listed below (an abbreviation used in reference to each institution is given in parentheses): The University of Kansas Museum of Natural History (KU); American Museum of

Natural History (AMNH); United States National Museum (USNM); Field Museum of Natural History (FMNH); Texas A&M University (TCWC); Los Angeles County Museum (LACM); Michigan State University (MSU); Escuela Nacional de Ciencias Biológicas (ENCB); Universidad Nacional Autónoma de México, Instituto de Biología (UNAM).

In most mammalogical literature, generic accounts are arranged according to the system used by Simpson (1945) or Hall and Kelson (1959) and referred to as "phylogenetic order." I have treated the genus having the most primitive dental characteristics (*Lonchophylla*) first, and have listed the others in order of increasing overall dental specialization. This arrangement differs from the two listed above, but facilitates an understanding of the relationships discussed in the last chapter.

Terminology and Dental Nomenclature

Detailed descriptions of characteristics of permanent teeth of the various genera and, for selected genera, the description of morphological and dimensional variation, will be difficult for the uninitiated to interpret without careful consideration of the following terms. Much of the dental nomenclature used herein is relatively new, having been proposed first by Van Valen (1966a: 7-9) and is a great improvement on the cumbersome, less complete nomenclature used in some earlier papers. Choate (1970) and Slaughter (1970) recently adopted Van Valen's terminology.

Two basic patterns of molar teeth are found in the Glossophaginae—the more primitive is the W-shaped ectoloph (*Glossophaga* and *Anoura*, for example), and the other is typified by the highly modified molars of *Choeronycteris* and several other genera in which the pattern has been lost completely. For reasons discussed elsewhere in this report, I conclude that the latter group of genera have lost the paracone from the upper molars and thus only a prominent

parastyle remains at the antero-labial margin of the teeth. This characteristic is given special attention here because earlier authors have referred to the parastyle as the "paracone" when discussing the dentition of several of the genera (Fig. 2). In upper molars characterized by a primitive or only slightly modified W-shaped ectoloph, it is convenient to write in terms of the anterior and posterior elements. These elements are triangular, or nearly so, and consist, respectively, of the parastyle-paracone-mesostyle and the mesostyle-metacone-metastyle. In text I often refer simply to "the anterior element of M1," or "both elements," and so forth. Consideration of the molars in terms of elements has an additional advantage in that it reflects in part the ontogeny of the teeth. The following terms, all of which apply to features that can be seen in occlusal views of the premolars and molars of glossophagine bats, are used herein:

- anterior cingular style*, small, anterior cusplet on upper premolars;
- main cone*, single, central cone of upper premolars;
- posterior cingular style*, small, posterior cusplet on upper premolars;
- postero-lingual cingulum*, ledge of varying size on last upper premolar in most genera;
- parastyle*, anterior-most cusplet of stylar shelf of upper molars;
- paracrista*, commissure connecting parastyle and paracone;
- paracone*, main cone of anterior element of the ectoloph;
- precentrocrista*, commissure connecting the paracone and the mesostyle;
- mesostyle*, cusplet at junction of anterior and posterior elements of the ectoloph;
- ectoflexus*, labial margin of tooth at mesostyle;
- postcentrocrista*, commissure connecting mesostyle and metacone;
- metacone*, main cone of posterior element of the ectoloph;

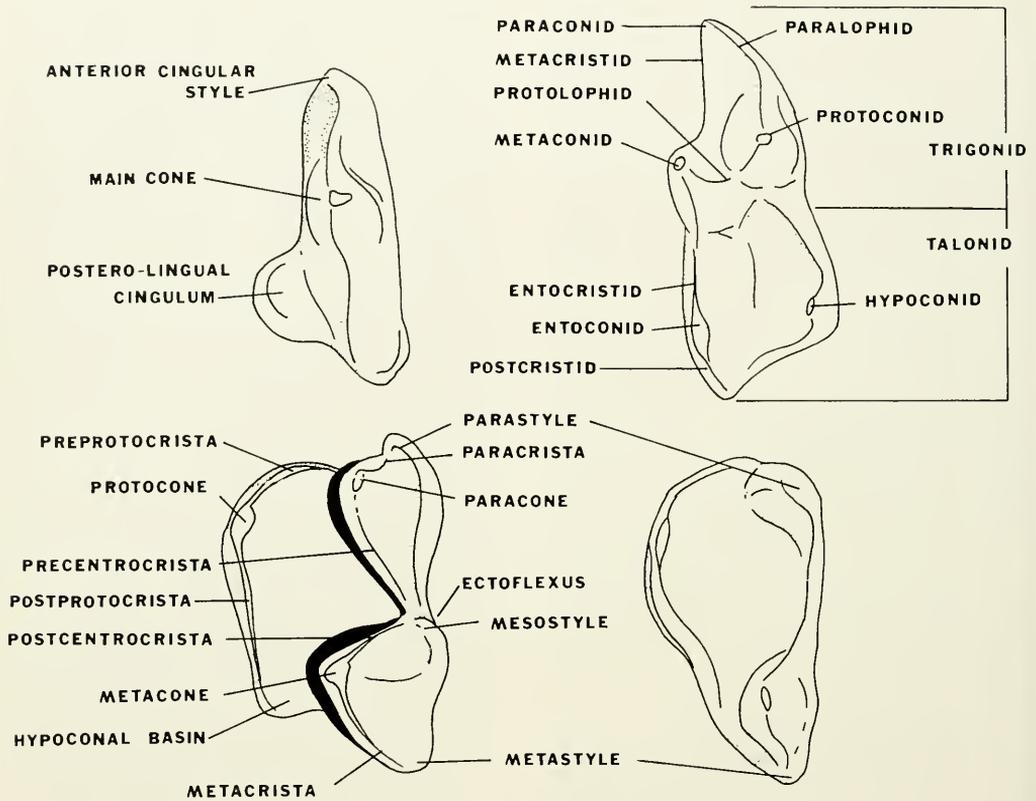


FIG. 2.—Dental nomenclature used in this paper; the third upper premolar (top left), first upper molar (bottom left), and first lower molar (top right) of *Anoura geoffroyi* are shown as examples representative of most of the glossophagine genera. The less complex first upper molar of *Choeronycteris mexicana* is shown for comparison (bottom right).

metacrista, commissure connecting the metacone and the metastyle;
metastyle, posterior-most styler cusp-let;
preprotocrista, antero-lingual margin between base of the paracone and the protocone;
protocone, generally indistinct cusp on antero-lingual margin;
postprotocrista, lingual margin posterior to the protocone;
hypoconal basin, shallow depression adjacent to the lingual base of the metacone;
paraconid, anterior-most projection of lower molars;
metacristid, ridge connecting the paraconid and the metaconid;
metaconid, main cone on lingual margin of base of the trigonid;

entocristid, ridge connecting the metaconid and the entoconid;
entoconid, low, ridge-like cusp on lingual margin of the talonid;
postcristid, ridge connecting the entoconid and the hypoconid;
hypoconid, small cusp on the postero-labial margin of the talonid;
protoconid, main cone on labial margin of base of the trigonid;
paralophid, ridge connecting the paraconid and the protoconid.

In addition to the above terminology used for morphological features of the premolars and molars, a series of directional terms also is used frequently in the text and these are defined as follows (mostly after Van Valen, 1966a:9):

anterior, toward the front of the

mouth (the term mesial often is used in dental research);

posterior, toward the rear of the mouth (the term distal often is used in dental research);

lingual, toward tongue;

labial, toward lips;

apical, away from the junction of the root and crown, in a vertical direction;

longitudinal axis, anterior-posterior center line of a tooth (occlusal view);

marginal, away from the longitudinal axis, in occlusal view.

Dental formulae are used sparingly in this report, and, when presented, simply are given as an abbreviated listing of teeth without phylogenetic implications. In the case of premolars, I occasionally have used a letter-number symbol (such as P4) to clarify the apparent phylogenetic status of a tooth. For example, the third upper premolar might be referred to as P4. There has been some disagreement regarding which of the upper incisors has been lost in the Microchiroptera. On this matter I agree with Handley (1959:100-103) and consider the I3 to be the missing tooth. Thus, the letter-number symbols for the upper incisors used occasionally herein do have phylogenetic implications. The upper case letters refer to upper teeth and the lower case letters to lower teeth, in accordance with conventional usage.

A moderate amount of medical and histological terminology is used in the chapters on deciduous teeth and pathology of the oral cavity. None of these terms is difficult, and all are standardized; a complete medical dictionary or a textbook on oral histology such as that edited by Sicher (1966) can be used for these terms.

Statistical Analysis and Measurements

The theory and methodology of the basic statistical procedures used in this investigation are given in Sokol and Rohlf (1969). Computations of coeffi-

icients of variation and the G-statistic were greatly facilitated through use of a set of statistical programs prepared by F. James Rohlf and the GE 635 computer system at the Computation Center of The University of Kansas. A two-way R x C test, using Yates Correction Factor, was used to test significance of discrete data, such as incidence of tooth loss and incidence of duplication. Correlation matrices based on 19 to 24 measurements of morphological features of the molars (depending on the genus) were prepared for analysis by using the NT-SYS (numerical taxonomy system of multivariate statistical programs) programs developed by F. James Rohlf, John Kispaguh, and Ronald Barteher of The University of Kansas for use with the GE 635 system. Raw measurements first were standardized by means of the "Stand" program and then a correlation matrix was prepared by the "Cordst" program, which computes matrices of the Pearson product moment correlation as well as distance coefficients. Measurements used in the analysis of variation in topographic features of the upper and lower molars and last upper premolar were taken by means of an ocular micrometer in a binocular dissecting microscope. Some of the individual measurements were easier to make than were others and thus there are unquestionably differences in accuracy; overall, however, the measurements were repeatable within reasonable limits. Specimens selected for measuring always were adults with unworn or only slightly worn teeth; individuals having greatly worn or damaged teeth were not included in the samples. All measurements were taken on the teeth of the right side of the jaws in order to avoid potential problems caused by asymmetry. Measurements taken on molars having a definite W-pattern, such as in *Glossophaga*, were different from those taken on the highly reduced molars of *Choeronycteris*. The measurements are defined below and illustrated in the generic accounts. Measurements taken on teeth of *Glosso-*

phaga, *Anoura*, *Leptonycteris*, and *Monophyllus* are listed below.

Last upper molar (M3 in all genera except *Leptonycteris*):

1. straight-line distance between the antero-labial tip of the parastyle and the lingual base of the paracone;
2. straight-line distance between labial edge of mesostyle and the anterior base of the paracone;
3. straight-line distance between mesostyle and parastyle, along labial margin of tooth;
4. straight-line distance between labial edge of mesostyle and postero-lingual base of metacone (least accurate measurement).

First and second upper molars (only M1 in *Leptonycteris*):

1. straight-line distance between the antero-labial tip of the parastyle and lingual base of the paracone;
2. straight-line distance between labial edge of mesostyle and anterior base of the paracone;
3. straight-line distance between mesostyle and parastyle, along labial margin of tooth;
4. straight-line distance between labial edge of mesostyle and postero-lingual base of metacone;
5. straight-line distance from anterior base of metacone to posterior tip of metastyle;
6. straight-line distance between metastyle and mesostyle.

Last upper premolar:

1. width across tooth at postero-lingual shelf.

All lower molars:

1. straight-line distance from anterior-most tip of paraconid to posterior base of metaconid;
2. width across tooth at bases of metaconid and protoconid;
3. straight-line distance between tip of paraconid and posterior base of protoconid;
4. straight-line distance from base of

metaconid to posterior tip of talonid, along the lingual margin.

The lower molars and last upper premolar of *Choeronycteris mexicana* were measured in the manner listed above but all of the upper molars, because of their reduced morphology, were measured as follows:

1. straight-line distance between posterior-most tip of posterior element (metastyle in M1 and M2) and anterior base of metacone;
2. straight-line distance between antero-labial base of metacone and anterior tip of parastyle;
3. straight-line distance across parastyle, from labial-most margin to base on lingual side;
4. width of molar, from labial-most margin of parastyle to lingual margin of preprotoecrista.

Histological Methods

Histological procedures were useful in the study of development of permanent teeth and the shedding of deciduous teeth and in the analysis of certain pathological conditions. Two excellent, detailed presentations of techniques for preparation of dental materials for histological study, which I used extensively, are those of Permar (1966) and Lillie (1965). The techniques selected are well known and widely accepted. All materials sectioned had been preserved in formalin and stored for more than one year in 70 per cent alcohol. After being selected for preparation, entire skulls and mandibles were carefully removed. The tissue was decalcified in five per cent nitric acid for 48 hours before being embedded in paraffin and piccolyte at 56.5° C. Sections were cut on a rotary microtome at 10 μ . The state of preservation of materials used was not always as good as it could have been if specimens originally had been preserved with histological studies in mind, but acquisition of fresh material to enable better histological preparation was difficult. It should be remembered when studying

the figures that the process of decalcification causes some distortion and, moreover, leaves a slightly expanded and empty space in place of enamel.

Two staining procedures were used. The first, Mallory triple, was used most frequently and with good success. This series of stains made the dentin and alveolar bone bright red and the non-mineralized connective tissue pale to deep blue. The keratinous outer layer of the oral epithelium stained orange and the remainder of the epithelium was stained deep blue or purple. Hematoxylin and eosin, which are useful general stains, also were used successfully but for my purposes were not as good as Mallory triple.

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with a drawing tube located in his laboratory. Linda Anne Phillips, my wife, prepared most of the figures used herein and helped me in many other ways throughout the course of the study.

DENTITION OF GLOSSOPHAGINE BATS

DECIDUOUS DENTITION

Few comparative studies of the morphology and ontogenesis of the deciduous dentition of bats have been conducted, and the moderately detailed descriptions that are available for a few species are widely scattered in the literature. Leche (1875, 1877, 1878), who apparently was the first to study seriously the primary dentition of bats, pointed out the potential utilization of deciduous dentition as a taxonomic characteristic in the Chiroptera. More recently, Friant (1963:100) has stated that the deciduous dentitions of the Chiroptera are comparable throughout the order.

The deciduous teeth of bats are highly specialized, strikingly different from permanent teeth, and are not functional in feeding. In most mammals the deciduous teeth are miniatures of the permanent teeth and are functional in the comminution of food material. Fossil bats are rare and shed little light on the course of evolution of chiropteran deciduous and permanent dentitions. In the only fossil bat with a deciduous tooth (the Eocene bat, *Archaeonycteris*), the deciduous premolar is an unspecialized copy of the permanent tooth (Revlod, 1917; Allen, 1939:169).

The evolutionary history of the deciduous teeth of bats is unknown, and trends in evolution of these teeth, as evidenced by Recent species, are unclear. Furthermore, published descriptions are inconsistent in detail and accuracy, and it is consequently difficult to derive much meaningful comparative information from them. According to Grassé (1955:1758), homodonty is the common pattern in chiropteran deciduous dentition, but Matthews (1950:13)

thought that deciduous teeth in the vespertilionid genus *Nyctalus* were an example of secondary heterodonty, and Dorst (1949:47) and Reeder (1953:2) were impressed by the variety of shapes in the deciduous teeth of *Pipistrellus* and *Myotis*, respectively. Generally, the deciduous teeth in bats seem modified for use as instruments for clinging to the female (Allen, 1939:169; Reeder, 1953:1; Friant, 1963:100; Slaughter, 1970), but in at least two genera (*Rhinolophus* and *Lavia*) all the deciduous teeth are resorbed before birth (Grassé, 1955:1758; Spillman, 1927; Dorst, 1953:84), and in others (*Mops*, a subgenus of *Tadarida*) at least some of the deciduous teeth are resorbed prenatally (Dorst, 1957a:135).

The deciduous dentitions of a few species representing three families of microchiropteran bats are reviewed in the following paragraphs. Whenever possible, I have restudied juvenile specimens of species discussed and have added my comments to those taken from publications of other authors. For descriptions of the deciduous teeth of a variety of Megachiroptera, see Miller (1907), Andersen (1912), and Friant (1951).

The first deciduous dentition to be described was of a widespread eastern European bat, *Vespertilio murinus* (Owen, 1845). The deciduous teeth in this bat total 22, a number typical of the Vespertilionidae and some other families as well. The lower deciduous incisors in *V. murinus*, like their permanent replacements, are trilobed, and although only one permanent upper premolar is found in this species, there are two deciduous upper premolars (Owen, 1845:432). The deciduous dentitions of several common North American genera

(*Myotis*, *Eptesicus*, and *Lasius*) were studied by Miller (1907). In both *Myotis* and *Eptesicus* the upper and lower deciduous incisors are trifold, thus resembling their permanent replacements (Miller, *loc. cit.*). In *Eptesicus*, which has only one permanent upper premolar, there are two deciduous premolars; the first is a small tooth that does not break the gingivum and, therefore, is nonfunctional, whereas the second, the predecessor of the permanent premolar, is somewhat larger and slightly premolariform (long and laterally compressed). Baker (1956:183), in describing the deciduous teeth of *Eptesicus fuscus pallidus* (based on six juveniles from Coahuila), stated that the deciduous dentition included "three incisors, one canine and three premolars" in each upper jaw but apparently he was mistaken because I find only two upper deciduous premolars and two upper deciduous incisors.

The chronological sequence of shedding and replacement of deciduous teeth in *Myotis lucifugus* was studied by Stegeman (1956). The rate of shedding was found to be variable; the lower incisors and upper and lower premolars were lost first and the canines and upper incisors last (Stegeman, *op. cit.*:60). All of the deciduous teeth in this species are retained for about 18 days postpartum; the outer upper deciduous incisors, which are the last deciduous teeth shed, are lost at approximately two months of age (Stegeman, *op. cit.*:61). The deciduous teeth of another species, *Myotis (Pisonyx) vivesi*, have been described in detail by Reeder (1953). The deciduous incisors in this species resemble slightly their permanent replacements, and the second upper and lower deciduous premolars are fairly complex, being somewhat premolariform.

As would be expected, the deciduous teeth of bats in the genus *Pipistrellus* have many of the characteristics of those in *Myotis* and *Eptesicus*. Two Old World species, *P. kuhli* and *P. nanus*, have trilobed deciduous incisors, but *P.*

kuhli differs from other vespertilionids studied to date in having a relatively unreduced, premolariform, first upper deciduous premolar that resembles the deciduous second upper premolar (Dorst, 1949:46). In another vespertilionid, *Nyctalus leisleri*, the upper canines differ from the other deciduous teeth in having greatly reduced lateral lobes (Matthews, 1950:13). Recent studies on an Asian vespertilionid, *Scotophilus*, have revealed that two upper trilobed deciduous incisors precede the single, simple, permanent upper incisor (Peterson, 1968:1081). This fact apparently has caused some taxonomic confusion in that the holotype of *S. kuhlii*, described as having two pairs of permanent upper incisors, is a juvenile with two deciduous pairs of incisors in place and a permanent pair essentially unerupted (Peterson, *loc. cit.*).

Several problems concerning the deciduous dentition of vespertilionids remain to be solved. In genera having three premolars (for example, *Myotis*), only two deciduous premolars have been found. Reeder (1953:2) thought that the first upper and lower permanent premolars in *Myotis vivesi* were those lacking deciduous precursors, and, judging from the illustration given by Stegeman (1956:59), such also is the case in *M. lucifugus*. Without histological studies it will not be known whether the missing deciduous premolars never form or are resorbed before birth.

The deciduous dentitions of a few species of the Molossidae have been studied. Harrison Allen (1895:35) reported simply that the deciduous teeth in *Molossus* are "of the same character . . . as in other bats." In *Tadarida brasiliensis* the deciduous upper incisors are relatively simple, terete teeth, whereas the lower incisors resemble their permanent replacements and, consequently, have flattened, bifid crowns (Miller, 1907:22). The deciduous canines in this species have an extra, small cusp on the anterior edge near the tip (Miller, *loc. cit.*). Although there are three perma-

nent lower incisors in *Tadarida*, Miller (1907:21) found only two lower deciduous incisors, one preceding the inner incisor and one preceding the second incisor. This may have been an artifact of the material available to Miller because Dorst (1957a:135) found three deciduous lower incisors in another species, *Tadarida (Mops) condylura* of Africa. In the latter species the upper deciduous incisors apparently are trilobed (Dorst, 1949:47 and 1957a:133), although the permanent incisors are not. The three lower deciduous incisors match, roughly, the degree of reduction of the permanent incisors in *T. condylura*; the inner deciduous incisor is largest and has a trilobed crown, the second is slightly smaller and bifid, and the third is a small, simple spicule (Dorst, 1957a:135). Possibly there is some geographic variation in the deciduous dentition of *Tadarida condylura*, because Dorst (1957a:134-135) reported that in specimens from the Congo the two upper deciduous premolars and one lower deciduous premolar did not penetrate the gingivum and were resorbed shortly after birth; therefore, the two upper deciduous incisors and canine and the three lower deciduous incisors were the only functional deciduous teeth. In a specimen of *T. condylura* from the southern part of Africa, Dorst (1949:48) found that the upper first premolar was a small spicule and the second was blade-like.

In comparison with that of vesperilionids and molossids, the deciduous dentition in the Phyllostomatidae generally is simpler, the teeth being reduced both in size and complexity. The overall simplicity of the deciduous teeth in phyllostomatids is in keeping with the comparatively reduced permanent dentition; only the Phyllostomatinae, among the subfamilies discussed here, have permanent teeth with complex coronal patterns.

The phyllostomatines are of interest because of the difference in shape of the

first deciduous incisors of the upper jaw in *Macrotus* in comparison with those of *Tonatia*, *Mimon*, *Chrotopterus*, and *Phyllostomus*. In *Phyllostomus* the second upper deciduous incisor is longer and more greatly curved than the inner, which is thin and tapers to a fine, recurved point at the tip (Miller, 1907:22). In *Mimon*, which I have studied, and in *Tonatia* (Dorst, 1957b:303) and *Chrotopterus* (Leche, 1878:10), the inner upper deciduous incisor resembles that in *Phyllostomus* in being smaller than the outer incisor and in having a fine, recurved point. In *Macrotus*, on the other hand, the first upper deciduous incisor is as large as the outer one and is forked, with the mesial lobe being somewhat larger than the lateral one (Nelson, 1966:143). Another interesting aspect of the deciduous teeth of *Macrotus* that was overlooked by Nelson (*loc. cit.*), is that the three lower incisors have only two permanent replacements. The first (inner) and second are trilobed, like their permanent replacements, whereas the third, which is shed but not replaced, is a small, simple spicule. *Carollia*, *Artibeus*, *Ametrida*, and *Desmodus* (the latter regarded herein as a phyllostomatid—see Forman *et al.*, 1968), are the remaining members of the family that have been studied. In *Carollia* the first upper deciduous incisors are thin and the apical ends come to a fine, recurved point (Leche, 1878:7-9), thus resembling the inner upper deciduous incisors in some of the Phyllostomatinae (see previous paragraph). In *Artibeus* and *Ametrida*, the first upper deciduous incisors are forked as in *Macrotus* (Leche, 1878:12-14; Miller, 1907:22). The deciduous teeth of vampire bats (*Desmodus*) are small and simplified; only two upper deciduous incisors, both of which are the same size and are simple hooked spicules, are functional (Miller, 1896). The remaining deciduous teeth are extremely small, barely penetrating the gingivum, and are resorbed shortly after birth.

Deciduous Teeth in the Glossophaginae

Because glossophagine bats having all or part of the normal deciduous dentition in place are not common in collections, the deciduous teeth of only three genera, *Glossophaga*, *Leptonycteris*, and *Choeronycteris*, are described in detail below. These genera, however, probably are representative of the Glossophaginae as a whole.

Glossophaga

Eight specimens of *Glossophaga soricina* with at least some of the deciduous teeth in place were available for study (KU 23664, 23668, 29613, 35214, 79433, 85618-9, 85629).

Bats of the genus *Glossophaga* have 22 deciduous teeth, two of which (the first upper premolars) are not followed by permanent replacements. The first and second upper deciduous incisors are situated immediately anterior to the alveoli of their developing permanent replacements. The inner upper deciduous incisors, which are slightly recurved, are tall, slender, and forked, with the mesial lobe being the largest (Fig. 3). The outer upper deciduous incisors are about the same size as the inner ones but differ, morphologically, in that they are recurved spicules with a small notch on the postero-lateral surface and are not forked. The upper deciduous canines are rooted at the postero-labial edge of the alveoli of the incoming permanent canines. The convex anterior surfaces of the crowns of the deciduous canines are pressed against the posterior surface of the crowns of the permanent replacements. The deciduous canines are relatively small, with the crowns being only slightly larger than those of the first upper deciduous incisors, and are strongly recurved (Fig. 3). The first upper deciduous premolars, which are tiny, slightly curved teeth that barely penetrate the gingivum (and therefore are non-functional), are rooted directly posterior to the deciduous canines and at the antero-labial edge of the alveoli of the

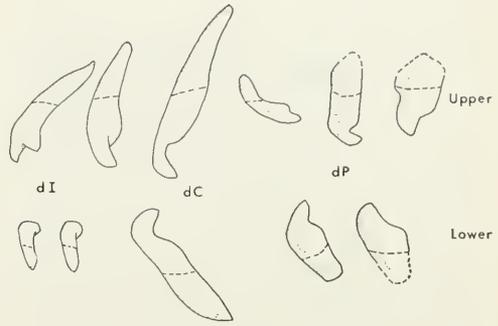


FIG. 3.—Labial view of individual deciduous teeth of *Glossophaga soricina*. The transverse dotted lines approximate the cervical region of each tooth and the dotted lines outlining the roots of some teeth were used when actual shape was unknown.

incoming first permanent premolars (P3). These deciduous premolars apparently represent the precursors of the permanent P2's, which no longer are present in *Glossophaga*. Consequently, the first deciduous premolars are shed and normally not replaced; exceptions are discussed in a later section. Leche (1878: 11-12) first noticed these deciduous premolars, which Thomas (1908:348) mistakenly thought had to be permanent premolars that were “. . . premature in development . . .,” rather than deciduous premolars. The second deciduous premolars, which are the precursors of the first permanent premolars (P3) are strongly recurved and slightly more than twice the size of the first deciduous premolars; they are rooted on the postero-labial edge of the alveoli of the first permanent premolars. The third upper deciduous premolars are high-crowned and somewhat blade-like, with a concave lingual surface (Fig. 3). They are located in the alveolar crest at the labial side of their incoming replacements.

The lower deciduous incisors are small spicules; the inner pair is slightly larger than the outer, but they are morphologically similar. The crowns of these teeth are expanded laterally and rounded apically (Fig. 3); in some individuals the crowns of the lower deciduous incisors have a faint apical groove that

causes them to appear bifid. The lower deciduous canines, which are located at the postero-labial edge of the alveolus of the incoming permanent canines, are recurved and closely resemble the upper deciduous canines. As in other glossophagines, deciduous precursors for the lower first premolars have not been found. If such deciduous teeth are formed at all, it is likely that they are resorbed before birth because of the advanced stage of eruption of the first premolar at time of parturition. The deciduous precursors of the second lower premolars are relatively broad and slightly hooked (Fig. 3); they are rooted directly above the site of development of their permanent replacements. The last lower deciduous premolars, the precursors of the third premolars (p4), are slightly blade-like and broad and are more nearly premolariform than are the other lower premolars.

The sequence of shedding, as determined from specimens listed above, is given in figure 10 and discussed in detail beyond.

Leptonycteris

Ten specimens of *Leptonycteris*—one of *L. nivalis* (KU 98390) and nine of *L. sanborni* (KU 95159-60, 95165-68, 95172-73, 99617)—having at least some deciduous teeth were available for study.

Bats of the genus *Leptonycteris* probably have 22 deciduous teeth, two of which (the first upper premolars) are not followed by permanent replacements. Figure 4 shows a labial view of each of the deciduous teeth; the upper deciduous incisors of *Leptonycteris* should be compared with those of *Glossophaga* and *Choeronycteris* in figures 3 and 5.

The inner upper deciduous incisors are greatly recurved and have notches on their lateral surfaces, making them forked as in *Glossophaga* (Figs. 3, 4). These teeth are located directly anterior to the alveoli of the developing inner permanent incisors. Without the great curvature shown in figure 4, the inner

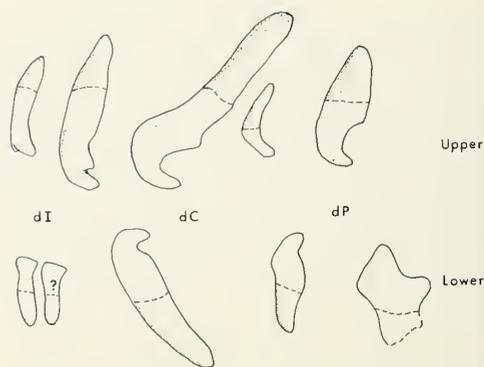


FIG. 4.—Labial view of individual deciduous teeth of *Leptonycteris nivalis*. The second lower deciduous incisor has not been seen but probably is much like the first deciduous incisor and thus has been drawn-in. The transverse dotted lines approximate the cervical region of each tooth and the dotted lines outlining the roots were used when the actual shape was unknown.

incisors probably would lack adequate surface for support from attachment of periodontal ligaments. The outer deciduous incisors are slightly compressed; the crown is curved posteriorly and has a notch below the apex (Fig. 4); these teeth are located directly anterior to the site of development of their permanent replacements. The upper deciduous canines, which are the largest of the deciduous teeth in *Leptonycteris*, are narrow (laterally compressed) and recurved, forming a posteriorly-facing hook. The deciduous canines are located posterior to the alveoli of the developing permanent canines and are, in fact, in contact with the crowns of the incoming canines. The first upper deciduous premolar is a small, peg-like tooth situated just posterior to the deciduous canines. These premolars, which are not replaced by permanent teeth, are rooted at the anterior lip of the alveolus of the first upper permanent premolar (P3). The second upper deciduous premolar is a narrow (laterally compressed), hooked tooth located at the labial edge of the alveolus of its permanent replacement. The second premolar essentially is a small replica of the upper deciduous ca-

nine (Fig. 4). The postulated third deciduous premolars have not been seen because they are lacking in the specimens available for study. This is not surprising because in related genera (*Glossophaga*, for example) this is the first deciduous premolar shed.

The inner lower deciduous incisors are small peg-like teeth located at the anterior lip of the alveolus of the inner permanent incisors. The outer deciduous incisors have not been seen; apparently they are shed early in life (see Fig. 10 and next section). The lower deciduous canines are smaller than the uppers but are narrow and hooked (Fig. 4); these deciduous teeth are rooted between the lower permanent canine and the first lower permanent premolar at the posterior lip of the alveolus of the canine. Only two lower deciduous premolars have been seen; probably the deciduous precursor of the first lower permanent premolar either is lost extremely early or is resorbed before birth. The deciduous precursor of the second lower permanent premolar has roots in the alveolar crest of the permanent tooth and is in contact with its antero-labial surface. This deciduous premolar is small, laterally compressed, and slightly hooked. The last lower deciduous premolar is nearly premolariform, consisting of a narrow cone with a small posterior heel. Like the precursor of the second lower premolar this tooth is rooted in the thin alveolar crest of its permanent replacement and is in contact with its antero-labial surface. The sequence of shedding, as determined from the specimens listed above, is given in figure 10 and discussed in the following section.

Choeronycteris

I examined 19 specimens of *Choeronycteris mexicana* in which at least some (but rarely all) of the deciduous teeth are present — AMNH 173664-65, KU 34548, 48234, 48236, 54944, 60177-78, 60180, 80149-50, 80170, 80782, 88274, 88276-7, 88279-80, 88282.

The total number of deciduous teeth

in *Choeronycteris mexicana* is 22, six of which (the first upper premolars and the lower incisors) are not replaced by permanent teeth.

The upper deciduous incisors are located directly anterior to the developing permanent incisors. The inner pair varies slightly in size and shape but generally these teeth are broad, ovoid in cross section, and have a roughly triangular, recurved crown. The outer incisors are simple, recurved pegs that are larger than the inner incisors and are round in cross section. The upper deciduous canines are large, hooked teeth, located at the posterior lip of the alveoli of the developing permanent canines; the deciduous precursors have a small notch on the posterior surface, about a third of the distance from the neck to the coronal apex. The first upper deciduous premolars are located slightly posterior to the deciduous canines at the anterior lip of the alveoli of the incoming first permanent premolars (P3). These deciduous teeth, which normally are not replaced by permanent teeth, are the smallest of the upper deciduous teeth and are no more than slightly recurved spicules that barely break through the gingivum and are nonfunctional. Stains and Baker (1954:438) mistakenly identified the first upper deciduous premolars as deciduous precursors of the first permanent premolars because specimens having all three upper deciduous premolars in place were unavailable to them. The second upper deciduous premolars, which are simple and slightly recurved teeth, are situated at the posterior lip of the alveoli of the developing first upper permanent premolars, which are their replacements. The third deciduous premolars, located at the medio-labial edge of the alveoli of the second upper permanent premolars (P4), are larger than the second deciduous premolars and are more premolariform, being narrow and blade-like (Fig. 5).

The lower deciduous incisors are tiny, slightly recurved spicules with rounded crowns; in *Choeronycteris* they

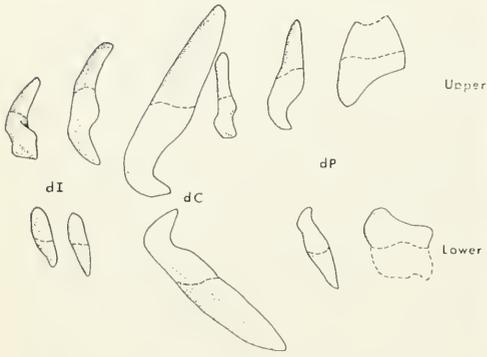


FIG. 5.—Labial view of individual deciduous teeth of *Choeronycteris mexicana*. The transverse dotted lines approximate the cervical region of each tooth and the dotted lines outlining the roots of some teeth were used when the actual shape was unknown.

are not followed by permanent teeth. One to four of these teeth, which only barely penetrate the gingivum (if at all) and undoubtedly are nonfunctional, persist in a majority of adults. The lower deciduous canines are slender, recurved to about the same extent as the upper deciduous canines (Fig. 5), and are located between the posterior surface of the incoming permanent canines and the anterior face of the permanent first premolars, which erupt relatively early (Fig. 6). Deciduous precursors of the first lower permanent premolars are unknown in *Choeronycteris*. If such deciduous teeth exist at all, they probably are resorbed prenatally. The first lower deciduous premolars are the deciduous precursors of the second lower permanent premolars (p3) and are small, slightly recurved spicules located directly above and slightly labial to the site where their permanent replacements will erupt. The second deciduous premolars, like the last upper deciduous premolars, are relatively long and blade-like and therefore somewhat premolariform (Fig. 5).

The sequence of shedding of the deciduous teeth in *Choeronycteris* is given in Figure 10 and discussed in detail in a section beyond.

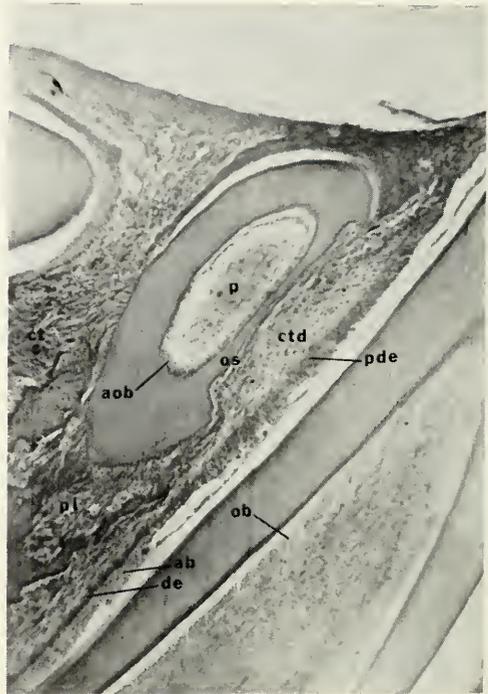


FIG. 6.—Longitudinal section through anterior portion of lower jaw (lateral aspect), showing prefuctional permanent canine on right, portion of root of deciduous canine in middle, and anterior tip of first permanent lower premolar on left. Note especially the area of altered connective tissue (ctd), and resorption of the deciduous tooth (os), and compare the odontoblasts of the permanent and deciduous canines (ob and aob). Other symbols, used here and in the following three figures, are: ct, connective tissue; p, pulp; pl, periodontal ligaments; ab, ameloblasts; de, dental epithelium; pde, proliferative mass of cells. Stained with Mallory triple.

Eruption of Permanent Teeth and Shedding of Deciduous Teeth

The term eruption often is used to mean "movement of permanent teeth into their adult position in the jaw." However, as has been pointed out by others (Weinmann, 1966:301, for example), movements of permanent teeth do not cease during the lifespan of the tooth and therefore all of the eruptive movements of the permanent teeth best are divided into three phases (after Weinmann, *loc. cit.*), as follows: 1) pre-eruptive phase during which the dental

organ completes development and enamel and dentin are formed; 2) prefunctional eruptive phase during which the root(s) forms and the new tooth moves to the occlusal plane; and 3) the functional eruptive phase, which begins after the tooth reaches the occlusal plane. These terms will be used, as defined here, in the following accounts.

Permanent teeth in the prefunctional eruptive phase and partially resorbed deciduous teeth in *Choeronycteris* are shown in figure 6. As the permanent teeth develop and move toward the gingivum, desmolytic action of the cells of the dental epithelium apparently causes the adjacent tissue to break down (Weinmann, 1966:303). Degradation of connective tissue between a developing permanent tooth and a deciduous tooth can be seen in figures 6 and 7; in the first, the most obvious area of alteration (ctd) is between the enamel epithelium along the posterior surface of the prefunctional lower permanent canine and the anterior surface of the root of the deciduous canine. Following maturation of the enamel, the ameloblasts become flattened and the basal cells of the enamel epithelium show great mitotic activity that results in a proliferative zone. When the occlusal tip of the crown breaks into the oral cavity, the proliferating epithelium of the erupting tooth fuses with that of the oral epithelium (Löe, 1967:416). Interestingly enough, the thick, irregularly shaped proliferative mass of cells below the outer layer of the enamel epithelium of the developing permanent teeth in *Choeronycteris* always was associated with areas of dissolution of connective tissue and of resorption of deciduous teeth. For example, in figure 6 the proliferative layer, which appears as a thickening of the enamel epithelium (pde), can be seen adjacent to the site of alteration of connective tissue and destruction of the deciduous lower canine. The enamel at this site was mature and thus columnar ameloblastic cells were lacking. In figures 7 and 8, an irregular proliferative mass of

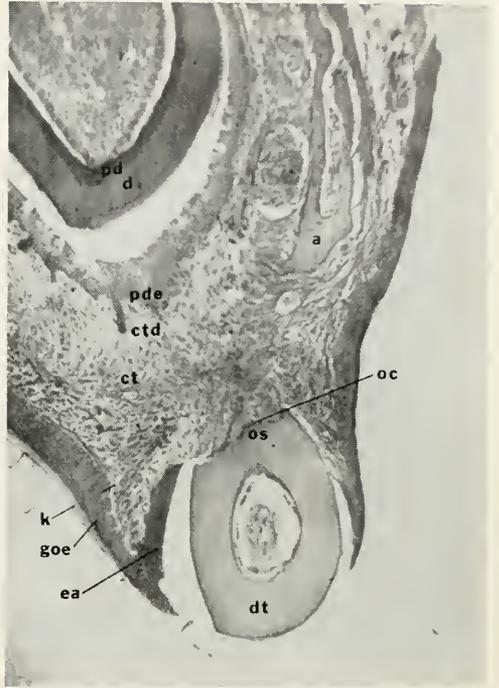


FIG. 7.—Cross section through upper jaw (anterior aspect), showing deciduous premolar (dt), and developing permanent premolar. Note the well defined area of alteration of connective tissue (ctd); the proliferative mass of cells of the dental epithelium (pde); the destruction of the deciduous tooth (os). Symbols not explained in the previous figure, are: a, alveolar bone; pd, predentin; d, dentin; oc, odontoclasts; k, keratinous layer of oral epithelium; goe, granular layer of oral epithelium; ea, epithelial attachment. Stained with Mallory triple.

relatively large, oval cells can be seen at the occlusal end of a prefunctional permanent premolar between the cells of the enamel epithelium and the enamel space. Columnar ameloblastic cells are lacking at these sites in both figures. Figure 9 is a view at high magnification in which the altered connective tissue (ctd) adjacent to an incoming lower permanent premolar clearly can be seen and compared with the normal connective tissue (ct). According to Fullmer (1967:355), microscopic examination suggests that the enzymic systems that promote or permit degradation of connective tissue are present within the

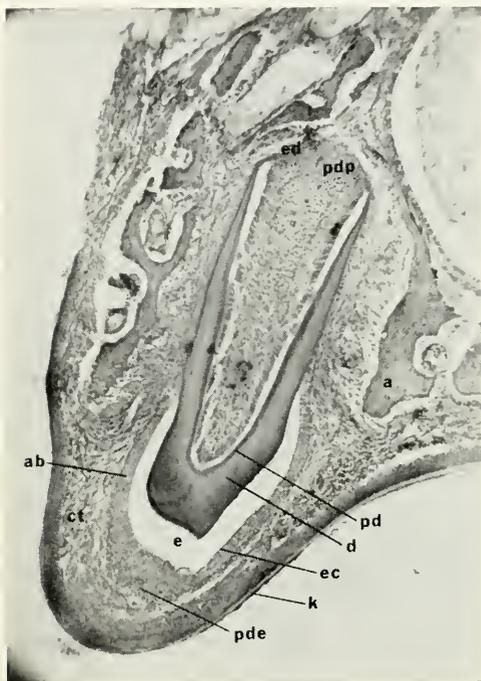


FIG. 8.—Cross section through upper jaw (anterior aspect), showing permanent premolar in prefunctional stage. Note the proliferative zone of the dental epithelium. Symbols not explained in previous figures are: pdp, proliferative zone of dental pulp; e, enamel space. Stained with Mallory triple.

connective tissue cells. It seems likely, however, that chemical activity of the proliferative mass of cells of the enamel epithelium also plays an important role. As a result of previous studies, it has been suggested that the proliferative zone produces an enzyme (possibly hyaluronidase) that leads to loss of the ground substance (acid mucopolysaccharids) between and within the collagenous fibers (Weinmann, 1966:303). The dense connective tissue thus is altered to loose, fluid-rich tissue with fine argyrophil fibers; this alteration can be seen in figures 6 and 9. The process of proteolysis that results in dissolution of connective tissue in the path of erupting permanent teeth apparently is not assisted by inflammatory cells, although lymphocytes have been found in the center of regions of degeneration (Fullmer,

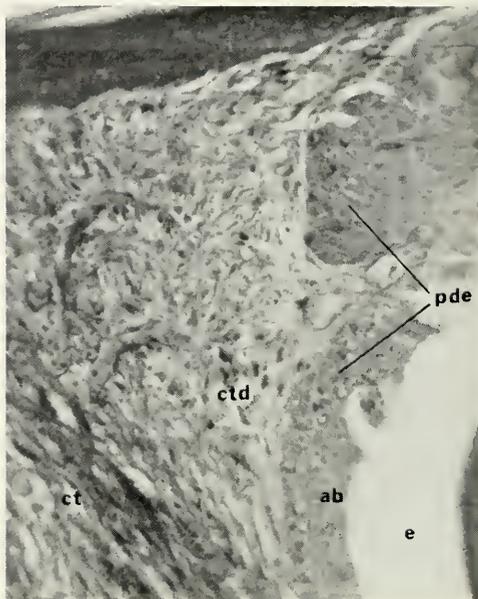


FIG. 9.—Proliferative mass of cells of the dental epithelium of a prefunctional lower premolar. All symbols are explained in Figures 7 and 8. Stained with Mallory triple.

1967:355). Inflammatory cells were not found in association with degeneration of connective tissue in the sections of *Choeronycteris* that I studied (see ctd in Fig. 7).

Pressure exerted by developing teeth is thought to cause cells of the loose connective tissue to differentiate into osteoclasts (see Aisenberg, 1966:320). Extensive resorption of cement and dentin of a lower deciduous canine and upper deciduous premolar is shown in figures 6 and 7. Because of the effect of pressure from developing permanent teeth on the shedding of deciduous teeth, sequence and time of shedding are related, at least in part, to degree of crowding and rate of eruptive movements and development of permanent teeth. The pulp of deciduous teeth of glossophagine bats possibly plays a role in the process of shedding. The cellular elements of the pulp of deciduous teeth are essentially the same as those of surrounding tissue; therefore, odontoclasts may differentiate from cells of the pulp (Aisenberg, 1966:326-327). Friant (1959:215) found that

centripetal resorption, resulting from alteration of odontoblasts to odontoclasts, was an important factor in the process of shedding of deciduous teeth in rabbits of the genus *Oryctolagus*. In man, the odontoblasts in the occlusal part of the pulp, at least, may appear to be normal and functioning even in a late stage of destruction of the deciduous tooth. I found slight centripetal resorption in one upper deciduous premolar in *Choeronycteris*; the odontoblasts of the deciduous teeth undergoing the destructive process appear to have been altered (Fig. 6).

The periodic acid-Schiff (paS) reaction frequently has been used in histochemical studies to demonstrate carbohydrate groupings in ground substance of teeth and bone (Burstone, 1966:360-361), and to show the presence of abundant carbohydrates in connective tissue undergoing degradation (Fullmer, 1967:357). Because resorbing bone and dentin are more intensely stained than is either normal bone or dentin (see Burstone, 1966), the periodic acid-Schiff reaction could be used to study possible centripetal resorption of the deciduous teeth in *Choeronycteris* and other glossophagine bats. Unfortunately the preserved materials available to me were unsatisfactory for paS studies.

In man, the process of shedding of deciduous teeth is not continuous and, consequently, in periods of "rest" some areas of resorption may be partially repaired by apposition of cementum or bone (Aisenberg, 1966:326). Repaired areas of tooth and alveolar bone were not found in *Choeronycteris*, possibly indicating that shedding in this bat is fairly rapid and perhaps continuous in comparison with the process in man.

The term "cutting" commonly is used to describe the passage of the crown of a permanent tooth through the oral epithelium and gingivum. Weinmann (1966) has commented on the inappropriateness of utilization of such a mechanistic term for an action that is largely chemical. In *Choeronycteris* the connec-

tive tissue is altered as the permanent tooth nears the oral epithelium. The proliferative layer of the enamel epithelium and the oral epithelium fuse, except at the greatest point of pressure where the oral epithelium degenerates to allow passage of the new tooth.

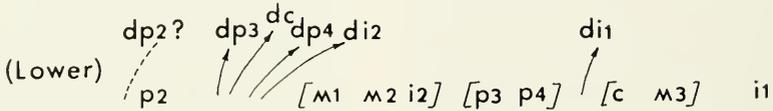
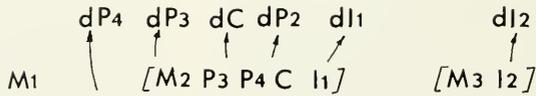
In the following paragraphs and in figure 10, the sequence of shedding of deciduous teeth and the eruption of permanent teeth in *Choeronycteris*, *Glossophaga*, and *Leptonycteris*, are described and diagrammed on the basis of specimens listed previously. Fortunately, most of the available specimens represent slightly different stages so that when arranged from smallest to largest the developmental sequences could be estimated.

Glossophaga

In *Glossophaga* as in *Choeronycteris*, the first lower premolar is the first permanent tooth to reach the functional eruptive phase. The first upper molar is the first of the upper teeth to reach this stage. In the lower jaw, the first and second molars and outer incisors complete the prefunctional eruptive phase together, and therefore reach the occlusal plane at essentially the same time. The eruptive movements of these teeth coincide with those of the second upper molars, premolars, canines, and inner incisors. The second and third lower premolars reach the functional eruptive phase slightly after the first and second lower molars and outer incisors but at approximately the same time as the upper canines and inner incisors. The axial movements of the lower canines and last lower molars bring these teeth into the occlusal plane coincidentally with the third upper molars and outer incisors. The inner lower incisors are the last of the permanent teeth to reach the functional eruptive phase. These teeth are in the preruleptive phase of development when the outer lower incisors are well into the prefunctional phase. The opposite is true of the upper incisors, where the inner teeth are con-

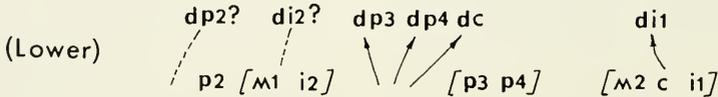
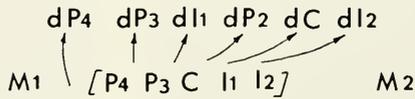
GLOSSOPHAGA

(Upper)



LEPTONYCTERIS

(Upper)



CHOERONYCTERIS

(Upper)

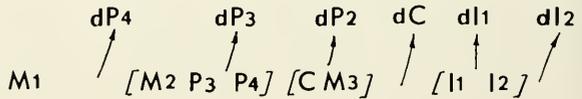


FIG. 10.—Comparative eruption and shedding sequences in three genera of glossophagines. Horizontal distance between units does not indicate time; the order and comparison between upper and lower teeth are chronological.

siderably more advanced than the outer pair.

In the lower jaw, the second and third deciduous premolars, canines, and outer incisors are shed quickly and at essentially the same time. Shedding of these teeth occurs slightly before the loss of the first and second upper deciduous premolars and canines but at the same time as the loss of the third upper premolars. In all instances these deciduous teeth are lost well before their permanent replacements have reached the functional eruptive phase. This is

because of the crowded nature of the developing tooth-row in *Glossophaga*; the thinness of bony support also contributes to the loss of the lower deciduous premolars, canines, and outer incisors, and the upper first and second premolars and canines. The upper deciduous incisors are lost when their permanent replacements complete the pre-functional eruptive phase. The inner lower deciduous incisors, on the other hand, are shed somewhat before their replacements complete axial movements into the occlusal plane.

Leptonycteris

As in *Choeronycteris* and *Glossophaga*, the first lower premolar is the first permanent tooth to reach functional eruptive phase. The first upper and lower molars, as well as the outer lower incisors, reach this stage of eruption coincidentally and only slightly behind the first lower premolars.

The first and second upper permanent premolars and the upper canines and incisors reach the functional eruptive phase at about the same time. Eruptive movements of these upper teeth coincide with those of the second and third lower premolars, although the latter apparently are slightly slower. The second upper and lower molars, the last of the cheek-teeth in *Leptonycteris*, are the final permanent teeth to reach the functional eruptive phase; movements of these teeth to the occlusal plane coincide. The lower permanent canines attain their functional eruptive phase at essentially the same time as the last lower molars; thus, the lower canines reach the occlusal plane well after the upper ones, which attain the functional eruptive phase concomitant with the upper permanent premolars and incisors. The lower inner incisors are the last of the permanent teeth to develop. These teeth are in the preeruptive phase when the outer lower incisors have nearly attained their functional position in the occlusal plane.

Because the first lower premolar is the first permanent tooth in the occlusal plane, its deciduous predecessor, if indeed there is one, must be resorbed before birth. The second and third upper deciduous premolars are the first of the upper deciduous teeth shed in *Leptonycteris* after birth. These deciduous teeth, and the second and third lower premolars as well, are under pressure from the permanent premolars while the latter still are in the prefunctional eruptive phase, because the permanent teeth develop directly below the deciduous teeth. The inner upper deciduous incisors are lost shortly before their perma-

nent replacements reach the functional eruptive phase. The first upper deciduous premolar (which is not replaced by a permanent tooth) and the upper deciduous canine are shed when the permanent canines have nearly (or completely) reached the functional eruptive phase. Probably this is because these deciduous teeth, which are located slightly posterior to the alveoli of the developing permanent canines, are not under direct pressure from the permanent tooth until late in its prefunctional eruptive phase. The lower deciduous canines are shed at the same time as the lower deciduous precursors of the second and third premolars. The inner lower deciduous incisors are the last of the deciduous teeth shed in *Leptonycteris*.

Choeronycteris

The first lower premolar is the first permanent tooth to reach the functional eruptive phase; its axial movements probably are nearly complete at birth. The first upper molar is the next to reach the functional eruptive phase. By the time that these two teeth have reached the occlusal plane, the remaining permanent teeth are in the following stages of development: the third upper and lower permanent molars and the first and second upper incisors are in the preeruptive phase; the second upper and lower molars, the first and second upper premolars and canines, and the second and third lower premolars and canines are in the prefunctional eruptive phase.

The second upper molars and the first and second premolars are the next of the upper permanent teeth to reach the functional eruptive phase. The second lower molar attains this phase of development at essentially the same time as the second upper molar. Axial movements of the second and third lower premolars are slightly slower than in the second lower molar, so these first two teeth reach the occlusal plane shortly after the latter, but at approximately the same time as the third lower molar. The

upper and lower canines and third upper molars reach the functional eruptive phase at approximately the same time, although the canines develop slightly ahead of the molars. The upper incisors are the last permanent teeth to develop and reach the functional eruptive phase in the genus *Choeronycteris*.

The third upper deciduous premolar, which is the predecessor of the second permanent premolar, is the first upper deciduous tooth shed, although a deciduous precursor of the first lower premolar is unknown. If it does exist it most likely is resorbed before birth. The second upper deciduous premolar and the lower deciduous premolars are the next deciduous teeth shed, being lost at essentially the same time, when their permanent replacements are about halfway through their prefunctional eruptive phase. The deciduous premolars replaced by permanent teeth are shed quickly because the permanent replacements develop directly below the deciduous teeth, causing resorption as soon as the permanent teeth begin their axial movements. The first upper deciduous premolar, which is not followed by a permanent replacement, persists slightly longer than do the other deciduous premolars because of its location at the anterior end of the alveolus of the permanent first upper premolar. The latter apparently has reached its functional eruptive phase before a combination of resorption of root and alveolar support and pressure from the incoming permanent canine cause the first deciduous premolar to be shed.

The lower deciduous canine is resorbed quickly because it is wedged between the permanent lower canine and first premolar (Fig. 6). On the contrary, no pressure is brought to bear on the upper deciduous canine by an incoming permanent premolar and, because it is located slightly posterior to the alveolus of its permanent replacement, it sometimes is not lost until well after the secondary canine has reached the functional eruptive phase.

Resorption of alveolar support plays a major role in the shedding of upper deciduous incisors, which are the last deciduous teeth shed in *Choeronycteris*, being lost when their permanent replacements attain the functional eruptive phase. The lower deciduous incisors usually are not shed in *Choeronycteris*; this matter is discussed further in the generic account.

Comparative Aspects

The deciduous teeth of *Choeronycteris*, *Glossophaga*, and *Leptonycteris* generally are similar (Figs. 3, 4, 5). One exception, however, is notable; the upper inner incisors in *Glossophaga* and *Leptonycteris* are forked, whereas those of *Choeronycteris* consist of a single shaft with a roughly triangular recurved apex (Fig. 5). Generally speaking, the upper deciduous incisors of *Choeronycteris* are like those of the phyllostomatine genera *Touatia*, *Mimon*, *Chrototerus*, and *Phyllostomus*, whereas the deciduous incisors of both *Leptonycteris* and *Glossophaga* are like those of *Macrotus*. Among the other phyllostomatids, the upper inner deciduous incisors of *Artibeus* and *Ametrida* also are forked and those of *Carollia* are simple, recurved hooks.

As can be seen in figure 10, which summarizes the eruption and shedding sequences in *Glossophaga*, *Leptonycteris*, and *Choeronycteris*, each of these genera has distinctive characteristics. The sequence of loss of deciduous teeth in each genus is related to the sequence of eruption of permanent teeth and the degree of crowding caused by the incoming teeth. In all three genera the first lower permanent premolar is the first of the secondary teeth to attain the functional eruptive phase; this tooth probably is in the prefunctional phase at the time of birth because even in the youngest specimens examined the first lower premolar was essentially functional. A deciduous precursor was not found in any of the genera, which probably means that this tooth, if it exists at all, is re-

sorbed before birth. Such prenatal resorption of deciduous teeth apparently is not uncommon in bats (Grassé, 1955: 175S; Dorst, 1953:85, 1957a:135).

The eruptive characteristics of the first upper molar are similar in *Glossophaga*, *Leptonycteris*, and *Choeronycteris*. In all three genera this tooth reaches the functional eruptive phase before any of the other permanent teeth. In *Leptonycteris* and in *Choeronycteris* the rate of development of the first upper molar is equal to that of the first lower molar, whereas in *Glossophaga* the first lower permanent molar apparently attains its functional stage slightly after the first upper molar. The reason for this difference is not clear. It is of further interest that in *Glossophaga* the second upper and lower permanent molars reach the functional phase at the same time as the first lower molar, whereas in *Choeronycteris* the second upper and lower molars do not attain their functional eruptive phase until after the first upper and lower permanent molars have done so. *Leptonycteris* differs from the other two genera in that the second upper and lower molars do not attain their functional phase of development until relatively late in the overall sequence of eruption and shedding. The late eruption of these teeth, which are the last molars in *Leptonycteris* and are reduced in size and structure, roughly coincides with the eruptive sequence of the third upper and lower molars in *Glossophaga*. In *Choeronycteris* the third lower molar reaches the functional eruptive stage slightly before the third upper molar.

Eruption of permanent incisors is noteworthy because of the differences among the three genera. In *Choeronycteris*, which lacks lower permanent incisors, the two upper incisors are the last of the permanent teeth to attain the functional stage, coming in together after the upper and lower canines. In *Leptonycteris* both upper incisors reach the final phase of eruption together, whereas in *Glossophaga* the inner incisors are slightly ahead of the outer pair.

In *Glossophaga* and *Leptonycteris* the outer lower permanent incisors reach the functional phase well before the inner teeth.

In summary, *Leptonycteris* and *Glossophaga* are more alike in their sequence of eruption than either is like *Choeronycteris*. *Leptonycteris*, with only two permanent molars, has essentially the same pattern as *Glossophaga*, with the second molars occupying the same sequential position as the third molars in the latter genus. *Choeronycteris* differs most from the other two in the sequential groupings in eruption.

PERMANENT DENTITION

The permanent dentitions typical of the species comprising each of the 13 nominal genera of the subfamily Glossophaginae are described in the following accounts. The genera of this subfamily are here divided into two groups on the basis of the morphology of the basicranial region and serological and cytological differences. The dentition, however, does not serve to divide the subfamily into the same basic groupings.

The first group of genera includes a variety of dental configurations. Six (*Lonchophylla*, *Lionycteris*, *Anoura*, *Glossophaga*, *Monophyllus*, and *Leptonycteris*) have fairly primitive molars in which the W-shaped ectoloph is retained; the remaining four genera in the first group (*Lichonycteris*, *Hylonycteris*, *Scleronycteris*, and *Platalina*) have greatly reduced dentitions (in the last three the W-shaped ectoloph has been lost). The second group (*Choeronycteris*, *Musononycteris*, and *Choeronycteris*) is comprised of kinds in which the dentition is greatly reduced and the W-shaped ectoloph lost.

Details of morphological variation and dental interaction were studied only in *Anoura*, *Glossophaga*, *Leptonycteris*, and *Choeronycteris*; samples of the remaining genera from a single locality, or adjacent localities, were too small for adequate statistical analysis.

Dental abnormalities are frequent in

glossophagines. Teeth occasionally are lost in the life of an individual. A wide variety of circumstances, including diseases, abnormal attrition, erosion, and possibly mechanical damage can cause the destruction of dental tissue. Accurate diagnosis of cause of loss of teeth is extremely difficult when specimens are available only as skulls free of soft tissue. It is thought, however, that most of the instances of loss of teeth discussed in this study resulted from erosion. The pathogenesis of erosion and other possible factors as well, are discussed in detail in the chapter on oral pathology.

Lonchophylla Thomas

Four species of long-tongued bats of the genus *Lonchophylla* currently are recognized: *robusta* is known from Costa Rica, Panamá, and Colombia (Cabrera, 1958:76; Walton, 1963:88); *thomasi* is known from Panamá, Venezuela, and Brazil (Cabrera, *loc. cit.*; Handley, 1966b:763); *mordax* has been recorded from Panamá, Brazil, Bolivia, and Perú (Handley, *loc. cit.*; Cabrera, 1958:75; Tuttle, 1970); and *hesperia* is known only from Perú (Cabrera, *loc. cit.*). Bats of the genus *Lonchophylla* generally are medium-sized glossophagines that have a moderately elongate muzzle and a short tail that protrudes slightly through the dorsal surface of a relatively unreduced interfemoral membrane. In coloration, these bats usually are brownish or orange-brown.

Goodwin (1946:312) thought *Lonchophylla concava* [= *L. mordax* (Handley, 1966b:763)] to be, at least to some extent, a nectar feeder. Supporting evidence, however, is lacking. Considering the dentition, it is likely that fruit and insects comprise a major portion of the diet of at least some species.

Miller (1907:139) briefly described the dentition of *Lonchophylla* and pointed out the unique features of the upper and lower incisors in bats of this genus. Allen (1908:36) also has commented on the dentition of these bats. Generally, the dentition in *Lonchophylla* is the most

primitive in the entire subfamily Glossophaginae. The teeth are large and robust, in comparison with most other glossophagines, and the incisors are unreduced. Bats of the genus *Lonchophylla* have 34 permanent teeth. The dental formula is: i 2/2, c 1/1, p 2/3, m 3/3; the molar teeth are relatively high-crowned and have a distinctly W-shaped ectoloph.

Upper incisors.—The four, large upper incisors nearly fill the available space between the canines. The two inner teeth are about as large as the outer pair, but differ morphologically in being slightly procumbent and in having a broad, blade-like crown. The second incisors are pointed and have a strongly oblique cutting edge.

Upper canines.—The upper canines are stout teeth that lack a longitudinal groove or ridge on the anterior face. The lingual surface of the canine is only slightly concave. Labial, lingual and anterior cingula are lacking but a large posterior cingular style is present.

Upper premolars.—The two upper premolars are not in contact and fill only approximately 80 per cent of the space between the canine and first molar. The first premolar (P3) is slightly smaller than the second and consists of a narrow, trenchant main cone and small anterior and posterior cingular styles. The second premolar (P4) is triangular in occlusal view because of the moderate postero-lingual shelf. The P4 is a relatively robust tooth that has anterior and posterior cingular styles; the latter is in contact with the parastyle of the first upper molar.

Upper molars.—All three upper molars are in contact but are not crowded. The first two are about the same size and are squared in occlusal outline, whereas the third is smaller (about 60% of first two) and more nearly triangular in outline. The first two molars have a distinctly W-shaped ectoloph and all three molars are relatively high-crowned. In the first two, the styler shelf is upturned so that the labial margin of the

tooth is nearly as high as the main cones (the paracone and metacone). The paracrista is a short, ridge-like commissure in both the M1 and the M2, and the paracone is relatively small and low. The mesostyle is part of the posterior element of the ectoloph and thus the precentrocrista ends at its base, below the level of the postcentrocrista. The metacone on all three upper molars is about the same size as the paracone. The third molar differs from the first two in having a more rounded parastyle, a lower labial margin, a greatly reduced mesostyle, and in lacking a metastyle. The protocone on all three teeth is a ridge-like cusp and all three have a distinct hypoconal basin.

Lower incisors.—The lower incisors are large, well-rooted teeth that are in contact and set in a shallow arc that takes up most of the available space between the canines. The four incisors are essentially the same size; all have a clearly trifold crown.

Lower canines.—The lower canines are stout teeth that are slightly recurved and tilted laterally. They have a narrow, antero-lingual cingular shelf that extends posteriorly to a place where it is broader and slightly upturned.

Lower premolars.—The three lower premolars are not crowded or in contact, but essentially fill the available space between the canine and first molar. All of the premolars are narrow and moderately high-crowned. The first premolar (p2) consists of a main cone with a slightly concave lingual surface and a small posterior cingular style; there is no anterior style. The second and third premolars resemble each other; both have an anterior as well as a posterior cingular style but only the p4 has a broad postero-lingual base.

Lower molars.—The three lower molars are all in contact. They are long and fairly narrow teeth and resemble each other morphologically. The first two are about the same size, but the third is smaller. The prominent paracoid is set on the longitudinal axis of

the tooth and the metaconid and protoconid are nearly side by side, although in the m1 the protoconid is slightly anterior to the metaconid. Both of these cones are high and prominent. The entoconid and hypoconid are prominent ridge-like cusps separated by a deep, V-shaped valley.

Dental Abnormalities

A small sample (49 specimens) of *Lonchophylla* was examined; therefore, the following comments on dental abnormalities may reveal little of their potential incidence in nature. Atavistic upper premolars were the only developmental abnormality found. In *Lonchophylla*, loss of teeth in life as a result of one or more factors appeared to be about the same in percentage of occurrence as in other glossophagines.

Hyperdontia

An adult female (FMNH 51732) of *Lonchophylla robusta* from Colombia has an extra upper premolar on the right side. The extra tooth is small, less than 50 per cent the size of a normal first upper premolar (P3), and is located anterior to the P3 and in contact with the posterior end of the canine. The supernumerary premolar has a single root and its crown is somewhat like a miniature premolar. Probably the extra tooth is an atavistic P2 because it clearly is neither an extra P3 that resulted from double initiation nor a deciduous tooth somehow retained in adulthood.

In an adult female (USNM 309389) of *Lonchophylla mordax* from Panamá, there are extra upper premolars located about halfway between the normal first premolars (P3) and the canines. These extra teeth are tiny peg-like spicules that have a single root. They are not deciduous teeth and not supernumerary first upper premolars; it is therefore likely that they are atavistic P2's. The crowns of the extra premolars are so small that they are not even as high as the adjacent cingular style of the P3's and probably did not penetrate the gingivum.

Loss of Teeth in Life

In the four specimens of *Lonchophylla thomasi* examined, two had lost the second upper incisors from both the right and left sides; in 13 specimens of *mordax* examined, one had lost the upper left first premolar (P3) in life. In the sample of 31 specimens of *robusta* (eight males, 22 females, one of unknown sex), the lower incisors were the teeth most often lost in life. The first lower incisors had been lost with a total incidence of 3.22 and the second incisors with a total incidence of 6.45. A male had lost an I2 as well as the left P4.

Lionycteris Thomas

Lionycteris spurrelli, the only known species, has been reported from Guayana, Brazil, Venezuela, Colombia, Perú, and Panamá (Cabrera, 1958:75; Handley, 1966b:763; Tuttle, 1970). It is a relatively small glossophagine with a moderately long muzzle and short tail that barely penetrates the unreduced interfemoral membrane.

Essentially nothing is known about the natural history of *Lionycteris spurrelli*. Tuttle (1970) reported that he obtained a specimen near a blooming cashew tree, but the diet is otherwise unknown. Judging from the highly specialized nature of the dentition, it is likely that the diet includes moderately hard materials such as fruit and insects.

Thomas (1913:270-271) briefly described the dentition of *L. spurrelli* and compared it with that of *Glossophaga* and *Lonchophylla*. He correctly thought that *Lionycteris* was related to these two genera, particularly to *Lonchophylla*. In many ways the dentition of *Lionycteris* is among the most primitive in the Glossophaginae, but in other ways certain teeth—particularly the premolars and upper incisors—are among the most highly specialized. This species has 34 permanent teeth; the dental formula is: i 2/2, c 1/1, p 2/3, m 3/3. The teeth are large and robust and, in comparison with the dentitions of other glossopha-

gines, the premolars are extremely high-crowned.

Upper incisors.—The four upper incisors are not in contact but fill the space between the canines (no median gap). The inner incisors are unusually high (slightly more than 50 per cent the height of the canines) and have a broad, barely oblique, blade-like apex and narrow base. The outer incisors, which are slightly less than one half the height of the inner teeth, have pointed crowns and moderately oblique edges.

Upper canines.—The upper canines are short and stout and lack a longitudinal groove and ridge on the anterior face. The lingual surface of the canine is slightly concave and there is a moderately large posterior cingular style.

Upper premolars.—The two upper premolars fill most of the space between the canine and first molar but are not in contact. The two premolars are remarkably similar in morphology and size; both are unusually high (slightly more than 50 per cent the height of the canines) and have a trenchant main cone that is nearly circular in cross-section at the base. The anterior and posterior cingular styles are small and the postero-lingual shelf, which is present on P3 as well as on P4, is of moderate size.

Upper molars.—The three upper molars are of moderate size and are in contact (or nearly so). The first two molars are squared in occlusal outline, whereas the third is somewhat smaller and somewhat triangular in outline. All three are morphologically similar and thus all have a W-shaped ectoloph. The ectoloph is distorted slightly, however, on the first molar because of a slight labial shift in the position of the paracone. The paracone and metacone are large, prominent cones on all molars. The parastyle is as high, although not as large, as the paracone. On the M1, the paraerista is quite short because of the nearness of the paracone to the labial margin of the tooth. The paraerista is longest on M3. The mesostyle is formed only by the posterior element of the ectoloph. Al-

though the M3 is generally unreduced, in comparison with the last upper molars in most of the other species of glossophagine bats, the metastyle of this tooth is smaller than its equivalent structure on the other two molars. The protocone is a small but distinct, ridge-like cusp on all three molars and the hypoconal basin is lacking.

Lower incisors.—The four lower incisors are large, well-rooted teeth. All are in contact and the space between the canines is completely filled. The crowns of all four teeth are oval in occlusal outline and all are trifold.

Lower canines.—The lower canines are relatively short, stout, teeth that are strongly recurved. The cingulum extends from the anterior end along the lingual surface to the posterior end of the tooth.

Lower premolars.—The three lower premolars are not in contact, but do fill the available space. All of the lower premolars, like the upper premolars, are unusually high, being more than 50 per cent of the height of the lower canines. The first premolar (p2) is slightly smaller than the other two and lacks a medio-lingual cusplet. All three teeth are approximately as wide as they are long, and all have anterior and posterior cingular styles. The second and third premolars have prominent medio-lingual cusplets.

Lower molars.—All three lower molars are in contact. The first and second are slightly larger than the third, but all are similar morphologically. The metaconid is large and nearly vertical and the protoconid, although lower than the metaconid, is prominent. The paraconid is upturned and has a small flange on the anterior-facing surface, which is largest on the m1. The entoconid is low and ridge-like and is separated from the high, prominent, hypoconid by a deep, V-shaped valley along the longitudinal axis of the talonid.

Dental Abnormalities

Twenty-five specimens of *L. spurrelli* from Panamá, Venezuela, Guayana, and

Brazil were studied. Although this small sample probably does not reflect the incidence of dental abnormalities in nature, several interesting examples of partial hyperdontia were found. The pattern of loss of teeth in life in this small sample appears to be much the same as in the other glossophagines.

Hyperdontia

An adult male (AMNH 97267) from Brazil has an extra tooth anterior to the normal first upper premolar (P3) on the right side. The extra tooth is only about 30 per cent the size of the P3 and, unlike the P3, has but one root. The crown of the supernumerary tooth is high and pointed and has a small notch on the posterior end that fits under and against the anterior cingular style of the P3. The extra tooth differs from the normal first premolar in size and number of roots and resembles it only slightly in coronal morphology. It seems likely that the extra premolar is an atavistic P2. The remainder of the dental arcade in this specimen was normal.

An adult female (USNM 385709) from Venezuela also has an extra permanent tooth anterior to the normal first upper premolar on the left side. In this specimen, the extra tooth is located slightly anterior to the P3, which is normal in all respects, but is not in contact with it. The abnormal tooth is only about 30 per cent the size of the P3 and has but one root. In coronal morphology, the supernumerary premolar is much like the extra premolar in the specimen described above and, like it, probably is an atavistic P2. The remainder of the dental arcade in the individual from Venezuela was normal.

An adult male (USNM 239477) from Brazil has an extra lower incisor on the right side. The supernumerary tooth, which probably resulted from double initiation of one of the lower incisors, is lodged between the first and second incisors (both of which appear to be normal) and in general appearance is most like the outer incisor. The extra lower

incisor is well rooted and is completely independent of the other teeth. Because of spatial limitations, it is turned so that its crown in occlusal view is nearly perpendicular to the crowns of the other teeth. The extra tooth differs from the others in lacking the trifid coronal apex. In order to accommodate the supernumerary incisor in the arc of lower incisors, the inner pair were pushed together so that they overlap. It is possible, of course, that an extra incisor such as this one could be an atavistic tooth. Considering that evidence for atavism as a cause of presence of extra lower incisors is considerably weaker than is evidence supporting atavism in upper premolars, I have not described this and other supernumerary lower incisors as atavistic. The remainder of the dental arcade in this specimen was normal.

Another adult male (AMNH 97265) from Brazil has an abnormality that was not found in any of the other glossophagine bats (more than 2400) examined. In this specimen, there is an extremely small, peg-like extra tooth posterior to the third upper molar on the right side. The abnormal tooth has a single root and its own alveolus; the crown is oval and lacks any distinguishing features. The tooth is so small that it certainly was covered by the gingiva in life. The M3 is normal in all ways, as are all other teeth in this individual. It is possible that the extra tooth resulted from some disturbance in the stage of morpho-differentiation.

Loss of Teeth in Life

In the 16 males examined by me, one first upper incisor, a lower canine, a lower first premolar (p2), and a lower third premolar (p4) had been lost in life. In the eight females, one first upper incisor had been lost in life. Although this sample is small, there is reason to suspect that loss of teeth from such factors as erosion and mechanical damage occurs in *Lionycteris* as in the other glossophagines.

Anoura Gray

The five nominal species of this genus of tailless bats, *Anoura geoffroyi*, *brevirostrum*, *cultrata*, *caudifer*, and *werckleae*, occur from the northern part of the western coast of México throughout southern México, Central America, and northern South America, and also on Trinidad and the Lesser Antillean island of Grenada (Hall and Kelson, 1959:119; Cabrera, 1958:74-75; Handley, 1960:463; Starrett, 1969:1; Jones and Phillips, 1970). Externally, the species are similar, being of moderate size, usually dark brownish or blackish in color (one exception), having a greatly reduced interfemoral membrane, the tail reduced or absent, and a slightly elongate muzzle.

Several authors have commented on the feeding habits of various species of *Anoura*. Although Goodwin (1946:312) has stated that *Anoura geoffroyi* is, in part at least, a nectar feeder with a long tongue "adapted for reaching into the corolla of various night-blooming tropical flowers," and that tailless bats are known to visit blossoms that do not secrete nectar and therefore might seek insects attracted to flowers, detailed information on feeding habits in nature is lacking. Goodwin and Greenhall (1961:247) included soft pulp of fruit in the diet of *Anoura geoffroyi* and reported that in captivity specimens have been maintained for two months on the soft parts of paw paw. Tamsitt *et al.* (1964:108) thought that permanent populations of *A. geoffroyi* could be supported at fairly high elevations by feeding on pear and other fruit trees as well as species of flowering plants. Starrett (*loc. cit.*) recently named a new species (*A. werckleae*) from Costa Rica and in doing so pointed out that it possibly utilizes the pollen of large yellow flowers of *Wercklea lutea*, which were found along a stream near the type locality. Starrett (1969:6) did not suppose that *Anoura werckleae* is completely dependent on flowers of *Wercklea lutea*, but noted that a "feeding relationship" could be demonstrated and on this basis sug-

gested that the "ranges of the two organisms [might] coincide."

The current taxonomic arrangement of the genus *Anoura* probably should be considered tentative; the genus is in need of careful review. Until recently the genus was divided into two genera, *Anoura* and *Lonchoglossa*; according to Miller (1907:137) the latter genus differed in having subterete outer upper incisors and the anterior upper premolar (P2) nearly in contact with the canine. Sanborn (1933:24) later reviewed the two genera and stated that "the teeth present no separate characters except size." He (*loc. cit.*) further noted that the position of the upper first premolars was extremely variable. Differences used to identify the nominal species are subtle and often include dental characteristics. Handley (1960:464) described the dentition of *cultrata* and pointed out the ways in which it differed from that of *geoffroyi* and *caudifer*. The most striking characteristics of the dentition of *cultrata* are the increase in size of canines and first lower premolar and reduction in size of the other premolars, both upper and lower. Another recently named species, *brevirostrum* of Perú, also has reduced premolars and, according to its describer (Carter, 1969:428), closely resembles *cultrata*. Carter (*loc. cit.*) noted that in *brevirostrum* the "hypocone" is weak on the first molar, "all but absent" on the second and completely lacking on the third. Apparently this author used the term hypocone to refer to the hypoconal basin. *Anoura werckleae*, which thus far is known from only two specimens, is said to be most like *cultrata*, but differs from it (dentally) in having a first upper premolar with a flattened crown and in having a nearly symmetrical first lower premolar (Starrett, 1969:3). Both of these dental characteristics should be reconsidered when more specimens are available because, judging from my studies, individual variation could account for both (see following paragraphs). The distinctive dental characteristics of the nominal species of

Anoura are minor, although when two species are sympatric (for example, *geoffroyi* and *cultrata* in Panamá) dental differences are sufficient for identification.

The dentition of bats of the genus *Anoura* has been described previously by Miller (1907:140-141) and discussed briefly by de la Torre (1961:40-41). All of the nominal species have 32 permanent teeth; the dental formula is: $i\ 2/0$, $c\ 1/1$, $p\ 3/3$, $m\ 3/3$. The teeth are large and fairly robust for a glossophagine; in comparison with the other genera, the molar teeth are most like those of *Lonchophylla*.

Upper incisors.—The four upper incisors are set in a shallow arc between the canines. The inner incisors, which are small, peg-like teeth with a rounded coronal apex, are separated by a median gap where the premaxillaries fuse. These teeth usually are set at a slight angle so that they are in contact with the outer incisors. The outer incisors are larger than the inner pair and have a slightly oblique, blade-like crown.

Upper canines.—The upper canines are stout, narrow teeth that have a slightly concave internal surface. There is a shallow longitudinal groove on the anterior-facing surface that is specifically variable. The posterior cingular style on the upper canines is about twice as large as the anterior one.

Upper premolars.—The three upper premolars are not in contact. The first premolar (P2) is a small and usually somewhat peg-like tooth (although there is variation in the crown) that has but a single root. The position of the P2 varies—in some specimens it is nearly in contact with the canine, whereas in others it is more nearly in the middle of the space between the second premolar and canine. The second premolar is long and narrow and has a trenchant main cone. The size of the anterior and posterior cingular styles is specifically variable. The third premolar (P4) is slightly larger than the second and, in addition to having anterior and posterior cingu-

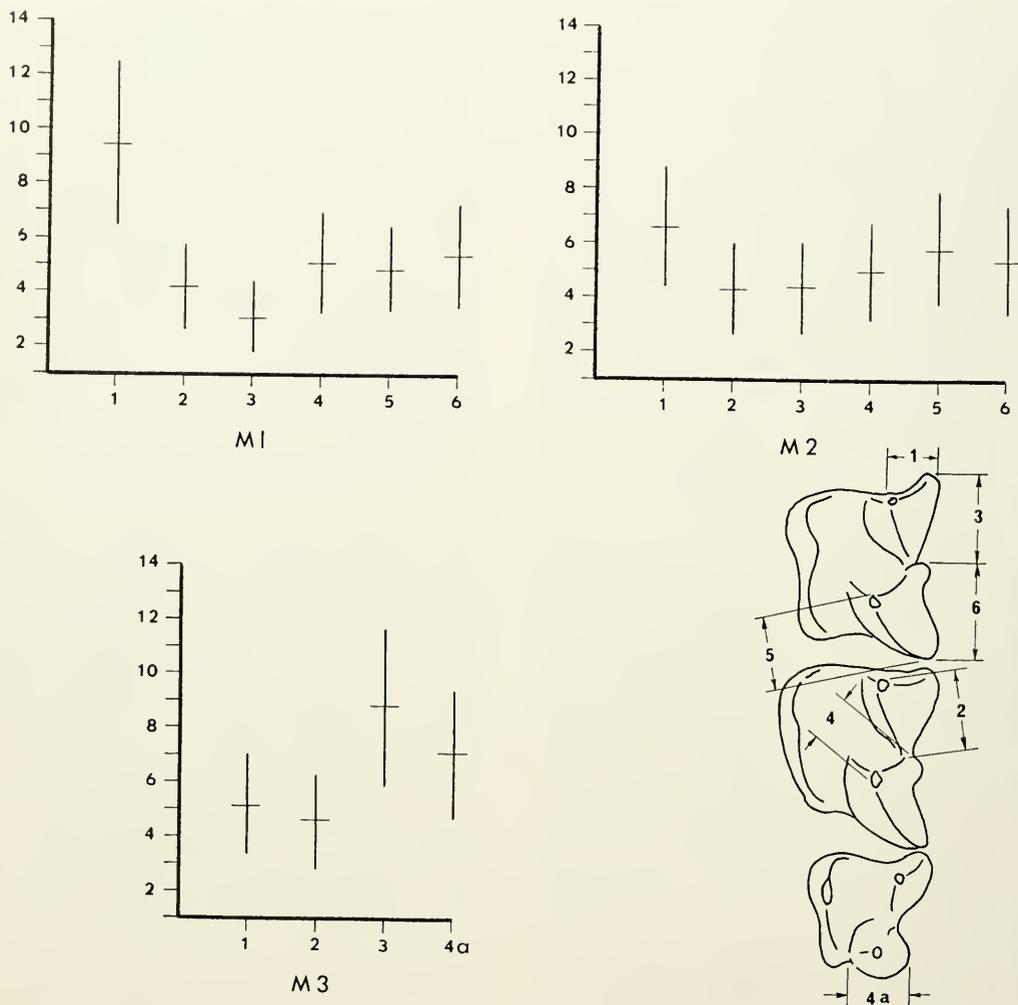


FIG. 11.—Graphs showing the coefficients of variation (horizontal bars) and two standard errors (plotted on ordinate) for measurements of morphological features of upper molars in *Anoura geoffroyi* (measurement number plotted on abscissa). The six measurements taken on each of the first two molars are shown in the inset. The first three of these measurements were taken also on the third molar; measurement 4a is unique to the M3.

lar styles, also has a small postero-lingual shelf.

Upper molars.—The three upper molars are in contact but are not crowded. The first two are squared in outline and about the same size, whereas the third is smaller (about 75 per cent the size of the first two) and nearly triangular in outline. The M1 and M2 are characterized by having a distinct W-shaped ectoloph with high, prominent cones and commissures. The metacone and para-

cone are especially prominent on the first two molars. The parastyle is lower and smaller than the paracone and the paracrista projects anteriorly. The pre-centrocrista ends at the base of the mesostyle, which on the first two molars is a prominent cone that is part of the posterior element of the ectoloph. The metacrista is slightly longer than the postcentrocrista and curves postero-labially. The third molar differs from the first two in lacking the metacrista

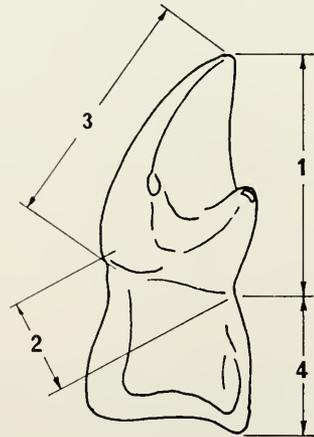
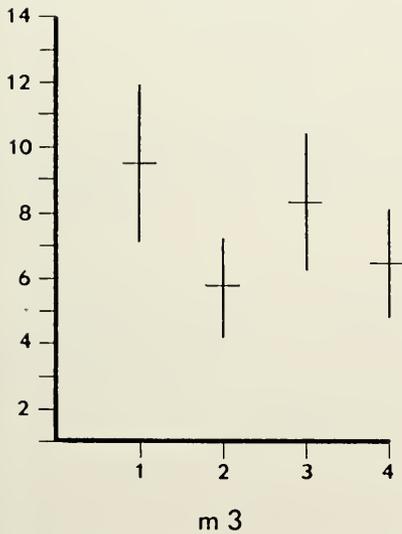
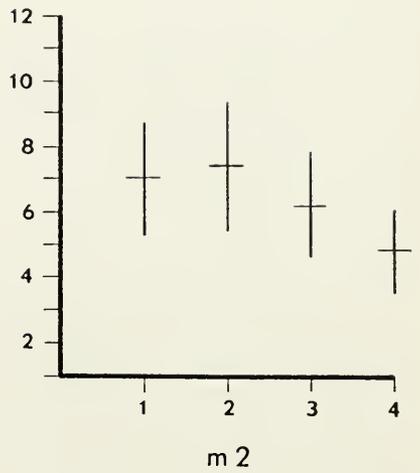
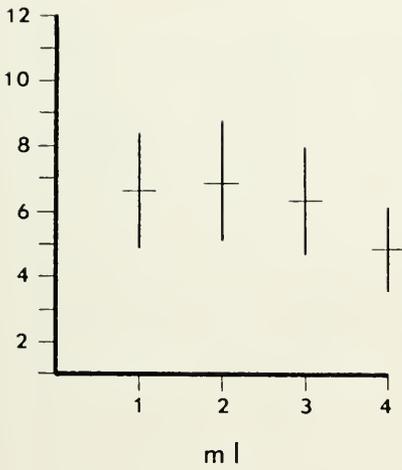


FIG. 12.—Graphs showing coefficients of variation (horizontal bars) and two standard errors (plotted on ordinate) for measurements of morphological features of lower molars in *Anoura geoffroyi* (measurement number plotted on abscissa). The four measurements taken on each of the three molars are shown in the inset.

and the metastyle. The mesostyle of the third molar is highly variable, but usually is small, being a low, rounded style rather than a prominent cone as in the M1 and M2. The protocone on all three upper molars is a ridge-like cusp; all three have a shallow hypoconal basin.

Lower canines.—The lower canines are strongly recurved; the lingual sur-

face is flat and they have only a small postero-lingual cingulum.

Lower premolars.—The three lower premolars are not in contact. Size and morphological features of the lower premolars are specifically variable. The anterior cingular style is lacking from the p2. The second lower premolar is long and narrow and has a trenchant main

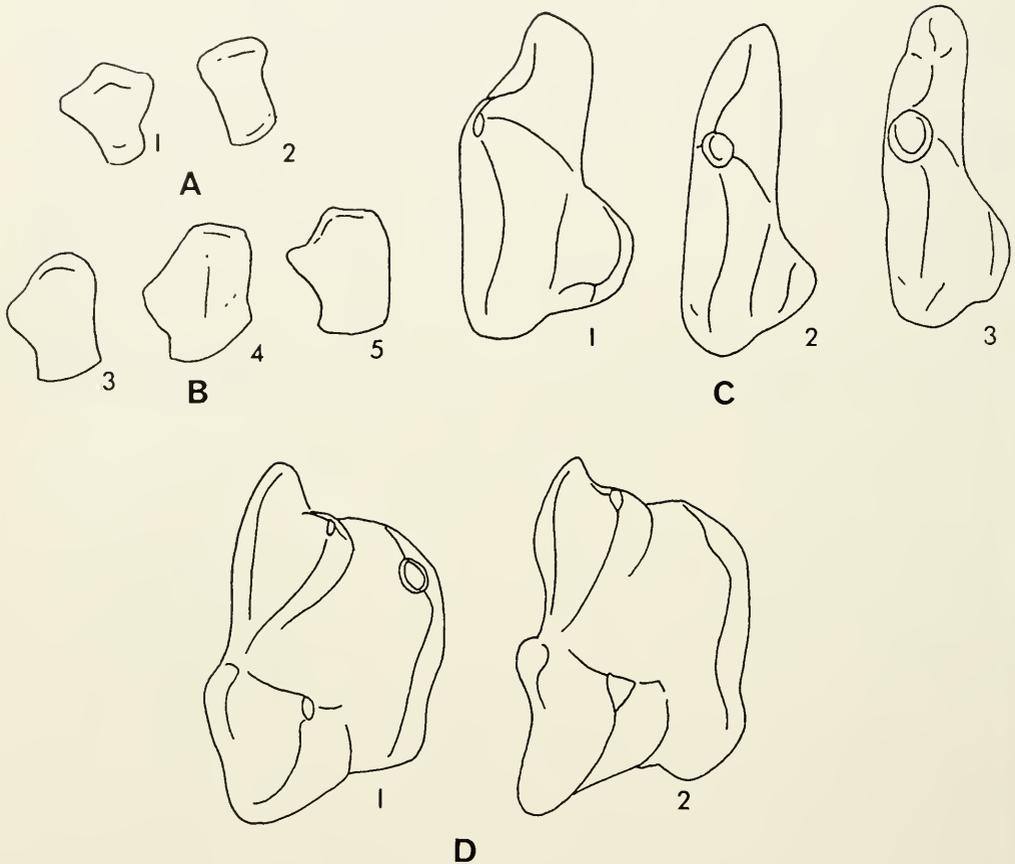


FIG. 13.—Examples of variation (occlusal view) in the first (A) and second (B) upper incisors, the third upper premolar (C), and the first upper molar (D) in *Anoura geoffroyi*. Specimens shown are: A, first incisor of KU 61024 (1), and KU 61027 (2); B, second incisor of KU 60983 (3), KU 60989 (4), and KU 61027 (5); C, third premolar of KU 60992 (1), KU 60986 (2), and KU 60998 (3); D, first molar of KU 60985 (1), and KU 60989 (2).

cone and both an anterior and a posterior cingular style. The third premolar differs in having a broad, somewhat flattened posterior style.

Lower molars.—The three lower molars are in contact; the first two are essentially the same size, whereas the third is about 25 per cent smaller. All of the lower molars are rectangular in occlusal outline and are similar morphologically. The metaconid is the largest cone and the protoconid, which is set slightly anterior to the metaconid, is the second largest. The paraconid is low and pointed and is almost on the longitudinal axis of each of the lower

molars. The entoconid and hypoconid are high, ridge-like cusps separated by a deep, V-shaped valley.

Morphological Variation

More than 100 specimens of *Anoura geoffroyi* from Chiapas, México, were used for study of morphological variation in the structure of the teeth in this genus. Thirty adult males from a single locality in Chiapas were used for statistical analysis of dimensional variation in the third upper premolars (P4), and the upper and lower molars. The dimensional variation in these teeth is summarized in figures 11 and 12.

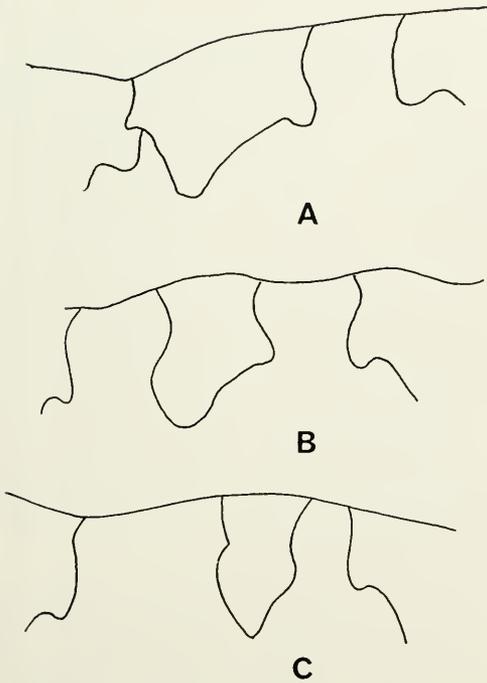


FIG. 14.—Examples of morphological variation in the crown of the first upper premolar (P2) in *Anoura geoffroyi*. Teeth, shown in lateral view, are: A, KU 61024; B, KU 61027; and C, KU 61025.

The inner upper incisors vary slightly in shape (Fig. 13). In most specimens these teeth are simple pegs with a flat, slightly expanded coronal apex. In a few individuals, for example KU 61024, the inner incisors are greatly expanded so that the apex of the crown is somewhat triangular when viewed posteriorly (Fig. 13). The upper outer incisors also vary in shape. In KU 61027, the notch on the lateral surface is considerably more prominent than in KU 60983; the most typical shape is exemplified by specimen KU 60989 (Fig. 13). The morphological variation in the upper incisors is difficult to study in detail because these teeth are subject to considerable alteration from attrition.

The first upper premolar (P2) varies in dimension, morphology, and position. In most individuals this tooth is a simple, slightly recurved peg. In specimen KU 61025, which is shown as an ex-

ample (Fig. 14), the first premolar is located only slightly anterior to the second premolar but in many individuals the first premolar actually is in contact with the canine. The largest, structurally most complex, first premolar found in the series from Chiapas is in specimen KU 61024. In this individual, the first premolar is somewhat like the second in that it has a main cone and posterior and anterior styles (Fig. 14).

The second upper premolar is the least variable of the upper premolars and the third is as variable as the first. The third premolar varies in dimension as well as morphology. Occasionally the tooth lacks an upturned anterior style (for example in KU 60986, Fig. 13), but the most striking individual difference is in the size of the postero-lingual shelf. In some specimens, such as KU 60992, the shelf is wide and broad and has a low ridge along the lingual margin, whereas in others (KU 60986) the shelf is considerably reduced in overall size and lacks a well defined ridge (Fig. 13). Variation in the shelf is reflected in the high coefficient of variation (11.03 ± 2.88) of the measurement of the tooth at its broadest place, which includes the shelf. Variation in size of the postero-lingual shelf is not an artifact of attrition because wear facets are found only on the apex of the main cone (Fig. 13).

The first upper molar is about as variable as the second, which it greatly resembles. The most noteworthy variation in dimension is in the length of the paracrista (Fig. 13), which has a coefficient of variation of 11.38 ± 2.96 . This variation reflects, at least partially, the variation in position of the paracone, which can be seen in figure 11. Although the length of the paracrista is highly variable, the remainder of the anterior element of the ectoloph is slightly less variable than is the posterior element (Fig. 11). The ectoflexus is moderately variable in the first upper molar, reflecting the variability in the size and shape of the mesostyle. In KU 60985, the mesostyle is rounded and extends la-

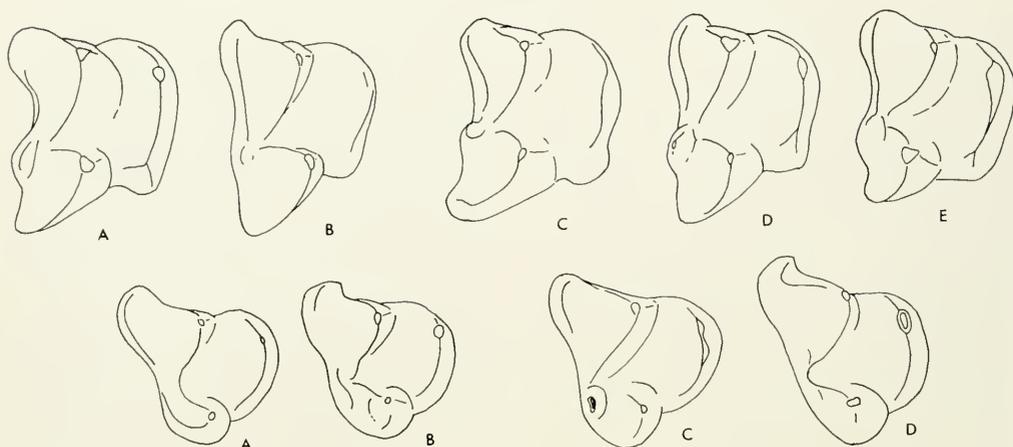


FIG. 15.—Examples of morphological variation (occlusal view) in the second and third upper molars in *Anoura geoffroyi*. Top row (second molar): A, KU 61041; B, KU 61036; C, KU 61034; D, KU 61035; E, KU 61030. Bottom row (third molar): A, KU 61023; B, KU 61025; C, KU 61022; D, KU 61024.

bially, whereas in the other example (KU 60989) it is lower and less prominent (Fig. 13). With exception of the mesostyle, the remainder of the posterior element of the ectoloph is fairly stable, with coefficients of variation ranging from 6.75 to 7.41.

Dimensionally, the second upper molar is only slightly less variable than the first; morphological variation (not reflected in the series of measurements analyzed) is somewhat greater (Fig. 15). The length of the paracrista, which is the most variable dimension of the first molar, also is the most variable of the second (CV, 8.57 ± 2.22). The shape of the parastyle, as well as the direction in which this part of the anterior element projects, is highly variable. In examples KU 61036 and KU 61035, the parastyle projects anteriorly, as it does in the first molar (Fig. 15). In KU 61041, however, the parastyle is rounded in occlusal view and the entire part of the element projects labially in much the same fashion as in *Glossophaga*. This variation is reflected in a coefficient of variation (6.33 ± 1.64) that is slightly higher than in the first molar, in which the position of the parastyle is fairly stable (CV, 5.09 ± 1.30). The ectoflexus of the upper second molar also is more variable than

in the first molar, because of differences in size and shape of the mesostyle and in direction of the parastyle. In some individuals (KU 61036, for example), the mesostyle is low and indistinct and the ectoflexus is relatively straight, whereas in others (KU 61041) the mesostyle is low but bulging labially, which, in conjunction with a labially directed parastyle, gives the ectoflexus a great amount of curvature (Fig. 15). In a few individuals (see KU 61035, Fig. 15), the mesostyle actually is a high-crowned cusplet with a distinct wear facet. The direction of the metastyle is another variable feature not adequately represented by a coefficient of variation. In some individuals the metastyle extends labially beyond the mesostyle (Fig. 15), whereas in others the metastyle is directed almost posteriorly (KU 61035), and does not extend as far as the mesostyle.

The third upper molar is slightly more variable than the first two. The length of the paracrista, in comparison with the same feature on the first and second molars, is only moderately variable (CV, 7.10 ± 1.84), due in part to stability of the shape of the parastyle (Figs. 11, 15). Although the shape of the ectoflexus is relatively stable, the

mesostyle varies greatly in size and shape; consequently, the base of the triangle formed by the anterior element of the ectoloph has the largest coefficient of variation (10.84 ± 2.82). In example KU 61022 the mesostyle is a high, rounded cusplet that is so major a feature that it has a distinct wear facet. In KU 61024 and KU 61025 the mesostyle is almost bipartite (Fig. 15), and in KU 61023 a mesostyle is essentially lacking. The metacone of the third upper molar is dimensionally variable ($CV, 9.07 \pm 2.36$); most of the variation in size apparently results from variations of the mesostyle. The precentrocrista, although relatively stable in length ($CV, 6.57 \pm 1.70$), varies morphologically. In KU 61022 the precentrocrista is a high, prominent ridge, whereas in KU 61023 it is low and rounded (Fig. 15).

The lower canines and premolars vary only slightly in *Anoura*. The third lower premolar varies in position and in the size of the posterior style.

The lower molars vary dimensionally but are fairly stable morphologically. The first lower molar is the least variable of the three; the trigonid is more variable in the m3 than is the talonid, which has a coefficient of variation of only 4.83 ± 1.24 (Fig. 12). The trigonid of the second molar is slightly more variable, especially in the length of the metaacristid and the breadth across the metaconid and protoconid, than the trigonid of the first molar but the talonid of the second has a coefficient of variation of 4.83 ± 1.24 , which is exactly that of the first molar. The lower third molar is more variable than either of the other two. In the third molar the length of the metaacristid is extremely variable ($CV, 9.51 \pm 2.46$) and the length of the talonid also is more variable than in the first two molars (Fig. 12).

Dental Interactions

A matrix of Pearson product moment correlation coefficients was prepared using the data discussed in the previous section. Overall, the coefficients of cor-

relation were fairly low; coefficients above 0.36 are significant at the critical level of 0.05 and those above 0.46 are significant at the critical level of 0.01. All of the dental measurements referred to in the following paragraphs are illustrated in figures 11 and 12. The molar teeth of *Anoura geoffroyi*, in comparison with those of the other genera for which coefficients of correlation were studied (*Glossophaga*, *Leptonycteris*, and *Choronycteris*), basically were more primitive in having a strongly W-shaped ectoloph. Furthermore, the prominent mesostyle is part of the posterior element rather than the product of both elements of the ectoloph.

When equivalent measurements are compared, the coefficients of correlation for measurements of the posterior elements of the first and second upper molars are greater than those for measurements of the anterior elements of the same teeth (Table 1). For example, the metastyle-mesostyle length of M1 has a significant ($P \leq .01$) coefficient of correlation of 0.48 with its equivalent measurement on M2, whereas the highest correlation between equivalent measurements of the anterior elements of M1 and M2 is only 0.21 (Table 1). The mesostyle-parastyle length of M1 does not correlate with that of either M2 ($r, 0.09$) or M3 ($r, 0.00$). It is interesting, however, that the parastyle-paracone length is the most variable dimension of the anterior element of the first molar (Fig. 11). In contrast, equivalent measurements of the anterior elements of the second and third molars are more highly correlated (having coefficients of correlation of 0.64, 0.27, and 0.40).

Within the anterior element of the first molar, only one of three correlations is significant (that of the paracone-mesostyle and mesostyle-parastyle lengths, which is 0.50). Apparently there is a direct mechanical relationship between these lengths; when the paracone-mesostyle length increases, the increase is at the labial margin and thus is reflected in the measurement of the

distance between the mesostyle and the parastyle. The position of the paracone of M1 varies somewhat but there is no apparent relationship between the parastyle-paracone and paracone-mesostyle lengths (r , 0.00). The within-element coefficients of correlation in the posterior element of M1 are greater overall than within the anterior element. The mesostyle-metacone and metacone-metastyle lengths are correlated (r , 0.47), as are the metacone-metastyle and metastyle-mesostyle lengths (r , 0.45). The first relationship possibly is related to slight variation of the position of the metacone along a lateral axis. Thus, when the metacone is shifted slightly in a lingual direction, both of the measurements of adjacent sides of the triangular-shaped element of the ectoloph are increased. The moderately positive correlation between the lengths of the metacone-metastyle and metastyle-mesostyle probably results from the fact that an increase in size of the metastyle proper would affect both of these measurements. As pointed out in the previous section, the anterior element of the second molar is less variable, overall, than that of the M1 (see Fig. 11). It is not surprising, therefore, that the patterns of intra-element correlations are different in M1 than in M2. For example, in the second molar, the distance between the parastyle and the paracone is correlated with the adjacent paracone-mesostyle length (r , 0.40), whereas there was no correlation between these same measurements in M1 (Table 1). There are no coefficients of correlation above 0.36 within the posterior element of the ectoloph of M2 (Table 1), the largest coefficient being only 0.22 for comparison of the distance between the mesostyle and metacone and the distance between the metacone and metastyle. The third molar is morphologically reduced and thus only the anterior element can be analyzed in terms of intra-element correlations. The only noteworthy relationship in this element is between the paracone-mesostyle and mesostyle-parastyle lengths (r ,

0.41). The relationship between these two is the only intra-element correlation common to the elements of all three upper molars.

Inter-element, within-tooth, correlations and lack of correlations also are interesting. In the first molar, none of nine inter-element combinations of measurements has a significant coefficient of correlation. One of nine combinations in M2 was significantly correlated (Table 1). The relationship between the lengths of the mesostyle-parastyle and mesostyle-metacone is noteworthy in the M2. Possibly because of the great variation in the size of the mesostyle in this tooth in *Anoura geoffroyi* (see examples in Fig. 15), there is a low negative coefficient of correlation (-0.28) when these two measurements are compared. When the mesostyle, which is part of the posterior element of the ectoloph, is large the distance between it and the parastyle is decreased. The inter-element relationships in M3 cannot be compared directly with those of either of the first two molars. In the third molar, the width across the reduced metacone is correlated only with the distance between the paracone and mesostyle (r , 0.56).

Inter-tooth comparisons between non-equivalent measurements are interesting in terms of recognition of possible morphogenetic fields. Analysis of these data for *Anoura geoffroyi* unfortunately is complicated by the fact that sequence of development and eruptive movements of the permanent teeth are as yet unknown. When all 36 combinations of equivalent and non-equivalent measurements of M1 and M2 are compared, seven have coefficients of correlation equal to, or greater than, 0.36 (Table 1), and when the 24 possible combinations between M1 and M3 are compared only two have significant positive correlations (≥ 0.36). It is especially noteworthy that the anterior element of the first molar has no correlations with the anterior element of either M2 or M3 (Table 1). The posterior element of the first molar, on the other hand, has two significant correla-

TABLE 2.—Correlation matrix for measurements of the three lower molars in *Anoura geoffroyi*. Abbreviations for measurements used in this and other correlation tables are: PAD, paraconid; MTD, metaconid; POD, protoconid. Measurements are illustrated in Fig. 12. Coefficients significant at the alpha level of 0.05 are marked with an asterisk and those significant at the 0.01 level are marked with a double asterisk.

	m 1				m 2				m 3			
	PAD-MTD	MTD-POD	POD-PAD	TALONID	PAD-MTD	MTD-POD	POD-PAD	TALONID	PAD-MTD	MTD-POD	POD-PAD	TALONID
m 1	1.00											
	0.33	1.00										
	0.06	0.40*	1.00									
	-0.08	0.49**	0.38*	1.00								
m 2	0.17	0.16	0.41*	-0.03	1.00							
	0.22	0.00	0.19	-0.13	0.06	1.00						
	-0.02	0.55**	0.36*	0.46*	0.26	-0.23	1.00					
	0.01	0.53**	0.56**	0.74**	0.08	0.08	0.41*	1.00				
m 3	-0.18	-0.05	0.29	0.03	0.51**	-0.16	0.22	0.20	1.00			
	0.02	0.12	0.39*	0.15	0.10	0.23	-0.12	0.24	0.09	1.00		
	0.05	0.27	0.31	0.19	0.66**	-0.07	0.39*	0.18	0.54**	0.02	1.00	
	0.00	0.47**	0.53**	0.59**	0.08	0.01	0.50**	0.61**	0.18	0.26	0.04	1.00

tions with the anterior element and three with the posterior element of the second molar and has two significant correlations with the anterior element of M3 (Table 1). Overall, all three upper molars appear to be in the same morphogenetic field.

Combinations for all measurements of the three lower molars of *Anoura geoffroyi* are given in the correlation matrix in table 2. When equivalent measurements are compared on an inter-tooth basis, two of the measurements (distance between the paraconid and metaconid and the width of the trigonid at the metaconid and protoconid) are not correlated with their equivalents (Table 2). For example, width of the trigonid of m1 and m2 are not correlated and the same measurements of m1 and m3 have a coefficient of only 0.12. The other two measurements (distance between the paraconid and protoconid and length of the talonid), however, are correlated with their equivalents (Table 2); length of the talonid of m1 when compared to that of m2 has a coefficient of 0.74, and when this measurement on m1 and m3 is compared the value is 0.59. It is interesting that the length of the paralophid (paraconid-protoconid) and the length of the talonid are the two measurements of the four taken on the lower molars that are most important in terms of occlusion.

The patterns of intra-tooth correlations are different in each of the lower molars (Table 2). In the first molar, the length of the metaconid (paraconid-metaconid length) is not correlated (r , 0.33) with the width of the trigonid. The width, in turn, is correlated with both the paralophid (paraconid-protoconid) and the length of the talonid, having significant coefficients of correlation of 0.40 and 0.49, respectively, with each of these measurements. In m2, the length of the paralophid and the length of the talonid are the only two measurements showing correlation (0.41), whereas in the third molar only the lengths of the

metaconid and paralophid are highly correlated (0.54).

Inter-tooth correlations, which are difficult to interpret in the absence of data on development and replacement, are mostly positive or lacking in the lower molars (Table 2). When the first two molars are compared, seven of 16 combinations have coefficients of correlation above 0.36, the highest being between the lengths of the talonids (r , 0.74). When m1 and m3 are compared, fewer (four of 16) correlations are above 0.36, but once again the highest correlation is between the lengths of the talonids (r , 0.59). Overall, the relationship between each of the lower molars is a positive one. Thus, the larger the m1, the larger the other two teeth will be.

A matrix of coefficients of correlation for all combinations of measurements of the upper and lower molars is given in table 3. The first upper molar has more significant correlations with all of the lower molars than do either of the other two upper molars (Table 3). The posterior element of the ectoloph of M1, which is considerably less variable than the anterior element (Fig. 11), has more correlations (11) with the lower molars than does the anterior element (six). Overall, the relationship between the sizes of the upper and lower molars is a positive one, with the M1 and m1 more or less directly influencing the dimensions of the other four teeth. The only noteworthy negative relationships involve the width (metaconid-protoconid) of the individual lower molars and the width of the elements of the ectolophs of the upper molars (which is a reflection of the positions of the main cones). For example, the lengths of the mesostyle-metacone and metacone-metastyle of M2, when compared to the width of m2, have negative coefficients of correlation of -0.33 and -0.32 .

In summary, in *Anoura geoffroyi* all of the molars appear to be in the same morphogenetic field. A complete understanding of their developmental relationships, however, must await the avail-

TABLE 3.—Matrix of coefficients of correlation for upper and lower molars in *Anoura geoffroyi*. The lower molars are plotted across the top; measurements are illustrated in Figs. 11 and 12. Coefficients significant at the alpha level of 0.05 are marked with an asterisk and those significant at the 0.01 level are marked with a double asterisk.

	m 1				m 2				m 3							
	PAD-MTD	MTD-POD	POD-PAD	TALONID												
M 1	PAC-PAS	0.15	0.01	0.14	-0.20	0.02	-0.18	0.05	-0.08	0.38*	-0.25	0.18	0.38*	-0.25	0.18	-0.01
	PAC-MES	0.14	0.30	0.09	0.18	-0.08	0.01	0.26	0.24	0.06	0.45*	0.16	0.06	0.45*	0.16	0.20
	MES-PAS	0.03	0.46**	0.35	0.20	-0.06	-0.07	0.40*	0.29	-0.05	0.42*	0.04	0.42*	0.42*	0.04	0.53**
	MES-MEC	0.22	0.31	0.34	0.11	0.40*	0.09	0.27	0.21	0.42*	0.04	0.55**	0.42*	0.04	0.55**	-0.05
	MEC-MTS	-0.02	0.43*	0.51**	0.40*	0.22	-0.07	0.57**	0.60**	0.34	0.08	0.48**	0.34	0.08	0.48**	0.32
MTS-MES	-0.26	-0.05	0.44*	0.29	0.27	0.21	0.16	0.33	0.30	0.27	0.44*	0.30	0.27	0.44*	0.01	
M 2	PAC-PAS	-0.01	0.26	0.18	0.31	0.14	-0.31	0.13	0.41*	0.31	0.14	0.30	0.31	0.14	0.30	0.29
	PAC-MES	0.28	0.26	0.30	0.10	-0.04	0.00	0.10	0.28	-0.13	0.18	-0.05	-0.13	0.18	-0.05	0.10
	MES-PAS	-0.09	0.03	0.26	0.31	-0.22	0.31	0.01	0.28	0.02	0.25	-0.08	0.02	0.25	-0.08	0.32
	MES-MEC	-0.03	0.26	0.25	0.24	0.33	-0.33	0.32	0.38*	0.56**	0.03	0.53**	0.56**	0.03	0.53**	0.17
	MEC-MTS	0.04	0.51**	0.20	0.19	0.24	-0.32	0.27	0.22	0.03	0.15	0.12	0.03	0.15	0.12	0.23
MTS-MES	0.03	0.06	0.28	0.21	0.18	0.21	0.21	0.16	0.23	0.20	0.10	0.23	0.20	0.10	0.10	
M 3	PAC-PAS	0.09	0.21	0.26	0.12	0.29	-0.19	0.14	0.31	0.42*	-0.04	0.41*	0.42*	-0.04	0.41*	0.17
	PAC-MES	0.32	0.29	0.40*	0.13	-0.04	0.08	0.21	0.27	0.11	0.20	-0.08	0.11	0.20	-0.08	0.51**
	MES-PAS	0.06	0.11	0.26	0.17	-0.12	-0.02	0.20	0.25	0.24	0.09	0.08	0.24	0.09	0.08	0.30
	MEC	0.22	0.17	0.19	0.16	0.02	-0.35	0.15	0.03	-0.05	0.25	-0.10	-0.05	0.25	-0.10	0.22

ability of material that will enable an analysis of the sequence of shedding of deciduous teeth and development and eruption of the permanent dentition.

Dental Abnormalities

No instances of hyperdontia were found in 364 specimens of *Anoura geoffroyi*, in 43 specimens of *caudifer*, or in 13 specimens of *cultrata*, and only two cases of anodontia resulting from dental agenesis (an incidence of 0.67), both in *geoffroyi*, were found. Abnormal loss of teeth in life, as the result of any of several factors, is fairly common in *Anoura*.

Dental Agenesis

An adult of unknown sex (USNM 252000) from Colombia lacked a lower left canine. An incomplete alveolus can be seen but there is no trace of a root; therefore, it is likely that this tooth never was present in life. Several other teeth (right and left upper premolars) had definitely been lost in life. Another specimen from South America, an adult female (USNM 370119) from Venezuela, lacked the lower right canine. The mandible at the site where the permanent canine should have been was rough but there was no trace of an alveolus. Furthermore, the side of the mandible, which normally is expanded slightly to accommodate the root of the canine, is narrow. Probably the canine was not present in life; the remainder of the dental arcade in this specimen was normal.

Loss of Teeth in Life

Teeth frequently are lost in life in *A. geoffroyi*, *caudifer*, and in *cultrata*. There are no significant differences in the incidence of loss between the first two species; only 13 specimens of the latter species were available for study. Comparative incidence of loss of teeth is summarized in Table 4. In *geoffroyi*, the first upper incisors are frequently lost (6.91 incidence in males), as are the first and second upper premolars (Table 4). The high incidence of loss

TABLE 4.—Comparative incidence of loss of teeth in life for *Anoura geoffroyi* and *A. caudifer*. Total numbers of teeth, given at bottom of table, were used to calculate the percentages. An asterisk indicates a significant difference ($P \leq .05$) in incidence of loss of teeth between sexes.

Teeth	<i>Anoura geoffroyi</i>		<i>Anoura caudifer</i>	
	Male	Female	Male	Female
Upper				
I1	6.91	2.10	2.50	2.17
I2	3.31	1.68	2.50	0
C	0.55	0.84	0	0
P2	8.84	5.46	2.50	2.17
P3	4.97*	1.68	2.50	0
P4	0.83	0	0	0
M1	0.28	0	0	2.17
M2	0.55	0	0	2.17
M3	0.28	1.26	0	0
Lower				
c	0	1.26	0	2.17
p2	0.55	1.26	0	0
p3	0.55	1.26	0	4.35
p4	0	1.26	2.50	2.17
m1	0	1.26	0	0
m2	0.55	0	5.00	6.52
m3	0.83	2.10	5.00	0
Totals	362	238	40	46

of the first premolars in life is due to a periodontal disease caused by macronyssid mites that infest the oral mucosa adjacent to these teeth. This disorder is discussed in detail in a later chapter on pathological conditions of the oral cavity. The disease is lacking in *caudifer* and the incidence of loss of the first upper premolars (P2) is considerably lower (2.50). In *geoffroyi*, the second upper premolar (P3) is lost significantly more often ($P \leq .05$) in males than in females. This is the only instance in either *geoffroyi* or *caudifer* wherein a given tooth is lost significantly more often in one sex than in the other. The lower second and third molars are lost fairly frequently in *caudifer* (Table 4), but the incidence is not significantly greater than in *geoffroyi*. The large sample of *geoffroyi* probably gives a better

approximation of the actual incidence of loss of the lower molars in nature.

The causes of loss of teeth in life, other than destruction from infection at sites of infestations of mites, include erosion, dental caries, and, possibly, mechanical damage. The first two factors are discussed in a later chapter.

Glossophaga É. Geoffroy St.-Hilare

This genus of long-nosed bats, with four nominal species (*Glossophaga soricina*, *alticola*, *commissarisi*, and *longirostris*), occurs throughout much of Mexico, Central America, the northern half of South America, and the southern Lesser Antilles (Hall and Kelson, 1959: 114; Cabrera, 1958:71-72; Gardner, 1962: 1-2). Bats of the genus *Glossophaga* are moderate-sized among the glossophagines, are generally brownish in color, have a moderately elongate muzzle, short tail, and an unreduced interfemoral membrane.

The omnivorous feeding habits of *Glossophaga* probably are better known than those of any other glossophagine genus, and thus are summarized in some detail here. According to Husson (1962: 133), *G. soricina* originally was incorrectly thought to be a blood-sucking bat, probably as a result of its long tongue. Apparently, however, insects, fruit, nectar, and possibly meat comprise the diet of these long-tongued bats. Hall and Dalquest (1963:228) found fruit pulp in stomachs of specimens from Veracruz and reported further that they caught bats in rat traps that had been baited with bananas. Stomachs of specimens of *soricina* collected on Trinidad contained fruit juices mixed with small insects; the latter were thought to have been trapped in nectar and thus taken incidentally (Goodwin and Greenhall, 1961:245). This species also has been seen on calabash flowers (*Crescentia cujete*), possibly indicating that the bats obtain nectar from this species (Goodwin and Greenhall, *loc. cit.*). According to Goodwin (1946:311), the long tongue also is used to lap liquid from the flowers of night-

blooming cacti. Walker *et al.* (1964: 283) reported that in captivity specimens of *soricina* actively hunt insects in flight and, in fact, seem to prefer insects at certain times of the year. These authors also stated that captive bats have been observed to drink water mixed with honey, and to eat fruit juices and pulp. Arata *et al.* (1967:654) found large-sized insects in stomachs of specimens of *soricina* obtained in Colombia; in the stomach of one individual they found matted hair still attached to flesh, which possibly indicates carnivorous feeding habits. It is clear from the foregoing statements that bats of the genus *Glossophaga* feed on a wide variety of foods. The stomach of *soricina*, as one might expect, shows some morphological and histological characteristics of strictly frugivorous bats (for example, *Artibeus*) and some of strictly insectivorous bats (Forman, 1971).

The dentition of bats in the genus *Glossophaga* has been described in moderate detail by Miller (1907:138). Generally, differences in dentition between the nominal species are subtle; Gardner (1962:2-4) and Jones (1966:454) have described some of the minor differences in the upper and lower incisors that can be used as taxonomic characters. Morphological features of the upper and lower molars essentially are the same in all of the nominal species. Hershkovitz (1949:438) has reported the occurrence of a supernumerary upper premolar in a specimen of *Glossophaga soricina* and with regard to loss of teeth in this genus, and in other glossophagines as well, has stated that the teeth are ". . . weak and frequently defective . . . when teeth are missing, the loss appears to be the result of some violence, most probably in connection with the bats' voracious attacks on soft pulpy fruit containing hard pits."

All species of *Glossophaga* have 34 permanent teeth; the dental formula is: i 2/2, c 1/1, p 2/3, m 3/3. The moderate-sized teeth are not crowded, but most are in contact with one another and thus fill the available space.

Upper incisors.—The four upper incisors are set in a shallow arc and nearly fill the space between the canines. The inner teeth are large, have a narrow base, and a broad crown with a slightly oblique cutting edge; usually they are slightly procumbent (the degree being specifically variable). The outer incisors are slightly smaller than the inner teeth and differ morphologically in having a pointed crown and strongly oblique edge.

Upper canines.—The upper canines are simple, stout teeth that lack a longitudinal ridge and groove on the anterior face. The canines have small anterior and posterior cingula and a strongly concave lingual surface.

Upper premolars.—The upper premolars fill the space between the canine and the first molar; usually they are in contact, but rarely they overlap. The first premolar (P3) is short and relatively broad, low-crowned, and lacks cingula. The posterior half is only slightly broader than the anterior half. The second upper premolar (P4) is low-crowned and bulkier than the first; the posterior half is broader than the anterior half because of the poorly defined postero-lingual cingular shelf.

Upper molars.—The upper molars all are in contact, or nearly so, but are not crowded. The first two are squared and essentially the same size. Both have a W-shaped ectoloph. The third molar is only about 75 per cent the size of the first two. The paracone and metacone are large and prominent on M1 and M2, and relatively smaller on M3. The paracrista is short and projects anteriorly on the first upper molar, being more labially directed than on M2. The paracrista is largest and longest on the third molar. The precentrocrista and postcentrocrista form a deep, broadly U-shaped valley between the paracone and metacone on all molars, and the mesostyle is formed by equal contributions from the anterior and posterior elements. The first and second molars have long, postero-labially directed metacrista; the metacrista and

metastyle are lacking on the M3. The protocone on all three molars is nothing more than a low ridge-like cusp; the hypocone is lacking but a shallow hypoconal basin usually is present.

Lower incisors.—The lower incisors are well-rooted, moderately high-crowned teeth that in some species are in contact and in others are separated. These teeth fill 75 to 80 per cent of the space between the lower canines. The crowns are triangular in occlusal view.

Lower canines.—These teeth are stout and recurved; they lack a labial cingulum, but have narrow posterior and anterior cingular ledges and a broad postero-lingual cingular shelf.

Lower premolars.—The lower premolars are low-crowned, broad, and completely fill the space between the first molar and canine. The first and second (p2 and p3) are narrower than the third and usually overlap slightly. The third premolar (p4) has a broad postero-lingual cingular ledge and a slightly concave lingual coronal surface.

Lower molars.—All three lower molars are morphologically the same, but the first two (which are essentially the same size) are slightly larger than the third. The protoconid and metaconid are the largest and highest cusps; the paraconid is reduced and low. The metacristid and paralophid are nearly parallel and the lingual margin of the trigonid is slightly concave. The metacristid is lower than the paralophid. The protoconid is a shallow, U-shaped valley between the metaconid and protoconid. The entoconid is large and nearly conical and is separated from the metaconid by a deep valley. The hypoconid is but a low ridge-like cusp that is separated from the lingual margin of the talonid by a shallow groove along the longitudinal axis of the talonid.

Morphological Variation

More than 200 specimens of *Glossophaga soricina* from Chiapas, México, were used for a study of morphological variation in the genus. Thirty adult

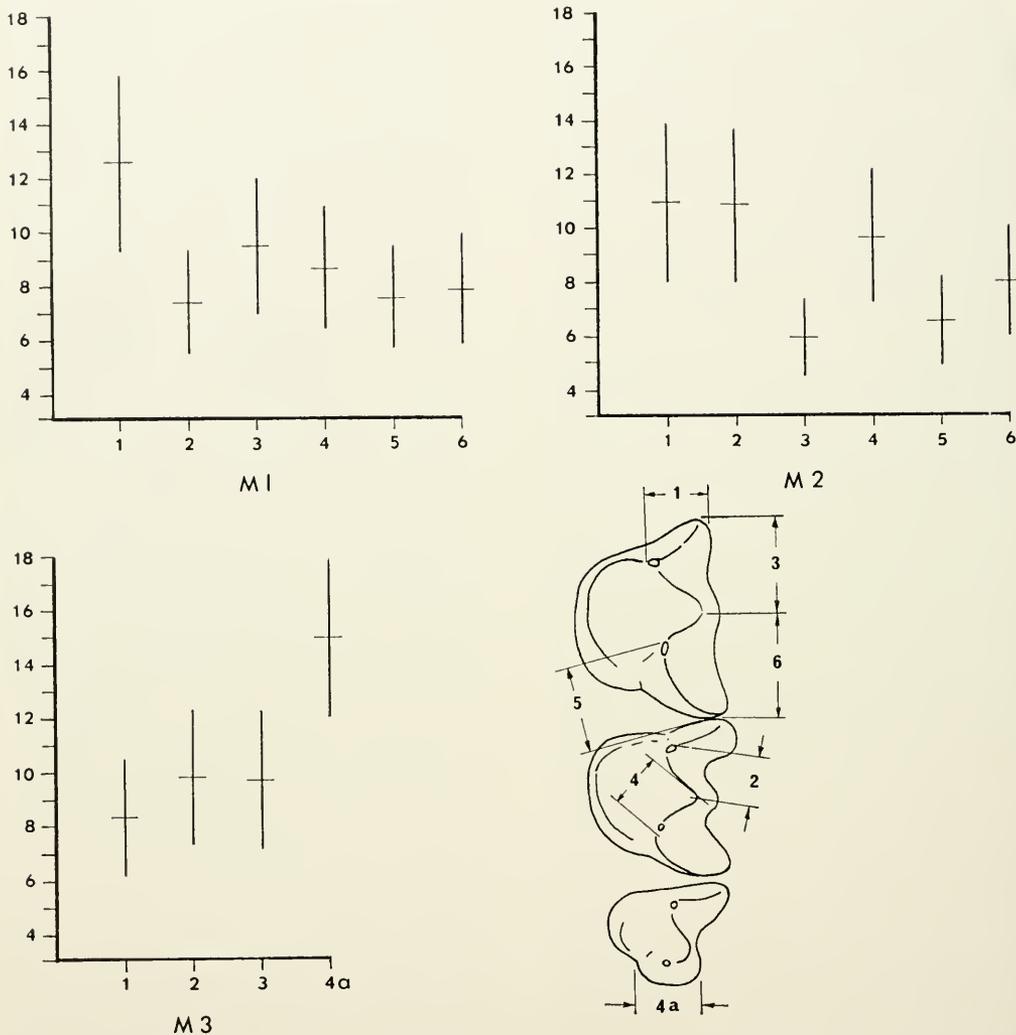


FIG. 16.—Graphs showing the coefficients of variation (horizontal bars) and two standard errors (plotted on ordinate) for measurements of morphological features of upper molars in *Glossophaga soricina* (measurement number plotted on abscissa). The six measurements taken on each of the first two molars are shown in the inset. The first three of these measurements were taken also on the third molar; measurement 4a is unique to the M3.

males from a single locality in Chiapas were used for the statistical analysis of dimensional variation in the third upper premolars (P4), and the upper and lower molars. The dimensional variation in these teeth is summarized in figures 16 and 17.

The upper incisors in *Glossophaga* vary only slightly in dimension and morphology. These teeth are especially difficult to study in this regard because

they are subject to attrition as well as destruction due to other causes. The second upper premolar (P4) is dimensionally and morphologically more variable than the first. In most specimens, there is a fairly broad postero-lingual cingular shelf on the second premolar but in a few individuals the shelf is lacking, or nearly so, and the tooth in occlusal view is laterally compressed. This structural variation is expressed in

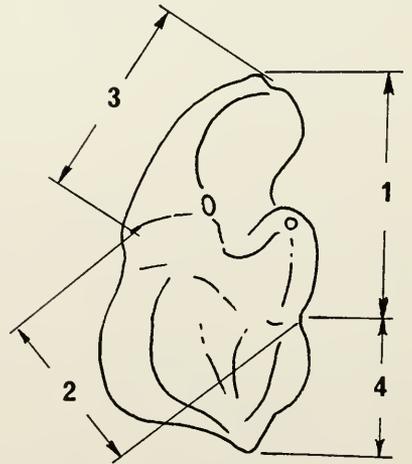
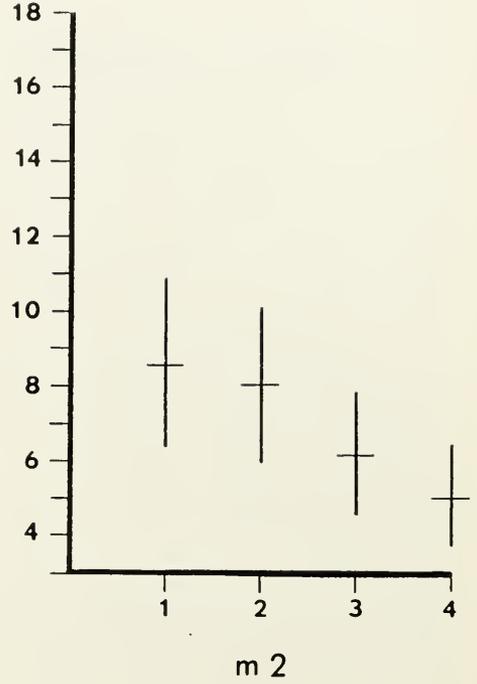
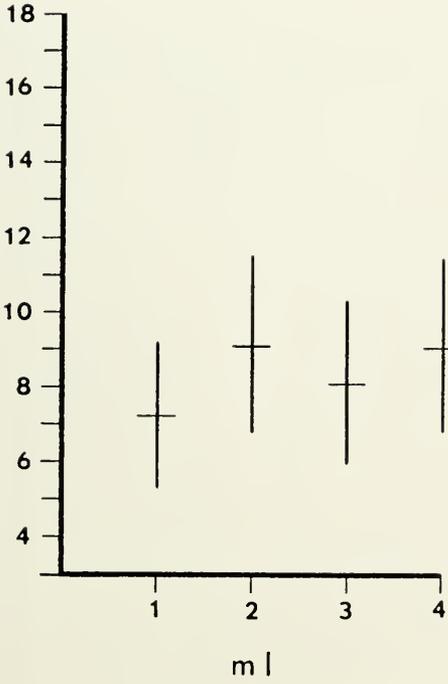


FIG. 17.—Graphs showing coefficients of variation (horizontal bars) and two standard errors (plotted on ordinate) for measurements of morphological features of lower molars in *Glossophaga soricina* (measurement number plotted on abscissa). The four measurements taken on each of the three molars are shown in the inset.

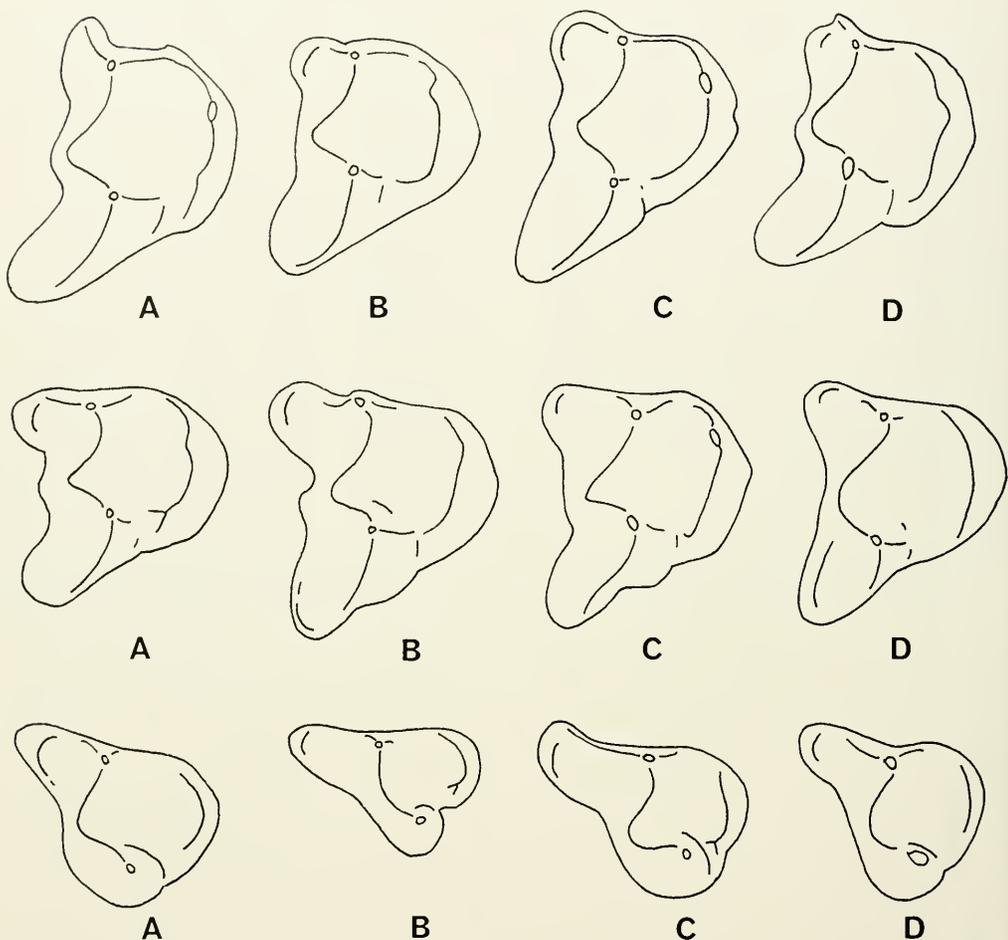


FIG. 18.—Examples of morphological variation in the upper molars in *Glossophaga soricina*. Top row (first molars): A, KU 60806; B, KU 60856; C, KU 68881; D, KU 60876. Middle row (second molars): A, KU 60866; B, KU 60831; C, KU 60841; D, KU 60864. Bottom row (third molars): A, KU 60840; B, KU 60835; C, KU 60863; D, KU 66850.

a fairly high coefficient of variation (9.94 ± 1.29) in measurements of the width of the tooth.

The first upper molar is highly variable in morphology as well as in dimension. The most striking variation is in the parastyle and paracrista which usually form a rounded bulge (such as in KU 60876 and KU 60856, Fig. 18), but in other specimens form a twisted, anteriorly projecting ridge (KU 60806, Fig. 18). This wide range of variation is reflected in a high coefficient of variation (12.51 ± 3.28) in length between the parastyle and paracone. The ectoflexus

is only slightly variable, especially in comparison with that of the second molar, but the outline and direction of the metaerista and metastyle are highly variable; this element is curved labially in KU 60806 and KU 60876, for example, whereas in KU 68881 it sweeps directly posteriorly (Fig. 18). In some individuals the metaerista and metastyle are somewhat reduced, and in the example figured the paracrista and parastyle also are unusually small (Fig. 18).

The second upper molar, overall, is slightly less variable than the first in *soricina* (Figs. 16, 18). As in the first

molar, the anterior element of the ectoloph is the most variable part of the tooth. The distance between the apex of the paracone and the tip of the parastyle yields a coefficient of variation of 10.95 ± 2.86 , which is slightly less than that of the same measurement of the first molar but high nevertheless. The morphological variation of the parastyle of the upper second molar is shown in figure 18; in KU 60866 the parastyle is small, rounded, and directed labially, whereas in KU 60831 it is considerably more prominent and slightly twisted anteriorly. In some individuals the parastyle is reduced and narrow (KU 60864, Fig. 18). Variation of the precentrocrista essentially equals that of the paracrista but greatly exceeds variation in the distance between the mesostyle and parastyle (Fig. 16). Thus, only two sides of the triangle formed by the anterior element of the ectoloph are highly variable, which reflects the variation in the position of the paracone itself. Examination of the examples in figure 18 will clarify the extent of this variation. The posterior element of the ectoloph is not as variable as the anterior element; the greatest dimensional variation in the posterior element is in the length of the postcentrocrista ($CV, 9.56 \pm 2.48$) and the least is in the length of the metacrista ($CV, 6.45 \pm 1.66$). The shape of the metacrista, the width of the metastyle, and the orientation of the posterior element of the ectoloph are somewhat variable (Fig. 18). For example, in KU 60864, in which the mesostyle is unusually small, the metastyle is directed almost posteriorly, whereas in KU 60866, in which the mesostyle is prominent, the metastyle is directed labially (Fig. 18). The hypoconal basin is variable to about the same degree as in the upper first molar. In some individuals the postprotocrista extends to the base of the metacone (KU 60881, Fig. 18), whereas in others it ends in a distinct basin (KU 60866 and KU 60864, Fig. 18). The ectoflexus is highly variable in the second molar, reflecting the variable shape

of the mesostyle itself, which in some individuals is barely distinguishable (KU 60864, Fig. 18) and in others prominent (KU 60866 and KU 60881, Fig. 18).

The third upper molar, the smallest in *Glossophaga*, is highly variable in outline (Fig. 18). Although the extremes illustrated in figure 18 would indicate that the anterior element of the ectoloph is dimensionally more variable than in the other two molars, such is not the case when large samples are studied. The distance between the mesostyle and the parastyle is more variable than in the first two molars ($CV, 9.63 \pm 2.50$) but the length of the paracrista is less variable than in either of the first two molars (Fig. 16). The position of the triangle that forms the anterior element of the ectoloph of the third molar varies relative to the longitudinal axis of the tooth. For example, in KU 60835 the paracrista is directed labially and in KU 60863 it is twisted slightly and directed almost anteriorly (Fig. 18). The ectoflexus is not as variable in the third molar as it is in the preceding two but the mesostyle varies considerably, nevertheless. In some individuals the mesostyle is a distinct bulge, whereas in others it is essentially indistinguishable (compare KU 60881 and KU 60863, Fig. 18). The hypoconal basin is present in some teeth but in others the postprotocrista connects with the base of the metacone. The width of the metacone is the most variable dimension in any of the molars in *Glossophaga soricina*. It is possible, however, that the high coefficient of variation (14.95 ± 3.84) reflects, in part, the difficulty in taking the measurement because of the lack of a metastyle for orientation. The variation in the size and shape of the mesostyle apparently is related to the degree to which the anterior and posterior elements of the ectoloph fuse during odontogenesis.

In *Glossophaga*, the lower incisors vary only slightly in dimension and are relatively stable morphologically. Spacing and size are consistent enough to be used as a mean of distinguishing be-

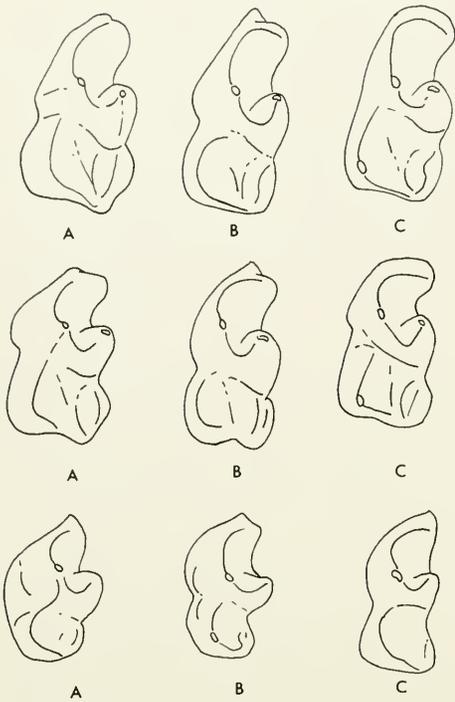


FIG. 19.—Examples of morphological variation in the lower molars in *Glossophaga soricina*. Top row (first molars): A, KU 60877; B, KU 60881; C, KU 60857. Middle row (second molars): A, KU 60877; B, 60881; C, KU 60857. Bottom row (third molars): A, KU 60855; B, KU 60883; C, KU 60857.

tween the nominal species. The lower canines, like the upper canines, vary only slightly. The lower premolars, which are simple teeth, vary only slightly in morphology. Of these teeth, only the third is noteworthy in that a few specimens have a small cingular lip on the posterior end of this tooth.

In the lower first molar the breadth across the metaconid and protoconid is the most variable dimension ($CV, 9.18 \pm 2.38$). This variation, in part, reflects the degree to which the metaconid is directed lingually. For example, in KU 60877 this cone is directed slightly lingually, but in KU 60857 it is nearly vertical (Fig. 19). In some individuals there is a small flange on the anterior-facing surface of the paraconid; in the examples shown in figure 19, this flange is most developed in KU 60881 and non-

existent in KU 60857. In the lower first molar the length of the metaconid is the least variable dimension of the trigonid (Figs. 17 and 19). The talonid varies greatly in length in part due to differences in the size of a small flange on the posteristid (directly posterior to the entoconid). In KU 60877, for example, the flange is large and would contribute greatly to the dimension of the fourth measurement, whereas in KU 60881 the flange is barely discernible and, therefore, the length of the talonid in this specimen is considerably less than in the other (Fig. 19). The coefficient of variation (9.14 ± 2.36) is much greater than in the second molar and slightly greater than in the third molar (Fig. 17).

The morphological and dimensional variation of the second molar is much like that of the first, except that dimensional variation, as reflected by coefficients of variation, is slightly less, especially in the length of the talonid (Fig. 17). As in the first molar, there is a variable flange on the anterior surface of the paraconid of the second molar. This flange, which is most prominent in KU 60881 (Fig. 19), usually is developed to about the same degree as in the first molar in the same individual. For example, in KU 60857, which lacked a flange on the first molar, the flange also was lacking on the second molar. The coefficient of variation of the length of the talonid of the lower second molar (5.02 ± 1.28) is considerably less than in the first molar, even though there is a variable flange on the posteristid (Fig. 19).

The third molar is the most variable of the lower molars, both morphologically and dimensionally. The length of the paralophid varies greatly ($CV, 10.17 \pm 2.46$), as can be seen in figure 17. In part, this variation is related to the position of the protoconid relative to the labial edge of the tooth and is reflected also by the high coefficient of variation in the width across the protoconid and metaconid ($CV, 9.61 \pm 2.50$). As in the

TABLE 5.—Correlation matrix for measurements of the three upper molars in *Glossophaga soricina*. Abbreviations for measurements used in this table are the same as those in Table 1. Measurements are illustrated in Fig. 16. Coefficients significant at the alpha level of 0.05 are marked with an asterisk and those significant at the 0.01 level are marked with a double asterisk.

	M 1						M 2						M 3			
	PAC-PAS	PAC-MES	MES-PAS	MES-MEC	MEC-MTS	MTS-MES	PAC-PAS	PAC-MES	MES-PAS	MES-MEC	MEC-MTS	MTS-MES	PAC-PAS	PAC-MES	MES-PAS	MEC
M 1	1.00															
	PAC-MES	1.00														
	MES-PAS	-0.21	1.00													
	MES-MEC	-0.01	0.32	1.00												
	MEC-MTS	0.21	0.25	0.17	1.00											
	MTS-MES	0.19	0.13	0.00	-0.03	1.00										
	PAC-PAS	0.57**	0.05	-0.05	-0.01	0.30	1.00									
	PAC-MES	0.25	0.24	0.26	-0.06	-0.05	0.25	1.00								
	MES-PAS	0.26	0.26	0.37*	0.37*	0.03	-0.02	-0.04	1.00							
	MES-MEC	0.24	0.29	0.25	0.08	0.01	0.32	0.35	0.48**	1.00						
	MEC-MTS	0.07	0.27	0.27	0.14	0.14	0.20	0.38*	0.24	0.26	1.00					
	MTS-MES	0.20	0.18	0.15	0.04	0.11	0.23	0.14	0.08	0.15	0.58**	1.00				
M 2	PAC-PAS	0.19	-0.08	0.00	0.12	0.18	0.01	0.39*	0.01	0.07	0.05	0.52**	1.00			
	PAC-MES	-0.12	0.23	0.29	0.16	0.02	0.10	0.18	0.24	0.30	0.29	0.67**	0.25	1.00		
	MES-PAS	0.08	0.26	0.37*	0.33	0.39*	0.17	0.25	-0.01	0.27	0.23	0.28	0.06	0.45*	1.00	
	MEC	-0.23	0.20	0.11	0.11	0.14	0.24	-0.17	0.18	0.45**	0.23	0.26	0.10	0.05	0.50**	1.00

first two molars, there is a small, variable flange on the anterior-facing surface of the paraconid (Fig. 19). A similar flange, found on the posteristid of the first molars, is lacking on the third. Most of the variation in the talonid of the third molar results from variation in size of the entoconid.

Dental Interactions

A matrix of Pearson product moment correlation coefficients that was produced using the data discussed in the previous section revealed an interesting series of interrelationships and examples of dental integration in the teeth of *Glossophaga soricina*. Most coefficients of correlation were low, which perhaps is not surprising in view of the great dimensional variation in the teeth. Coefficients of correlation of 0.36 and above are significant at the critical level of 0.05, and those of 0.46 and above are significant at the 0.01 level. All measurements referred to in the following paragraphs are illustrated in figures 16 and 17.

When equivalent measurements of the upper three molars are compared, correlations between individual measurements of the anterior element of the first molar and those of the second are notably greater than when the individual measurements of the posterior elements are compared (Table 5). For example, measurement of the paracone-parastyle length of M1 has a coefficient of correlation of 0.57 with the same measurement of M2, whereas the length of the mesostyle-metacone of M1 is not correlated with the equivalent measurement of M2 (r , 0.08). The dimensional relationship between the anterior elements of all three upper molars is greater than the correlation between the posterior elements of the first and second molars. In the anterior element of M1 the first measurement (paracone-parastyle) either is not correlated or shows slight negative correlation with the other two sides of the triangular element of the ectoloph; when compared to the measurement of the distance between the mesostyle and

parastyle, the coefficient of correlation is -0.21 . The position of the paracone is variable in M1, as pointed out in the previous section, and thus the distance between the paracone and parastyle has a high coefficient of variation (12.51). The pattern of correlation within the posterior element of the first molar is about the same as that found within the anterior element (Table 5). For example, there is no correlation between the metacone-mesostyle length and the distance between the metastyle and mesostyle (r , -0.03).

The intra-element relationships found in M2 and in M3 differ somewhat from those of the first molar. In the second molar the lengths between the parastyle and paracone and paracone and mesostyle are correlated (0.38), but as in M1 the paracone-parastyle and mesostyle-parastyle lengths are not correlated (-0.04). The apparent reason for this pattern can be seen in figure 16. As pointed out in the previous section, the paracone-parastyle and paracone-mesostyle measurements in M2 are highly variable, whereas the mesostyle-parastyle measurement has a low coefficient of variation. In the anterior element of M3 yet another pattern is found; the paracone-parastyle length is well correlated ($P \leq 0.01$) with both of the other two measurements (0.58 and 0.49, see Table 5). One aspect of intra-element relationships that is common to the anterior elements of all three upper molars is that of high correlation between the paracone-mesostyle and mesostyle-parastyle. The coefficients of correlation between these measurements in M1, M2, and M3, are, respectively, 0.50, 0.47, and 0.48. This strong, consistent correlation probably results from the fact that when the paracone-mesostyle length is greater the mesostyle is broader; increase in size at this site results in an increase in the measurement of the distance between the mesostyle and the parastyle. Not surprisingly, the same pattern is found in the posterior elements of M1 and M2; as the metacone-metastyle length increases

so does the distance between the metastyle and mesostyle (Table 5).

Inter-element, within-tooth, correlations and lack of correlations also are interesting and several patterns are involved. The mesostyle-parastyle length in the second molar is correlated with the distance between the mesostyle and metacone of the posterior element (r , 0.49) probably for the same reason that the paracone-mesostyle length of the anterior element is correlated with the mesostyle-parastyle length. The mesostyle-parastyle length in M1 and M2 is not correlated, however, with the mesostyle-metastyle length; in M1 the r value is 0.003 and in M2 it is 0.15 (Table 5).

Inter-tooth comparisons between non-equivalent measurements also are noteworthy because correlations in these instances can indicate control from a common source rather than direct mechanistic relationships. When the mesostyle-metacone length of the first molar is compared to the mesostyle-paracone length of second and third molars, the correlations show the same pattern (0.37 with M2 and 0.33 with M3). When the distance between the mesostyle and metacone of M1 is compared with the parastyle-paracone measurement of the same tooth, the coefficient of correlation is low (Table 5). The metacone-mesostyle length of the first molar is well correlated with the paracone-parastyle length of the second molar (0.46); this relationship is possibly direct because the first molar develops and attains the functional eruptive phase somewhat before the second molar (Fig. 10). The greater the posteriorly-directed length of the metastyle of M1, the more the parastyle of the second molar will have to be directed labially in the crowded upper jaw of *Glossophaga*. When the parastyle is directed labially, the distance between the paracone and the parastyle of M2 is increased (see KU 60841 and KU 60864, Fig. 18).

Among the upper molars, the within-tooth correlation coefficients (when all combinations are considered) are lowest

in the first molar and highest in the third (Table 5). Within the first molar only two of 15 combinations have a coefficient of correlation above 0.36, whereas within the second molar eight of 15 are above 0.36 and in the last molar, which is morphologically reduced and therefore has fewer possible combinations, four of six exceed that figure. Although the third molar is reduced and is considerably smaller than the first two, it does not appear to be in a separate field of morphogenetic influence. Indeed, the overall correlation with the second molar is slightly higher than the overall correlation between the first and second molars (Table 5). Coefficients of correlation of four of 36 possible combinations between M1 and M2 are 0.36 or more, as are four of 24 combinations between M2 and M3. The amount of overall inter-tooth correlation apparently decreases with the increase of distance between the individual teeth because, whereas four of 24 combinations between M2 and M3 were above 0.36, only two of 24 were above 0.36 when the first and third molars were compared.

Combinations for all measurements of the three lower molars of *Glossophaga soricina* are given in the correlation matrix in table 6. When equivalent measurements are compared on an inter-tooth basis in the lower molars, the coefficients of correlation between the first, second, and third molars are low. For example, the width across m1 at the metaconid-protoconid has a coefficient of correlation of only 0.27 with the same measurement in the second molar and is not correlated with the measurement in the third molar (r , 0.18). Another example is length of the talonid, which is not correlated with the length of the same feature in either m1 (r , 0.08) or in m3 (r , 0.11). When equivalent measurements in the second and third molars are compared, the width (metaconid-protoconid) has a significant coefficient of correlation (0.38) as does the length of the talonid (0.44).

TABLE 6.—Correlation matrix for measurements of the three lower molars in *Glossophaga soricina*. Abbreviations for measurements used in this table are the same as those in Table 2. Measurements are illustrated in Fig. 17. Coefficients significant at the alpha level of 0.05 are marked with an asterisk and those significant at the 0.01 level are marked with a double asterisk.

	m 1				m 2				m 3			
	PAD-MTD	MTD-POD	POD-PAD	TALONID	PAD-MTD	MTD-POD	POD-PAD	TALONID	PAD-MTD	MTD-POD	POD-PAD	TALONID
m 1	1.00											
	0.40	1.00										
	0.26	0.33	1.00									
	0.17	0.22	0.24	1.00								
m 2	0.24	0.37*	0.32	0.17	1.00							
	0.31	0.27	0.32	0.54**	0.22	1.00						
	0.14	0.34	0.19	0.14	-0.09	0.30	1.00					
	-0.28	0.04	-0.17	0.08	-0.20	0.10	-0.14	1.00				
m 3	0.20	0.18	0.13	-0.20	0.23	0.15	0.08	-0.13	1.00			
	-0.01	0.18	0.52**	0.32	0.21	0.38*	0.31	0.18	0.19	1.00		
	0.33	0.15	0.37*	-0.03	0.28	0.24	0.44*	-0.26	0.44*	0.37*	1.00	
	0.21	0.44*	0.41*	0.11	0.07	0.04	0.09	0.44*	0.00	0.33	0.07	1.00

Overall, the patterns of intra-tooth correlations are different in each of the lower molars. The degree of correlation between the width of the teeth (metaconid-protoconid) and the length of the paralophid (protoconid-paraconid) is one exception, however, because in all three molars the values are above 0.30 (Table 6), although the coefficient of correlation is significant only in m3 (r , 0.37). In the m1, width across the tooth is correlated with length of the metaconid (paraconid-metaconid), whereas neither the width of the m2 nor the width of the m3 is correlated with its metaconid (0.40, 0.22, 0.19, respectively). It is noteworthy that in conjunction with this decrease in coefficient of correlation, there is an increase in the coefficients of variation for the length of the metaconid (paraconid-metaconid) as follows: 7.25 in m1, 8.58 in m2, and 9.79 in m3. As shown in table 6, the coefficients of correlation of the within-tooth combinations of measurements are highest in the third molar (two of six above 0.36) and lowest in the second (none of six above 0.36). The third molar, which is dimensionally the most variable of the lower molars (Fig. 17), also develops and attains the functional eruptive stage well behind the m1 and m2 (Fig. 10). Development and eruption of the second molar is concomitant with that of the first. This characteristic of odontogenesis in *Glossophaga* results in interesting correlations between teeth. For example, the two measurements of length of the trigonid (paraconid-metaconid and paraconid-protoconid) of the third molar show low, but possibly noteworthy, negative correlation with the length of the talonid of both the first and second molars (Table 6). When compared with the talonid of the first molar, the metaconid (paraconid-metaconid) of m3 has a negative coefficient of correlation of -0.20 and when compared to the talonid of the second molar, the paralophid of m3 has a low negative coefficient of correlation of -0.26 . These negative values possibly result from the

relatively short mandibular length and the subsequent crowding of developing teeth in *Glossophaga*. Limitation of space in conjunction with the direct influence of the presence of two molars (m1 and m2) having almost completed odontogenesis (mature enamel) probably affects the cell masses of an as yet unmineralized third molar. The reverse of this inter-tooth pattern also is noteworthy. The width (metaconid-protoconid) of the m2 correlates well with the length of the talonid of m1 (r , 0.55). This indicates that the larger the first molar, the larger will be the trigonid of the second. The talonid of the third lower molar, because it is part of the last tooth in the sequence, responds positively to several sizes, including the width and length of the trigonid of m1 (Table 6).

In summary, these interactions are as follows: 1) the first two lower molars develop at approximately the same rate and attain the functional eruptive stage together (Fig. 10); 2) the overall size of the m1 affects the two main elements of the m2 differently in that the trigonid responds positively to overall size of m1 and the length (but not the width) of the talonid responds negatively or not at all (r , -0.28); 3) the size of the trigonid of the m2 is correlated (positively) with the trigonid of m3, which develops well after the first two lower molars; 4) the size of the talonid (length) of m2 has either no effect or, possibly, a slight negative effect on the length of the trigonid of m3 (r , -0.20), and a strong, significant, positive effect on the length of the talonid (r , 0.44), which is the last element of the lower molar to form. The operatives in this series of morphogenetic interrelationships among the lower molars in *Glossophaga* are incompletely known but certainly are mechanistic in part. As in the upper molars, all of the lower molars apparently are in the same morphogenetic field; two of 16 combinations of measurements of m1 and m2 have significant coefficients of correlation as do

TABLE 7.—Matrix of coefficients of correlation for upper and lower molars in *Glossophaga soricina*. The lower molars are plotted across to top; measurements are illustrated in Figs. 16 and 17. Coefficients significant at the alpha level of 0.05 are marked with an asterisk and those significant at the 0.01 level are marked with a double asterisk.

	m 1				m 2				m 3			
	PAD-MTD	MTD-POD	POD-PAD	TALONID	PAD-MTD	MTD-POD	POD-PAD	TALONID	PAD-MTD	MTD-POD	POD-PAD	TALONID
PAC-PAS	0.41*	0.22	-0.17	0.15	0.04	0.43*	-0.04	0.03	-0.05	-0.15	0.07	-0.01
PAC-MES	-0.27	-0.09	-0.11	0.37*	-0.09	-0.03	-0.17	0.36*	-0.26	0.00	-0.32	0.15
MES-PAS	-0.16	0.09	0.19	0.25	-0.05	0.03	-0.16	0.09	0.00	0.27	-0.12	-0.03
MES-MEC	-0.07	0.32	0.18	0.17	0.12	0.03	-0.01	0.06	-0.06	-0.07	0.01	0.22
MEC-MTS	0.30	0.15	0.21	0.19	0.21	0.16	-0.06	-0.10	-0.20	0.18	0.00	0.30
MTS-MES	0.27	0.10	0.39*	0.29	0.20	0.48**	-0.15	0.28	-0.08	0.30	-0.18	0.42*
PAC-PAS	0.35	0.16	0.05	0.03	0.21	0.21	-0.15	0.24	0.15	0.08	0.12	0.24
PAC-MES	-0.07	-0.03	-0.04	0.24	-0.14	0.28	-0.16	0.28	-0.11	-0.02	-0.19	0.07
MES-PAS	0.05	0.11	-0.08	0.42*	-0.07	0.18	-0.18	0.06	-0.32	-0.13	-0.15	0.02
MES-MEC	0.07	0.11	-0.02	0.37*	0.14	0.32	-0.33	0.53**	-0.24	0.21	-0.14	0.17
MEC-MTS	-0.15	-0.08	-0.07	0.13	0.36*	-0.06	-0.50**	0.32	-0.05	0.07	-0.31	0.20
MTS-MES	0.13	0.32	-0.05	0.19	0.22	0.25	0.03	0.56**	-0.16	0.31	-0.12	0.42*
PAC-PAS	0.16	0.33	-0.01	0.01	0.30	-0.26	-0.12	0.06	-0.14	-0.12	-0.01	0.31
PAC-MES	-0.01	0.17	0.17	0.20	0.23	-0.20	-0.40*	0.11	-0.26	-0.06	-0.44*	0.34
MES-PAS	0.20	0.42*	0.07	0.03	0.23	-0.20	-0.40*	0.03	-0.08	-0.20	-0.27	0.19
MEC	-0.05	-0.05	0.18	0.22	0.11	-0.08	-0.24	-0.10	-0.45*	0.02	-0.36*	0.25

TABLE 8.—Comparative incidences (in parenthesis), by sex, of certain congenital abnormalities in dentition of *Glossophaga soricina*. A significant difference ($P \leq .01$) between sexes was found only in incidence of hyperdontia of lower incisors.

Abnormality	Number and incidence	Abnormality	Number and incidence
Hyperdontia		Partial anodontia	
upper premolars	male = 1 (0.41) female = 5 (1.46)	upper incisors	male = 2 (0.82) female = 0
upper incisors	male = 0 female = 1 (0.29)	lower incisors	male = 4 (1.63) female = 0
lower incisors	male = 7 (2.86) female = 0	third upper molars	male = 1 (0.41) female = 2 (0.58)
		third lower molars	male = 1 (0.41) female = 3 (0.88)

four of 16 combinations of measurements between m1 and m3 (Table 6). Slightly fewer combinations between the second and third molars are significant (three of 16).

A matrix of coefficients of correlation for combinations of measurements of the upper and lower molars is given in table 7. The first upper molar, which in *Glossophaga* apparently completes odontogenesis and attains the functional eruptive stage before even the first lower molar (Fig. 10), has seven coefficients of correlation of 0.36 or higher (out of 72 possible combinations) with measurements of the lower molars (Table 7). More of these correlations are with the first and second lower molars (three each) than with the third (one). The second upper molar also has seven coefficients of correlation above 0.36; four are with the second lower molar and only two are with the m1. The third upper molar, which develops and reaches the occlusal plane after the first two molars, at approximately the same time as the m3, has a total of six correlations with the lower molars that are significant ($P \leq .05$).

The first upper molar has no significant negative coefficients of correlation with the lower molars. Overall dimensions of the three upper molars have an equal number of negative correlations with the second and third lower molars

(three each) and none with m1. The lengths of the paralophid (protoconid-paraconid) of the second and third lower molars, which occlude directly with the first and second upper molars, have high negative coefficients of correlation (up to -0.50) with the posterior element of the ectoloph of M2 and the anterior element of M3 (Table 7). The greatest number of negative correlations are with lengths of the trigonids of m2 and m3. This would be expected, considering the fact that overall the size of the individual upper molars correlates positively with the size of the first lower molar, which in turn clearly is interrelated to size of the various elements of the second and third lower molars.

Dental Abnormalities

The following three kinds of abnormal conditions are moderately common in the genus *Glossophaga*: 1) hyperdontia resulting in extra upper premolars, extra upper incisors, and extra lower incisors; 2) congenital agenesis of lower incisors, upper incisors, upper third molars, and lower third molars resulting in partial anodontia; and 3) abnormal loss of teeth in life. The incidences of the first two kinds of abnormal condition are given in table 8, and the comparative incidence of the third kind is summarized in table 9.

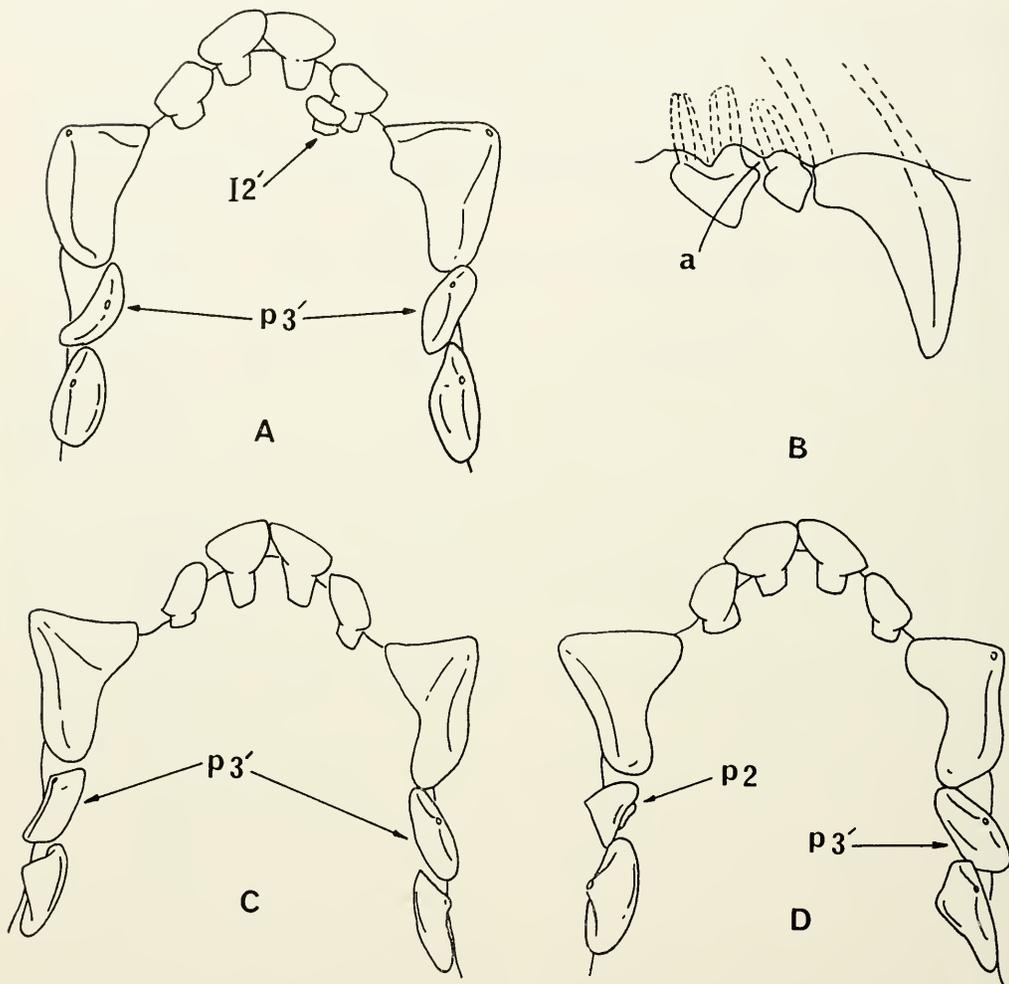


FIG. 20.—Examples of supernumerary premolars and incisors in *Glossophaga soricina*. A, KU 60880—occlusal view of supernumerary right and left first premolars ($P3'$) and supernumerary, ectopic second incisor ($I2'$); B, KU 91571—lateral view of atavistic upper premolar ($P2$) having one root rather than two as in the normal $P3$, the area denoted by "a" is shown in the histological view in Fig. 21; C, KU 102312—occlusal view of supernumerary right and left first premolars ($P3'$); D, KU 102350—occlusal view of an atavistic $P2$ and a supernumerary first premolar ($P3'$).

Hyperdontia

Hyperdontia was found in 14 specimens of *Glossophaga soricina* (818 were examined), but in none of 101 specimens of *commissarisi* or in 136 specimens of *alticola*. Although most of the specimens having one or more extra teeth were in a large series from Chiapas, México, the geographic differences are not significant.

Eight specimens (five females and three males), six from Chiapas and two

from Sinaloa, having one or more extra premolars were examined and are described below. The difference between incidence of extra upper premolars in the sexes is not significant ($P \leq .05$). Four examples of abnormal configurations are shown in figure 20; three examples illustrate extra premolars resulting from double initiation of the developmental process, whereas the fourth (specimen KU 91571) shows an atavistic tooth ($P2$).

An adult female from Chiapas (KU 60880) has an extra upper premolar on both sides anterior to the first premolar (Fig. 20). The extra teeth, which probably resulted from double initiation, have two roots and the general morphological features of normal upper first premolars. Both teeth are slightly smaller than normal first premolars (about 80 per cent their size), and are set at an angle to the toothrow; the one on the right is in contact with the postero-lingual surface of the canine and the antero-labial surface of the next premolar (Fig. 20). In addition to supernumerary upper premolars, this specimen also has an ectopic second upper incisor on the left side. This latter abnormality is discussed further in a following paragraph.

Another adult female from Chiapas (KU 60847) has supernumerary upper premolars on the right and left, anterior to the normal first premolars. The extra teeth are slightly smaller than the normal first premolars but have two roots and the same morphological configuration and, therefore, probably resulted from double initiation. Both of the extra teeth, which are in contact with the canines and following premolars, are crowded and the one on the left side is slightly out of line with the remainder of the toothrow. The other teeth in this specimen are normal.

An adult male (KU 60855) from the same locality as the preceding specimen, has an extra upper premolar on the right side. The extra tooth, which is set at an angle with its posterior end slightly overlapping the antero-labial surface of the first premolar and its anterior end in contact with the canine, is about 75 per cent the size of a normal first premolar; it has two roots and essentially the same morphological configuration and, therefore, probably resulted from double initiation.

Another adult male from Chiapas (KU 102312) has supernumerary upper premolars on the right and left (Fig. 20). These extra teeth, which are located directly anterior to the normal

upper first premolars, are only slightly smaller than the normal teeth and have two roots and the same morphological configuration as the normal teeth. Due to lack of space, the extra teeth are set at a slight angle with their anterior ends in contact (or nearly so) with the postero-lingual surface of the canines and their posterior ends overlapping the antero-labial surface of the first premolars. The remainder of the dental arcade is normal in this individual.

An adult female from Chiapas (KU 60841) has an extra upper premolar on the left side between the canine and first upper premolar. The extra tooth is slightly smaller than the usual P3, being only about 80 per cent as large, but has two roots and the same morphological features as the normal first premolar. The remainder of the dental arcade is normal in this specimen.

In an adult female from Sinaloa (KU 75204) there are two extra upper premolars, one on each side posterior to the canines. The extra premolars are about 90 per cent the size of normal upper first premolars, but are double rooted and morphologically like the first premolars. These extra teeth, which are crowded between the canine and first premolars, probably resulted from double initiation of development. In this individual, the lower right first molar had been lost in life but the remainder of the dental arcade was normal.

One adult female from Chiapas (KU 102350) is especially interesting; it has a supernumerary upper premolar on the left that apparently resulted from double initiation because it has two roots and morphologically appears to be a "normal" first premolar and, on the right, has a small tooth with but one root that apparently is an atavistic premolar representing P2. The small, extra premolar is about 25 or 30 per cent the size of a normal first premolar and consists of a single, laterally-compressed cone with a slightly concave lingual surface. This tooth is slightly crowded and set at an angle with its posterior end overlapping

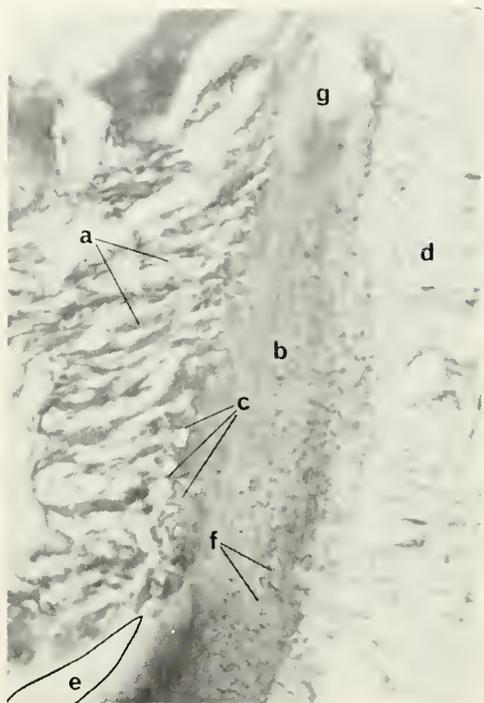


FIG. 21.—Longitudinal section (labial view) of posterior half of root of an atavistic P2 in a specimen of *Glossophaga soricina* (RRP 928): a, oblique periodontal ligaments; b, dentin; c, irregular area where periodontal ligaments meet dentin in apparent absence of cementum; d, scattered, diffuse periodontal ligaments in the pulp cavity; e, the enamel space; f, areas of poorly mineralized dentin; g, apex of root. Area shown here corresponds to "a" of Fig. 20. Stained with Mallory triple.

the normal first premolar (P3) on the antero-labial side (Fig. 20). The supernumerary premolar on the left probably resulted from double initiation because it resembles in all ways the normal first premolar except that it is only about 90 per cent the size of a normal tooth. This extra premolar is greatly crowded and in contact with both the canine and first premolar (Fig. 20). The remainder of the dental arcade in this specimen is normal.

An adult female from Campeche (KU 91571) has an extra premolar on the upper right side between the first upper premolar and upper canine. This extra tooth is small, has a rounded coronal

shape, and is single rooted; thus, it has the characteristics of an atavistic tooth and possibly represents the P2, which is characteristically lacking in *Glossophaga*. The positioning of the extra premolar and the shape of the crown and root in comparison with a normal first premolar (P3), is shown in Fig. 20. This tooth was not studied histologically but a similar tooth, in a specimen from Sinaloa, has been studied and the shape of the tooth, its relationship to the canine and first premolar (P3), and its histological features, are shown in Fig. 21 and discussed in the following paragraph.

An uncatalogued specimen, bearing field number RRP 925, was found to have atavistic upper premolars on both sides. In this individual, which is an adult male from Sinaloa, the small, extra upper premolars had one root and their coronal morphology differed considerably from that of a normal first upper premolar (Fig. 20). The specimen, which was stored in 70 per cent alcohol, was examined grossly and then histologically, using the methods described in the chapter on Methods and Materials. The crown and single root of the right atavistic premolar are shown in Fig. 20; the normal upper first premolar and the canine also can be seen to each side of the abnormal tooth. The roots of the first premolar (P3) are normal in all respects, whereas the root of the extra tooth is incomplete. The abnormal tooth lacks a cementum layer and therefore the horizontal periodontal ligaments attach directly to the dentin, producing an irregular surface (Fig. 21). The apical end of the root is completely open and typical pulp is lacking; instead, the dense periodontal ligaments normally found at the apex of a root extend approximately one half the distance into the pulp cavity. Apparently the atavistic teeth were being destroyed because the anterior-facing internal surface of the root of one tooth is incomplete (Fig. 21). Perhaps the most important aspect of the histological analy-

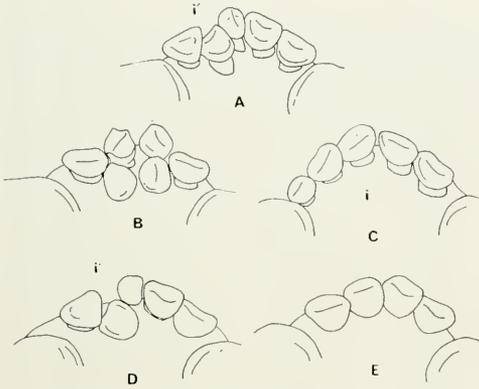


FIG. 22.—Examples of supernumerary lower incisors in four specimens of *Glossophaga soricina*. A, KU 95754—extra incisor (*i'*) located between the inner incisors; B, KU 60935—duplicated inner incisors; C, KU 87312—extra incisor (*i'*) posterior to second incisor on left side; D, KU 102323—extra incisor (*i'*) between the inner incisors; E, KU 102312—normal configuration of lower incisors.

sis is the fact that the upper first premolars (P3), unlike the atavistic tooth, were found to be normal in all respects. The remainder of the dental arcade in this specimen was normal and the gingivae did not appear to have been inflamed or otherwise abnormal.

Upper incisors.—Only one specimen, KU 60880, which was mentioned previously, was found to have an extra upper incisor. In this specimen, the ectopic second incisor is about 25 per cent the size of a normal second incisor and has essentially the same morphological features (Fig. 20). The lack of additional specimens with this abnormality indicates that the occurrence is extremely low in *Glossophaga*.

Lower incisors.—One or more extra lower incisors were found in seven specimens, all males, of *Glossophaga soricina* from Chiapas, Guatemala, and Sinaloa. The apparent lack of this abnormal condition in females is significant ($P \leq .05$). Four examples of hyperdontia of lower incisors are shown in figure 22 and compared with the normal condition.

In an adult male from Sinaloa (KU

95754) there are five lower incisors (Fig. 22). The extra tooth is located on the left side, near the mandibular symphysis. This tooth possibly resulted from a split during the proliferative stage rather than from abnormal initiation because neither it nor the tooth to its left appears to be normal. The innermost incisor on the left is smaller in size and differs in coronal morphology from the second tooth, which is more like a normal first incisor. The innermost tooth is rotated so that the long axis of the crown (in occlusal view) is parallel to the midline of the skull (Fig. 22) rather than at a right angle to it.

An adult male from Chiapas (KU 60935) has six lower incisors. In this individual there apparently was double initiation of both the right and left inner incisors (Fig. 22). The outer incisors are normal in size and morphology as well as in position relative to the canines. The four inner incisors are set with two in front and two in the rear; the four are approximately the same size and have the same shape although the orientation of the anterior two is slightly different from that of the posterior two. The remainder of the dental arcade in this specimen was normal.

In an adult male from Guatemala (KU 64895) there are five lower incisors. The two incisors on the left and the outer incisor on the right are normal in size, shape, and position, but the right inner one is split into two separate, small teeth that together approximately equal a normal inner incisor in size. The two teeth are set side by side within the arc formed by the incisors and are not crowded. The remainder of the teeth in this individual are normal.

An adult male from Chiapas (KU 102323) has an extra lower incisor on the left side between the apparently normal left and right inner incisors (Fig. 22). The extra tooth is smaller (85%) than normal lower incisors and does not bear morphological similarity with any of them. The space occupied by the extra tooth has caused the left inner

incisor to be pushed out of line and slightly rotated so that the surface normally facing anteriorly is directed somewhat laterally (Fig. 22). The remainder of the dental arcade is normal in this individual.

Another adult male from Chiapas (KU 102346) has an extra incisor on the left side. The configuration of the lower incisors, and the characteristics of the supernumerary tooth itself, resemble closely the condition of the preceding specimen (Fig. 22).

An adult male from Jalisco (KU 87312) has a supernumerary lower incisor located on the left side between the outer incisor and the canine (Fig. 22). This is the only individual in which this configuration was found. The extra incisor is smaller (about 75% the size of the normal outer incisor) than normal teeth and has a flat occlusal surface rather than the usual shape with a distinct cutting edge. Because of the position of the supernumerary tooth, the left side of the arc is crowded and the outer incisor, which is normal in all respects, slightly overlaps the inner one (Fig. 22).

An adult male from Nayarit (KU 39543) has only four lower incisors but the inner ones are approximately twice the normal size. These large incisors appear to have a double crown and the root, although not completely divided into two separate segments, is doubled in width and partially separated by a vertical indentation. This kind of abnormality possibly resulted from a disturbance in the morpho-differentiation phase (Schour and Massler, 1966:37). The large size of the inner incisors has caused the lower incisors to be crowded and the two inner ones to project slightly anteriorly. The remainder of the dental arcade in this specimen is normal.

Dental Agenesis

Partial anodontia attributed to agenesis was found in 13 of 818 specimens of *Glossophaga soricina*, but in none of 101 specimens of *G. commissarisi* nor in 136

specimens of *G. alticola*. Congenitally missing teeth are not easily recognized because sometimes when teeth are lost in life the hard tissues are so well repaired that it appears teeth never were present. For the purposes of this analysis of partial anodontia, specimens were selected conservatively and consequently the actual incidence is more likely to be higher than lower. Upper and lower incisors and upper and lower third molars were the only congenitally missing teeth in *G. soricina*. No cases of total anodontia were found and no significant differences in the incidence of partial anodontia between sexes or geographic localities were noted.

An adult male from Puebla (KU 60826) lacks the upper left and the lower right first incisors. No trace can be seen of these two teeth; the alveolar bone is smooth and transillumination does not reveal the presence of sockets. An adult male from Chiapas (KU 102334) lacks all lower incisors and the upper left second incisor as well. In this individual there is no sign of root fragments or sockets representing these teeth and the alveolar bone of the mandible between the canines is flattened and rugose. In an adult male from Nicaragua (KU 70630) the lower incisors on the right side are lacking; no trace of these teeth can be seen.

An adult male from Chiapas (KU 60921) lacks the lower inner incisors and the upper right third molar. The shelf of bone posterior to the second molar, which usually holds the third molar, is narrow and thin on the right side but on the left is normal and the third molar is in place. A similar condition was found in KU 82545, an adult female from Veracruz; the upper right third molar was lacking and the supporting shelf narrow and thin. The remainder of the dental arcade in this specimen was normal. In a specimen from Nicaragua (KU 97604) the upper left third molar and the lower left third molar both are missing. The alveolar bone at the sites where these teeth should have been is

TABLE 9.—Comparative incidence of loss of teeth in life for *Glossophaga soricina*, *G. alticola*, and *G. commissarisi*. Total number of teeth, given at bottom of table, were used to calculate percentages. An asterisk indicates a significant difference ($P \leq .05$) in incidence of loss between sexes.

Teeth	<i>G. soricina</i>		<i>G. alticola</i>		<i>G. commissarisi</i>	
	Male	Female	Male	Female	Male	Female
Upper						
II	1.52*	0.22	1.69	2.13	0	0
I2	1.24*	0.22	1.69	2.13	0	0
C	0	0.11	0.56	0	0	0
P3	0	0.22	0	0	0	0.94
P4	0.14	0.44	0.56	1.06	0	0
M1	0.14	0.22	0.56	2.13	0	0
M2	0.14	0.22	0	0	0	0
M3	0.28	0.33	0.56	0	0	0
Lower						
i1	2.07*	0.67	2.81	4.26	3.13	1.89
i2	2.49*	0.67	1.12	3.19	3.13	0.94
c	0.97*	0.11	0	2.13	0	0
p2	0.69	0.22	0.56	2.13	1.04	0
p3	1.24*	0.22	0.56	3.19	2.08	0
p4	0	0	0.56	2.13	1.04	0.94
m1	0.41	0.33	1.69	2.13	0	0
m2	0.28	0.55	2.25	1.06	0	0
m3	0.55	0.55	3.93	1.06	0	0
Totals	724	902	178	94	96	106

smooth and there is no sign of resorption. The most extensive anodontia involving third molars was found in an adult female from Nicaragua (KU 70636) in which the upper and lower molars were never present; the alveolar bone is smooth. An adult female from México (KU 27989) lacks the lower right third molar, and an adult female from Sinaloa (KU 94093) lacks both lower third molars.

Loss of Teeth in Life

Incidence of loss of teeth in life in *Glossophaga soricina*, *alticola*, and *commissarisi* is summarized in table 9. Significant differences in the kind of tooth lost, the incidence of loss by sex, and the incidence of loss by the different species all were analyzed by means of an R x C test of independence using the G-statistic and Yates Correction Factor.

In *soricina*, the upper and lower in-

cisors are the teeth most often lost in life. These teeth are lost significantly more often in males than in females ($P \leq .05$); for example, the outer lower incisors had been lost in 2.49 per cent of 362 males and in only 0.67 per cent of 451 females (Table 9). The lower second premolar (p3) also is lost significantly more often in males than in females ($P \leq .05$), whereas the incidence of loss of the upper premolars, the upper molars, and the lower molars is the same for both sexes. Interestingly enough, the lower canines are lost significantly more often in males than in females (0.97 per cent as compared with 0.11), but the upper canines are rarely lost in either sex (Table 9). None of the specimens examined by me had lost the lower third premolars (p4) in life and none of the males had lost one or more upper canines or first premolars (P3).

The pattern of tooth loss in *alticola* is quite different from that seen in *sori-*

cina (Table 9). The difference in incidence of loss of upper and lower incisors, for example, is not significant between the sexes. Indeed, none of the differences between sexes proved to be significant in *alticola*. In comparison with *soricina*, the lower second and third molars are lost significantly more often in *alticola* ($P \leq .05$ and $P \leq .01$, respectively)—a striking difference borne out by the incidence of loss, which is only 0.55 per cent for the lower third molar in *soricina* and 3.93 per cent for the same tooth in *alticola*.

Glossophaga commissarisi differs from both of the other two species (Table 9). In *commissarisi* apparently the lower incisors are the only teeth lost with high frequency; in males the incidence was 3.13 and in females 1.89 for the inner lower incisors (Table 9). This difference is not significant (G-statistic=0.012). None of the specimens of *commissarisi* examined by me had lost any of the upper or lower molars.

Although remarkable differences between species and between sexes within species were found, the incidence of loss of teeth in life is not geographically variable. For example, 8.55 per cent of 117 males of *G. soricina* from Chiapas had lost one or more teeth in life as compared with 10.81 per cent (37 specimens) from Nicaragua, 6.00 per cent (50 specimens) from Sinaloa, and 7.14 per cent (28 specimens) from Veracruz. Series sufficiently large for geographical comparisons in *alticola* and *commissarisi* were not available.

Monophyllus Leach

The two species of the long-tongued genus *Monophyllus*, *redmani* and *plethodon*, are endemic to the Antilles. The first species is known from Jamaica, Cuba, Hispaniola, and Puerto Rico, whereas the second is known from Puerto Rico, Anguilla, Barbuda, Antigua, Dominica, St. Lucia, St. Vincent, and Barbados (Schwartz and Jones, 1967; Choate and Birney, 1968:405-406). These bats are medium-sized glossopha-

gines that are easily recognized by their short tail, which extends freely beyond the edge of the greatly reduced inter-femoral membrane. The muzzle in species of the genus is only moderately elongate.

Little is known about the feeding habits of either species. Probably fruit and insects constitute most of the diet (Walker *et al.*, 1964:287). Possibly *Monophyllus plethodon*, which occurs in the Lesser Antilles, competes with *Glossophaga longirostris* because the two are much alike and usually do not occur on the same island.

The dentitions of the two species differ little; Schwartz and Jones (1967:3) stated that the gap between the first and second upper premolars is wide in *M. redmani* and narrow in *plethodon*. They stated further (*loc. cit.*) that they had “. . . been unable to determine any other . . . consistent . . . dental details,” and synchronous cohabitation of Puerto Rico by *redmani* and *plethodon* is probably the strongest proof of their specific status. Choate and Birney (1968:405) described some subtle differences in the lower molars of two subspecies of *plethodon*, but size generally is the most useful intraspecific characteristic. The dentition of these long-tongued bats has been described briefly by Miller (1907:139) and Anthony (1925:29-35). The two species each have 34 permanent teeth; the dental formula is: $i\ 2/2$, $c\ 1/1$, $p\ 2/3$, $m\ 3/3$. In general appearance the teeth of *Monophyllus* are most like those of *Glossophaga*, but in detail they are considerably different. The teeth are only moderately reduced and the cheek-teeth fill the available space. Details of morphological variation and dental interaction were not studied in *Monophyllus*.

Upper incisors.—The upper incisors are of moderate size and nearly fill the area between the canines. Although the inner and outer pairs are about the same size, they differ morphologically in that the inner incisors are nearly vertical and have a broad crown, whereas the outer

teeth are pointed, have sharply oblique crowns, and are tilted anteriorly so as to be in contact with the inner pair. There is a small gap between the two inner incisors.

Upper canines.—The upper canines are stout teeth with a concave internal surface. These teeth lack an internal (lingual) cingulum but have small, up-turned cingular styles at the anterior and posterior ends. There is a deep longitudinal groove on the anterior face of the canines and a sharp, longitudinal ridge.

Upper premolars.—The two upper premolars are not in contact or crowded and both are narrow and high-crowned. The first premolar (P3) has a narrow, trenchant crown and small anterior and posterior styles, whereas the second (P4) has a high, narrow crown and a small anterior style but also has a fairly broad postero-lingual cingular ledge.

Upper molars.—The upper molars are moderate in size and all are in contact. The first two are morphologically similar (M2 is slightly smaller), and are squared in occlusal outline. The third molar is morphologically reduced and is more nearly circular in occlusal view. The ectoloph of M1 and M2 is W-shaped; the paracone and metacone are high and prominent cones on both teeth. The parastyle is rounded but large and the paracrista is short. The mesostyle in occlusal view is a lateral (labial) bulge and is composed of equal contributions from the anterior and posterior elements of the ectoloph. The metastyle of the first two molars is flared postero-labially. The third molar differs in having a less prominent parastyle, which is relatively low and extends in a labial rather than an antero-labial direction, and in having a low reduced metacone that lacks a metacrista and metastyle. The protocone on all three molars is nothing more than a low, ridge-like cusp on the lingual margin of the tooth. The first two molars are unique among those of glossophagines in having a hypoconal wing or "buttress." In these two teeth the pos-

tero-lingual margin slopes downward to the hard palate rather than connecting directly with the base of the metacone.

Lower incisors.—The lower incisors are small, peg-like teeth that have low, rounded crowns. In occlusal view all four are nearly circular in outline. The inner teeth are separated by a narrow gap and the outer teeth are almost in contact with the lower canines.

Lower canines.—The lower canines are relatively large teeth that are tilted laterally and only slightly recurved. The anterior face is rounded, whereas the posterior surface is concave. The lingual cingulum forms a rounded ledge.

Lower premolars.—The three lower premolars are not crowded but the first (p2) is in contact with the canine. Although all of the premolars are about the same size, they differ from one another morphologically, with the second (p3) and third (p4) being most alike. The first premolar consists of a long, thick main cone lacking upturned anterior and posterior styles. The labial surface is convex and the lingual surface is concave. The second premolar has a high, trenchant main cone with straight sides and prominent anterior and posterior styles. The third premolar is like the p3 but has a broad, flared postero-labial surface.

Lower molars.—The lower molars are not crowded or in contact but fill the available space. All three are similar morphologically but the m1 is largest and the m3 smallest. The protoconid and metaconid are prominent cones; the protoconid is set slightly lingual to the longitudinal axis and the metaconid on the lingual margin. The paraconid also is slightly to the lingual side of the longitudinal axis. The entoconid and hypoconid are prominent, pointed cusps separated by a deep V-shaped valley.

Dental Abnormalities

Three kinds of dental abnormalities were found in the 106 specimens of *Monophyllus redmani* and *plethodon* that I examined. One specimen, having

TABLE 10.—Comparative incidence of loss of teeth in life for *Monophyllus redmani* and *M. plethodon*. Total numbers of teeth, given at bottom of table, were used to calculate the percentages. An asterisk indicates a significant difference ($P \leq .05$) in incidence of loss between sexes.

Teeth	<i>Monophyllus redmani</i>		<i>Monophyllus plethodon</i>	
	Male	Female	Male	Female
Upper				
I1	0	1.92	12.50	3.33
I2	0	0	6.25	0
C	0	0	6.25	3.33
P3	1.19	0	6.25	0
P4	0	0	0	0
M1	0	0	31.25*	3.33
M2	0	0	6.25	3.33
M3	0	0	6.25	0
Lower				
i1	21.42	15.38	12.50	23.30
i2	13.09	5.76	31.25	13.33
c	0	0	12.50	10.00
p2	0	0	6.25	0
p3	0	0	6.25	0
p4	0	0	6.25	0
m1	0	0	12.50*	0
m2	0	0	0	0
m3	0	0	0	0
Totals	84	52	16	30

two of these abnormal conditions (incomplete duplication of a permanent tooth and partial anodontia) is described below. The third abnormality, loss of permanent teeth in life, is fairly common in both species of *Monophyllus*, just as it is in most other glossophagines.

The only instances of anodontia and incomplete duplication were found in an adult female of *plethodon* (USNM 106098) from St. Lucia. The second lower incisors are lacking in this individual and no alveoli or alveolar crypts can be seen, even when the anterior end of the mandible is transilluminated. Apparently, therefore, these teeth never were present in life. The lower left third premolar (p4) consists of two large cones joined in the middle; the tooth has three roots that are arranged linearly. The anterior cone of the abnormal tooth is higher and broader than the posterior one. It is possible that a disturbance in the morpho-differentiation stage caused

the partial dichotomy of this tooth (see Schour and Massler, 1966:37). Although the third lower premolar is unusually large, there is no sign of compensatory attrition in this specimen.

Loss of Teeth in Life

Loss of teeth in *Monophyllus* is summarized in table 10. The apparently high incidences of loss of teeth may be more a reflection of the small sample sizes available than an indication of the actual occurrence in nature.

Upper teeth of *Monophyllus redmani* are only rarely lost in life, judging from the 75 specimens examined (Table 10). The lower incisors, however, frequently are lost; the incidence of loss for the inner incisors was 21.42 per cent in males and 15.38 in females. The second incisors are lost somewhat less frequently (Table 10). The available sample of specimens of *plethodon* was extremely

small, but indications are that individual teeth in this species are lost more frequently than are teeth in *redmani*. For example, the total incidence of loss of individual teeth in 15 females of *plethodon* was significantly greater than incidence of loss in *M. redmani* ($P \leq .05$).

In *Monophyllus plethodon* the first upper and lower molars were found to be missing significantly more often ($P \leq .05$) in males than in females (Table 10). Because of the small sample of this species, however, these data might not be indicative of the actual condition in nature.

Macronyssid mites infest the oral mucosa in *Monophyllus redmani* (see chapter on pathology), but unlike the situation in either *Leptonycteris* or *Anoura*, the first upper premolars only rarely are lost as a result of destruction of the adjacent hard palate and soft tissues. Indeed, only a single individual of the 75 examined had lost an upper premolar (P3) as a result of this disorder.

Leptonycteris Lydekker

The three nominal species of long-nosed bats of this genus, *Leptonycteris nivalis*, *sanborni*, and *curasoae*, occur from the southwestern United States (Texas and Arizona) southward throughout much of México into Guatemala and on several islands off the northern coast of South America (for example, Curacao and Aruba). *Leptonycteris curasoae* is known only from the islands, whereas the other two species occur on the mainland and are sympatric over a wide area. Externally, the nominal species are similar, although differences in pelage are useful in identification of *nivalis* and *sanborni*. In comparison with other glossophagines, bats of the genus *Leptonycteris* are large; the tail either is lacking or so reduced as to be essentially imperceptible externally, the interfemoral membrane is greatly reduced, and the muzzle is only moderately elongate.

Little is known about the feeding habits of any of the species of *Lepto-*

nycteris but probably the diet includes fruit, pollen, and insects. The stomachs of six specimens of *sanborni* from Arizona contained 92 per cent pollen and eight per cent insect remains (Hoffmeister and Goodpaster, 1954:58). These authors (*loc. cit.*) reported that the head of nearly every specimen collected by them was covered with yellow pollen that apparently came from Jimson weeds. Detailed studies of feeding habits and other aspects of the ecology of long-nosed bats, especially in areas where *nivalis* and *sanborni* are sympatric, should prove valuable.

As in other species of glossophagine bats, the dentitions of the three species of *Leptonycteris* are similar and, in fact, alone may not suffice for identification. Miller (1907:137) indicated that the genus *Leptonycteris* could be distinguished from *Lichonycteris* by virtue of having only two lower premolars; on a later page (p. 142) he gave the correct dental formula for *Leptonycteris*, which has three lower premolars. Partially because of the lack of obvious dental differences, the taxonomic history of the genus *Leptonycteris* has been confusing. Hoffmeister (1957) reviewed the genus and arranged the available specimens as subspecies of one species, *L. nivalis*. He did not use dental characters to distinguish between the kinds but did note that the teeth of "*L. nivalis curasoae*" were larger than those of "*L. nivalis sanborni*." Later, Davis and Carter (1962) recognized the specific status of the three forms and pointed out that the Mexican ranges of *nivalis* and *sanborni* overlapped broadly. Some features of the upper incisors were included among the taxonomic characteristics (Davis and Carter, 1962:196-197) but none of these features is truly diagnostic. One of the best ways to distinguish between the two species is by means of the size and shape of the presphenoid ridge. In *nivalis* the posterior part of the ridge is low and almost flattened, whereas in *sanborni* the ridge is prominent and rounded. The name "*Leptonycteris ni-*

valis yerbabuenae," which was applied to a long-nosed bat from Guerrero by Martinez and Villa (1940), has caused some difficulties as to assignment because the type specimen has been lost (Alvarez, 1966). *Leptonycteris yerbabuenae* currently is recognized as a valid specific name only by Villa (1966: 252) and Goodwin (1969:72-73).

The dentition of the genus *Leptonycteris* has been briefly described by Miller (1907:142-143) and discussed by de la Torre (1961:40-41). All of the species have 30 permanent teeth; the dental formula is: $i\ 2/2$, $c\ 1/1$, $p\ 2/3$, $m\ 2/2$. The teeth of the species of *Leptonycteris* are relatively small and narrow, and are reduced in number; the first upper premolar (P2) has been lost and the last upper and lower molars are M2 and m2.

Upper incisors.—The upper incisors are relatively large teeth that fill the space between the canines. The inner incisors are narrow teeth with a broad, slightly oblique crown; the cervical region and root are round. The outer incisors also are narrow but have a strongly oblique, pointed crown and an oval cervical and root region.

Upper canines.—The upper canines are stout, narrow teeth with an internal surface that is slightly concave. The canines lack labial and lingual cingula but have a postero-lingual shelf and an upturned antero-lingual cingulum. The canines have a well defined longitudinal groove and ridge on their anterior face.

Upper premolars.—The upper premolars are long and narrow; they are not in contact but fill 60 to 70 per cent of the available space. The teeth are nearly the same length but the second (P4) is broader. Both have two roots. The first premolar consists of a high, trenchant main cone and small, upturned anterior and posterior styles. The second premolar differs in having a moderate postero-lingual shelf.

Upper molars.—The upper molars are in contact and fill the available space. The first is long and narrow and the W-shaped pattern of the ectoloph

thus is elongate. The second molar is morphologically reduced and is roughly triangular in occlusal view. In the first molar the parastyle usually is directed anteriorly and the paracrista is narrow and short. The paracone is not especially prominent and is variable in position so that the anterior element of the ectoloph is the more elongate. The mesostyle of the M1, and that of the M2 as well, is formed by both the anterior and the posterior elements and is low and somewhat U-shaped in occlusal view. The metacone is the largest, most prominent cone on the first molar and the metacrista and metastyle are directed posteriorly from it. The parastyle of the second molar is a distinct, bulb-shaped style and the paracone is low and ridge-like. The metacone of M2 is rounded and large and a metacrista and metastyle are lacking. The protocone on both molars is low and ridge-like. Also, both molars have a shallow hypoconal basin.

Lower incisors.—The lower incisors are small, peg-like teeth; there is a small space between the inner pair. The inner incisors usually are somewhat smaller than the outer teeth, the crowns of which are more nearly rectangular in occlusal view.

Lower canines.—The lower canines are stout, slightly recurved teeth that have a narrow cingular shelf from the anterior end along the lingual surface to the posterior part of the tooth.

Lower premolars.—The three lower premolars are not in contact but fill the available space. All are approximately the same size although the first is lower and broader than the other two. The second and third premolars (p3 and p4) are narrow and long and each has small, upturned anterior and posterior styles.

Lower molars.—The lower molars are long, narrow teeth that are in contact with one another. The first is slightly larger than the second but morphologically the two are much the same. The paraconid is usually in line with the protoconid and thus the paralophid is short-

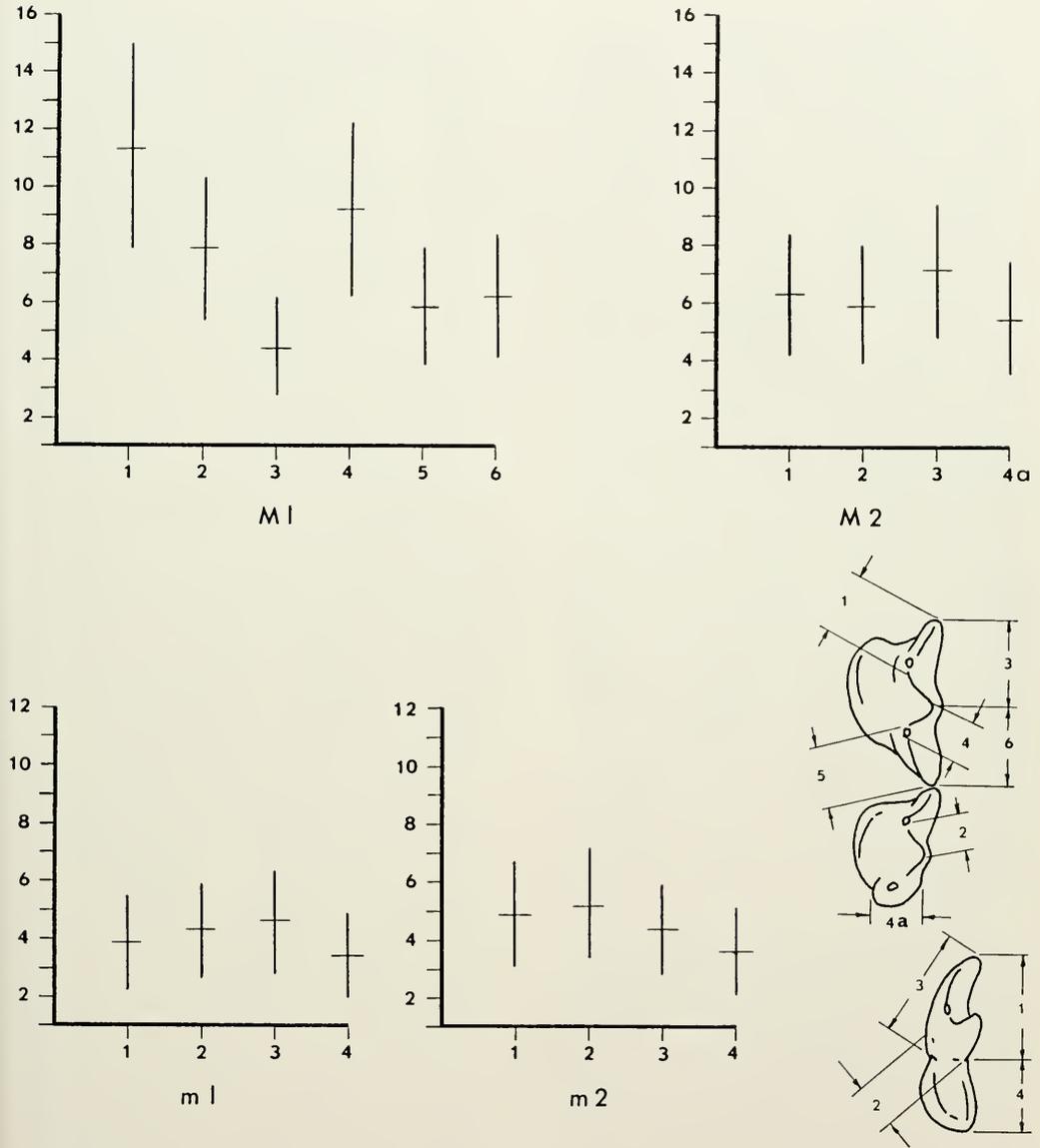


FIG. 23.—Graphs showing coefficients of variation (horizontal bars) and two standard errors (plotted on the ordinate) for measurements of morphological features of the upper and lower molars of *Leptonycteris sanborni* (measurement number plotted on the abscissa). Measurements taken on the two upper molars are shown in the inset; the first three measurements were taken on both teeth, measurement 4a is unique to M2. The four measurements taken on each of the lower molars also are shown.

er than the metaacristid. The protoconid and metaconid are high and prominent and the former is set slightly anterior to the latter. The entoconid is a long, low ridge and the hypoconid is a distinct, rounded cusp.

Morphological Variation

A series of 157 specimens of *Leptonycteris sanborni* from Jalisco was used for a study of morphological and dimensional variation in the dentition. Thirty adult males from a single locality in

Jalisco were used for the statistical analysis of dimensional variation (Fig. 23).

The upper incisors vary slightly in *Leptoncyteris* but, as in most glossophagines, morphological and dimensional variation in these teeth is difficult to study because of the amount of attrition and high incidence of erosion. The upper first premolar (P3) varies in shape and in structure (Fig. 24). In most individuals the first premolar in occlusal view has a convex lingual surface and a concave labial surface. In some, however, the shape of the inner and outer surfaces is reversed so that the lingual surface is concave. The most noteworthy morphological variation in the first premolar concerns the presence or absence of a lingual buttress that extends from the coronal surface dorsally into the hard palate (Fig. 24). In KU 59611 the buttress is greatly developed and prominent, being located only slightly posterior to the middle of the tooth (Fig. 24). The buttress is much smaller in KU 59616 (Fig. 24) and is located just anterior to the posterior root of the premolar (well posterior to the middle of the tooth). The commonest condition is that exhibited by KU 34231 (Fig. 24), in which the lingual buttress is lacking.

The upper second premolar (P4) varies morphologically as well as dimensionally. The most notable morphological variation is in the size and position of the postero-lingual cusplet, which is a characteristic feature of the last upper premolar in most genera of glossophagine bats. In some individuals the shelf formed by the cusplet is long and narrow (KU 59611, Fig. 24), whereas in others it is a short but broad projection with an upturned lingual edge (KU 59616, Fig. 24). The great amount of individual variation in this feature is reflected in a high coefficient of variation (11.28 ± 2.95) in the measurement of the width of the tooth at this point.

The upper first molar in *Leptoncyteris* has been considerably modified from the primitive condition in glossophagines; the anterior element of the ecto-

loph has nearly lost its triangular shape as a result of a labial shift in the position of the paracone. Individual differences in the position of the paracone, relative to the parastyle, are reflected in the extremely high coefficient of variation of the length of the paracrista ($CV, 13.36 \pm 3.51$). The range of variation is shown in figure 24; in KU 59610, for example, the paracone is shifted labially so that the W-shaped pattern of the ectoloph is somewhat spread out, whereas in KU 59596 the paracone is closer to the longitudinal axis of the tooth and the W-shaped ectoloph is preserved. Although the parastyle varies individually in shape, in all four examples illustrated in figure 24 it is directed anteriorly. This generally is true of the parastyle of the upper first molar in *Leptoncyteris*. The variation in the position of the paracone and length of the paracrista, which results in a high coefficient of variation, is also reflected in the variation in the length of the precentrocrista ($CV, 9.83 \pm 2.56$) but, interestingly enough, not in the length of the base of the triangle formed by the anterior element of the ectoloph; the variation in the length of the base (mesostyle to parastyle) is the least of any dimension of the tooth (Fig. 24). In the examples in figure 24, it can be seen that the paracone shifts, and the length of the paracrista and precentrocrista varies accordingly, but the labial base of the element remains essentially the same. The mesostyle in the first molar is a labial bulge formed almost equally by the anterior and posterior elements of the ectoloph of the tooth. Occasionally, the elements do not fuse completely during development, so the mesostyle is split into two components as in KU 59580 (Fig. 24). The ectoflexus varies only slightly in the first molar, which is one reason for the low coefficients of variation for the labial base of both the anterior and posterior parts of the ectoloph (Fig. 23). The pattern of variation in the posterior element is much the same as in the anterior one (Fig. 23), with the postcentrocrista be-

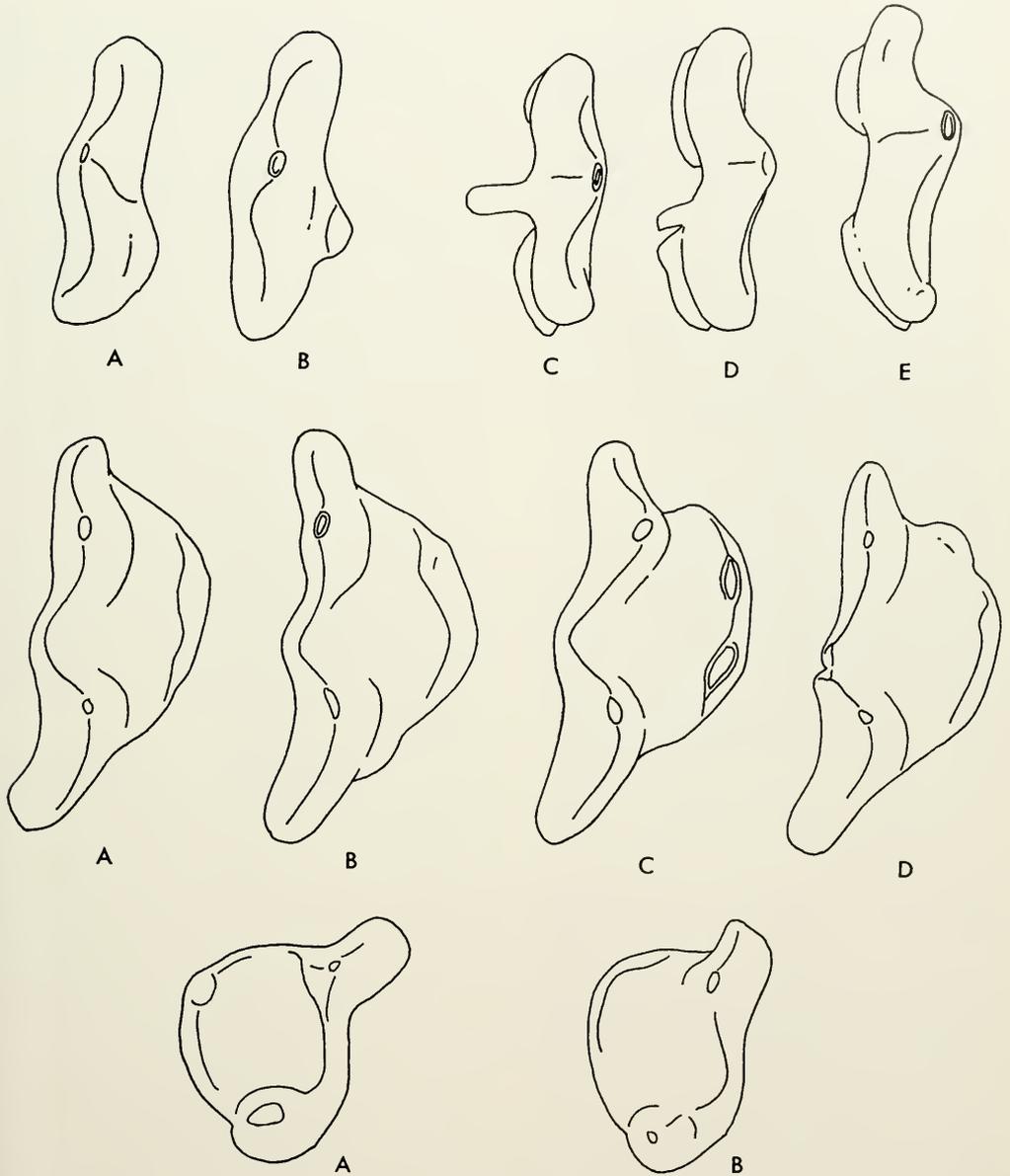


FIG. 24.—Examples of morphological variation in the upper premolars and molars in *Leptonycteris sanborni*. Top row (second premolar, P4): A, KU 59611; B, KU 59616. Top row (first premolar, P3): C, KU 59611; D, KU 59616; E, KU 34231. Middle row (first molar): A, KU 59616; B, KU 59610; C, KU 59596; D, KU 59580. Bottom row (second molar): A, KU 59569; B, KU 59597.

ing the most variable length ($CV, 11.21 \pm 2.93$) and the metacrista the least variable ($CV, 7.83 \pm 2.04$). The shape and size of the metastyle is stable and this accounts for the relatively low coefficient of variation in the metacrista.

The upper second molar, which is the last molar in *Leptonycteris* and is reduced in size and morphological features, is less variable than the first molar as is shown in the graphical presentation of coefficients of variation (Fig. 23).

This is in sharp contrast with the pattern in *Anoura* and *Glossophaga* (Figs. 11, 16), even though the last upper molars in the three genera have the same morphological features. The major difference, of course, is that in *Anoura* and *Glossophaga* the last upper molar is the third molar, whereas in *Leptonycteris* it is the second. The size and shape of the parastyle of the last molar in *Leptonycteris* is somewhat variable. The two examples (Fig. 24) perhaps overemphasize the variation, however, because the coefficients of variation of measurements of the parastyle in 30 adult males generally are low (Fig. 23).

Variation in the lower incisors, which mostly involves their presence or absence, is discussed in the following section. The first and second lower premolars vary in much the same way; in both of these teeth the curvature, especially of the lingual surface, varies from nearly straight to concave. The third lower premolar (p4) varies slightly in shape and thickness and in size of the flattened posterior heel. In some individuals the anterior part of the last premolar is narrow and tapered (occlusal view) and the posterior heel rounded, whereas in others the anterior part of the tooth is broad and the posterior part is flat and wide.

The lower molars in *Leptonycteris* are considerably less variable than are the uppers (Fig. 23). In other genera—for example, *Anoura* and *Glossophaga*—the lower molars are essentially as variable as the upper molars. In *Leptonycteris*, however, the third upper and third lower molars have been lost and, although the upper second molar is highly modified structurally, the second lower molar is much like the first. The following comments, therefore, concern both the first and second lower molars. The trigonid is slightly more variable than the talonid (Fig. 23). In the second molar, the position of the protoconid varies and consequently the coefficient of variation for the base of the trigonid is slightly higher in this tooth than in the

first molar (CV, 7.28 ± 1.89 and 6.30 ± 1.63 , respectively). The degree to which the hypoconid is flared labially also varies in both lower molars.

Dental Interactions

A matrix of Pearson product moment correlation coefficients was prepared using the data discussed in the previous section. Overall, the coefficients of correlation were low; coefficients above 0.36 are significant at the critical level of 0.05 and those above 0.46 are significant at the 0.01 level. All of the various dental measurements referred to in the following paragraphs are illustrated in figure 23. The molar teeth in *Leptonycteris* are unusual, in comparison with those of most other glossophagines, in that only two upper and two lower molars are present and that the M2 is morphologically reduced—consisting of an anterior element and a broad, rounded posterior element composed only of a metacone (Fig. 24).

When equivalent measurements of the two upper molars are compared, there essentially is no correlation in size (Table 11). Thus, for example, the coefficients of correlation between the paracone-parastyle length of M1 and that of M2 is only 0.09. The individual measurements of the posterior elements of the first molar cannot be compared directly with equivalent measurements on the M2 because of the reduced nature of the latter tooth, but when the three measurements of the posterior element of M1 each are compared to the width across the metacone of M2 (which is an index of the size of the reduced posterior element of the tooth) a series of significant coefficients of correlation reveal the generally direct relationship between the two (0.40, 0.49, 0.37).

Within the first molar, the anterior element of the ectoloph is highly variable, especially with regard to the position of the paracone (Figs. 23 and 24). The position of the paracone apparently varies along a more or less anterior-posterior axis and thus has a low, negative

TABLE 11.—Correlation matrix for measurements of the two upper molars in *Leptoncycteris sanborni*. Abbreviations for measurements used in this table are the same as those in Table 1. Measurements are illustrated in Figure 23. Coefficients significant at the alpha level of 0.05 are marked with an asterisk and those significant at the 0.01 level are marked with a double asterisk.

	M 1						M 2			
	PAC-PAS	PAC-MES	MES-PAS	MES-MEC	MES-MTS	MES-MEC	PAC-PAS	PAC-MES	MES-PAS	MES-MEC
PAC-PAS	1.00									
PAC-MES	-0.24	1.00								
MES-PAS	0.07	0.62**	1.00							
MES-MEC	0.13	0.29	0.34	1.00						
MES-MTS	0.16	0.26	0.28	0.65**	1.00					
MTS-MES	0.40*	0.13	0.30	0.56**	0.67**	1.00				
PAC-PAS	0.09	0.11	0.02	-0.15	-0.28	-0.06	1.00			
PAC-MES	0.05	0.06	0.12	0.14	0.11	-0.07	0.19	1.00		
MES-PAS	0.13	0.14	0.09	-0.05	-0.06	-0.05	0.56**	0.52**	1.00	
MES-MEC	-0.13	0.06	0.28	0.40*	0.49**	0.37	0.04	0.21	0.14	1.00

TABLE 12.—Correlation matrix for measurements of the two lower molars in *Leptonycyteris sanborni*. Abbreviations used in this table are given in Table 2. Measurements are illustrated in Figure 23. Coefficients significant at the alpha level of 0.05 are marked with an asterisk and those significant at the 0.01 level are marked with a double asterisk.

		m 1				m 2			
		PAD-MTD	MTD-POD	POD-PAD	TALONID	PAD-MTD	MTD-POD	POD-PAD	TALONID
m 1	PAD-MTD	1.00							
	MTD-POD	0.34	1.00						
	POD-PAD	0.37*	-0.10	1.00					
	TALONID	0.49**	0.21	0.06	1.00				
m 2	PAD-MTD	0.56**	-0.07	0.19	0.29	1.00			
	MTD-POD	0.43*	0.73**	-0.24	0.30	0.19	1.00		
	POD-PAD	0.48**	0.33	0.37	0.24	0.29	0.25	1.00	
	TALONID	0.37*	0.18	0.02	0.35	0.31	0.51**	0.18	1.00

coefficient of correlation with the paracone-mesostyle length (-0.24). The length of the paracone-mesostyle is highly correlated (0.62) with the distance between the mesostyle and parastyle; this relationship is a direct one that results from the fact that an increase in labial extension of the ectoflexus will increase both measurements. The dimensional relationships within the posterior element of the ectoloph of M1 are considerably different from those of the anterior element. All sides of the triangular-shaped posterior element are well correlated (≥ 0.56) with one another (Table 11). Overall, the posterior element is not as variable as the anterior one (Fig. 23).

Certain dimensions of the anterior and posterior elements are slightly correlated with each other but generally the inter-element correlations are low (Table 11). The parastyle-paracone length is relatively well correlated with the mesostyle-metacone length (0.40); this possibly is related in part to the moderately strong negative correlation between the lengths of the paracone-parastyle and the paracone-mesostyle because, when the latter measurement is small, the mesostyle is located more anteriorly than otherwise and thus the

length from the metacone to the mesostyle is increased. Intra-tooth correlations in the second upper molar are slightly different from those in the M1. The size of the anterior element of M2 essentially is not correlated with that of the morphologically reduced posterior element, but within the anterior element the paracone-mesostyle length is highly correlated ($P \leq .01$) with that of the mesostyle-parastyle (0.52), and the latter also is correlated with the parastyle-paracone length (0.56).

Interactions among the upper molars clearly reflect the differential in their development and time of eruption (Fig. 10). The size of the anterior element of the ectoloph of the first molar does not correlate with size of the elements of the second molar (Table 11). The posterior element of M1, however, is correlated with the width of the reduced posterior element of M2 (coefficients of 0.40 , 0.49 , and 0.37). The most noteworthy interaction is an apparently mechanistic one between the posterior element of M1 and the anterior element of the second molar, which undergoes odontogenesis well after the formation of the posterior element of M1 (Fig. 10 and Table 11). The larger the posterior element of M1, especially in length of the metacrista

(metacone-metastyle), the smaller the parastyle-paracone length of the anterior element of the second molar ($r, -0.28$).

The intra-tooth relationships in the lower molars are somewhat more straight forward than in the upper molars. A matrix of coefficients of correlations for all combinations of measurements of the lower molars is given in table 12. The length of the talonid in m1 is correlated ($r, 0.49$) with the length of the metaacristid (paraconid-metaconid length). In the trigonid of the first lower molar the length of the metaacristid is correlated with the length of the paralophid. The pattern of intra-tooth correlations is different in the m2; in the second molar only one of six coefficients of correlation is significant ($P \leq .01$), whereas in m1 two of six are significant (Table 12). In the first molar the highest correlations are within the trigonid or between measurements of the metaacristid (paraconid-metaconid) and the length of the talonid (Table 12). In m2, on the other hand, the strongest correlation is between the length of the talonid and the width of the trigonid across the metaconid and protoconid ($r, 0.51$). All of the combinations of measurements within the trigonid have relatively low coefficients of correlation (0.19 to 0.29).

The importance of slight differences in the intra-tooth pattern is emphasized when the inter-tooth relationships are considered. In *Leptonycteris*, the two lower molars are morphologically similar and, although they are in contact, are not crowded; in fact, there is adequate mandibular space for yet a third lower molar posterior to m2. This is in sharp contrast to the upper molars where the spatial factor is great because the two upper molars fill all of the available space. The two lower molars undergo odontogenesis and eruptive activity separately (Fig. 10) but even so, overall are strongly correlated dimensionally (Table 12). Indeed, when all combinations of measurements of the two teeth are compared, six of 16 have significant coefficients of correlation (≥ 0.36). For

example, the widths of the trigonids (across the metaconid and protoconid) of m1 and m2 have a coefficient of correlation of 0.73. As pointed out earlier, the length of the talonid of m2 is correlated with the width of this tooth (0.51), which in turn is correlated with the width of m1. The general relationship between the lower molars, therefore, is a positive one and the individual dimensions of the second lower molar are more closely related to those of the first molar than to each other. Thus, the proportions within the m2 essentially are more the result of the sizes of elements of the m1 rather than the result of any individual dimensions within the second molar itself. The potential importance of this interaction comes to view when one considers the relationships between the upper and lower molars.

The sizes of the elements of the first upper molar and those of the first lower molar, both of which develop and erupt at the same time in *Leptonycteris* (Fig. 10), are significantly correlated in eight of 24 possible combinations (≥ 0.36). By way of comparison, the M1 has only three of 24 noteworthy correlations with the M2, and all of these are with the posterior elements of that tooth (Table 13). The first upper molar has four coefficients of correlation above 0.36 when compared to m2, but these correlations apparently are the result of the strong interaction between m1 and m2. The second upper molar, on the other hand, has only one significant ($P \leq .01$) correlation with the first lower molar, but has five with the trigonid and the talonid of the second lower molar (Table 13). In summary, the pattern of integration in the molars of *Leptonycteris* is established initially by the size of the first teeth to reach the occlusal plane (M1 and m1). The second upper molar responds to the size of the first in two ways; the anterior element responds negatively for mechanical and spatial reasons and the posterior element responds positively so that the larger the posterior element of M1, the larger that

TABLE 13.—Matrix of coefficients of correlation for upper and lower molars of *Leptonycteris sanborni*. The lower molars are plotted across the top; measurements compared are those illustrated in Figure 23. Coefficients significant at the alpha level of 0.05 are marked with an asterisk and those significant at the 0.01 level are marked with a double asterisk.

		m 1				m 2			
		PAD-MTD	MTD-POD	POD-PAD	TALONID	PAD-MTD	MTD-POD	POD-PAD	TALONID
M 1	PAC-PAS	0.18	-0.03	0.01	0.37*	0.41*	0.11	-0.03	0.01
	PAC-MES	0.11	0.38*	0.00	0.09	0.02	0.29	0.45*	0.11
	MES-PAS	0.53**	0.34	0.20	0.25	0.37*	0.20	0.46**	0.10
	MES-MEC	0.36*	0.37*	0.23	0.34	0.15	0.15	0.19	0.06
	MEC-MTS	0.34	0.27	0.15	0.63**	0.00	0.23	0.30	0.08
	MTS-MES	0.38*	0.20	0.20	0.62**	0.25	0.23	0.22	0.12
M 2	PAC-PAS	-0.11	-0.02	0.00	-0.08	0.14	0.19	0.10	0.31
	PAC-MES	0.23	0.11	0.00	0.04	0.23	0.20	0.42*	0.26
	MES-PAS	0.17	0.23	-0.09	0.24	0.27	0.47**	0.40*	0.64**
	MEC	0.49**	0.29	0.00	0.34	0.32	0.41*	0.24	0.35

of M2. The proportions of the second lower molar result, in large measure, from sizes of the individual features of the m1 rather than from a pattern of intra-tooth relationships.

Dental Abnormalities

Partial hyperdontia, incomplete duplication of permanent teeth, and partial anodontia resulting from agenesis are found occasionally in some species of the genus *Leptonycteris*. In addition to these congenital disorders, teeth frequently are lost in life as the result of erosion, periodontal disorders, and dental caries. Erosion probably is the most common cause of loss of teeth.

Hyperdontia

Hyperdontia was found only in *Leptonycteris sanborni*; bilateral supernumerary upper premolars were found in one specimen and unilateral duplication of a lower premolar was found in another. The incidence of complete duplication of at least one tooth in *sanborni*, was 0.48 for sexes combined, and, because both cases were in males, the

incidence for males alone was calculated as 0.65.

In an adult male from Guerrero (UNAM 8835), there are extra first upper premolars on each side. The extra teeth are duplicates of the "normal" first premolars but are only about half their size. The supernumerary teeth are located between the canines and first premolars; the latter are normal in position and in morphology. The remainder of the dental arcade in this individual is normal.

In an adult male from Veracruz (KU 23693) the lower right second premolar (p3) is divided into two parts, neither of which appears to be a "normal" tooth. The anterior part, which is about 50 per cent larger than the posterior part, consists of a main cone and an anterior cingular heel; the posterior surface of the main cone is slightly flared. The posterior part consists of a main cone and the fairly well developed posterior heel. Both the anterior and posterior "teeth" have two roots and apparently are not connected. This abnormal condition probably did not result from a double initiation because neither part forms a

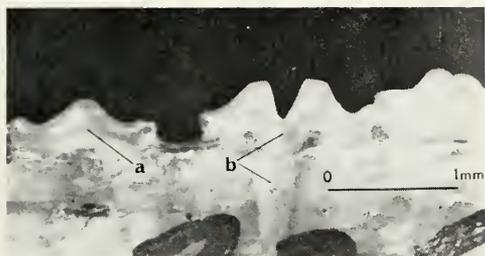


FIG. 25.—An adult male of *Leptonycteris sanborni* (KU 23693) having an incompletely duplicated lower third premolar (p4) on the left side. This abnormal tooth, which normally resembles the second premolar (a), consists of two main cones that share a common root (b).

complete tooth. It is more likely that some disturbance during morpho-differentiation caused a split in the developing tooth (see Schour and Massler, 1966: 37). In this same specimen, the lower left third premolar (p4) is incompletely duplicated. This kind of abnormality, which is not considered by me to be hyperdontia, was found in three specimens of *sanborni*, thus having an incidence of 0.72 for sexes combined and an incidence of 0.97 for males alone. In KU 23693 the abnormal third premolar consists of two main cones, the anterior one having an anterior cingular heel and the posterior one having a posterior cingular heel, that are connected and share a common root located in the middle of the tooth (Fig. 25). The two abnormal premolars in this specimen apparently did not hamper its survival because the remainder of the dental arcade is normal and none of the teeth show unusual attrition.

Bilateral incomplete duplication was found in an adult male from Jalisco (KU 34154). In this individual, the right and left second upper premolars consist of two main cones, an anterior and a posterior cingular heel, and two postero-lingual ledges (the anterior being considerably smaller than the posterior). The overall size of the abnormal premolars is about 25 per cent greater than that of normal second premolars in *Leptonycteris sanborni*. The remainder

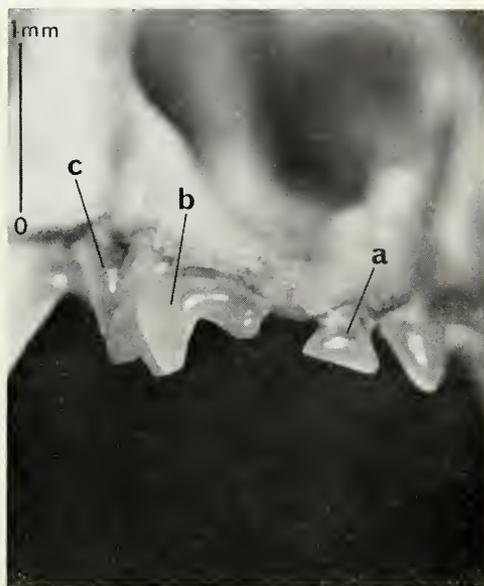


FIG. 26.—An adult male of *Leptonycteris sanborni* (KU 34137) with a normal left upper first incisor (a) and an abnormal tooth (b) in place of the right first incisor. The second incisor on the right side (c) is turned sideways and is crowded between the canine and abnormal tooth.

of the dental arcade in this specimen was normal.

Another adult male from Jalisco (KU 34137) has an abnormal upper first incisor on the right side (Fig. 26). This unusual tooth is about three times larger than a normal inner incisor and bears no resemblance to one. The abnormal tooth has a cone on the lateral side and a cingular basin on the medial and internal surfaces (Fig. 26); the root is extremely large. The most likely explanation of this tooth is that it is the result of an abnormal initiation of upper canines because its size and the morphology of its cervical region resemble slightly the normal upper canine in the species. The second incisor on the right is normal but because of the size of the abnormal tooth directly anterior to it, is turned so that its long axis (in occlusal view) is nearly at a right angle to the axis of the cheek-teeth (Fig. 26). The remainder of the teeth in this individual are normal in all respects.

TABLE 14.—Comparative incidence of loss of teeth in life for *Leptonycteris nivalis* and *L. sanborni*. Total numbers of teeth, given at bottom of table, were used to calculate the percentages.

Teeth	<i>Leptonycteris nivalis</i>		<i>Leptonycteris sanborni</i>	
	Male	Female	Male	Female
Upper				
I1	0	0	3.57	0.93
I2	0	0	1.14	1.39
C	0	0	0.32	0.46
P3	6.41	6.36	1.30	0.93
P4	1.28	4.55	0.65	0
M1	1.28	0.91	0.81	0
M2	2.56	0.91	0.97	0
Lower				
i1	6.41	0.91	29.55	29.63
i2	2.56	0	15.10	11.57
c	0	0	0.16	0.46
p2	0	0	1.14	0.46
p3	0	1.82	0.65	0
p4	0	0	0.16	0
m1	3.85	0	0.65	0
m2	5.13	0	0.65	0
Totals	78	110	616	216

Dental Agenesis

Agenesis of cheekteeth is uncommon in *Leptonycteris*. In but one specimen, an adult male of *nivalis*, an upper molar was congenitally missing (incidence of 1.28 for this tooth in males and of 0.53 for sexes combined). In the same species, the inner lower incisors failed to develop with an incidence of 3.85 in males and 0.91 in females, whereas the second incisors were congenitally lacking with an incidence of 1.28 in males. In *sanborni* it was difficult to determine whether missing lower incisors had been lost in life or failed to develop, because the incidence of loss of these teeth is unusually high. The incidence of anodontia in the upper incisors is 1.30 in males; all females examined either had incisors in place or had lost them in life.

Loss of Teeth in Life

Certain teeth frequently are lost in life in *Leptonycteris nivalis* and *sanborni*; incidences are summarized in table 14. In *nivalis*, the first upper premolar (P3)

is lost with an incidence of 6.41 in males and 6.36 in females. These high incidences are the result of infestations of oral mites (Macronyssidae) that are a primary etiological factor in destruction of periodontal tissues. The remaining upper cheekteeth, although lost occasionally, are considerably less prone to loss resulting from infestations of mites, erosion, and dental caries. The lower incisors in *nivalis*, which are relatively robust and well rooted teeth, are lost in life fairly frequently; incidence for lower inner incisors in males is 6.41 and in females is 0.91. This difference is not significant. The remaining lower teeth, with exception of the lower first and second molars in the males examined by me, are lost rarely. The apparently high incidence of loss of lower molars in males (3.85 and 5.13 for the first and second, respectively) is not significantly greater than the apparently rare loss of these teeth in the small sample of females.

In *Leptonycteris sanborni*, for which the available sample was considerably

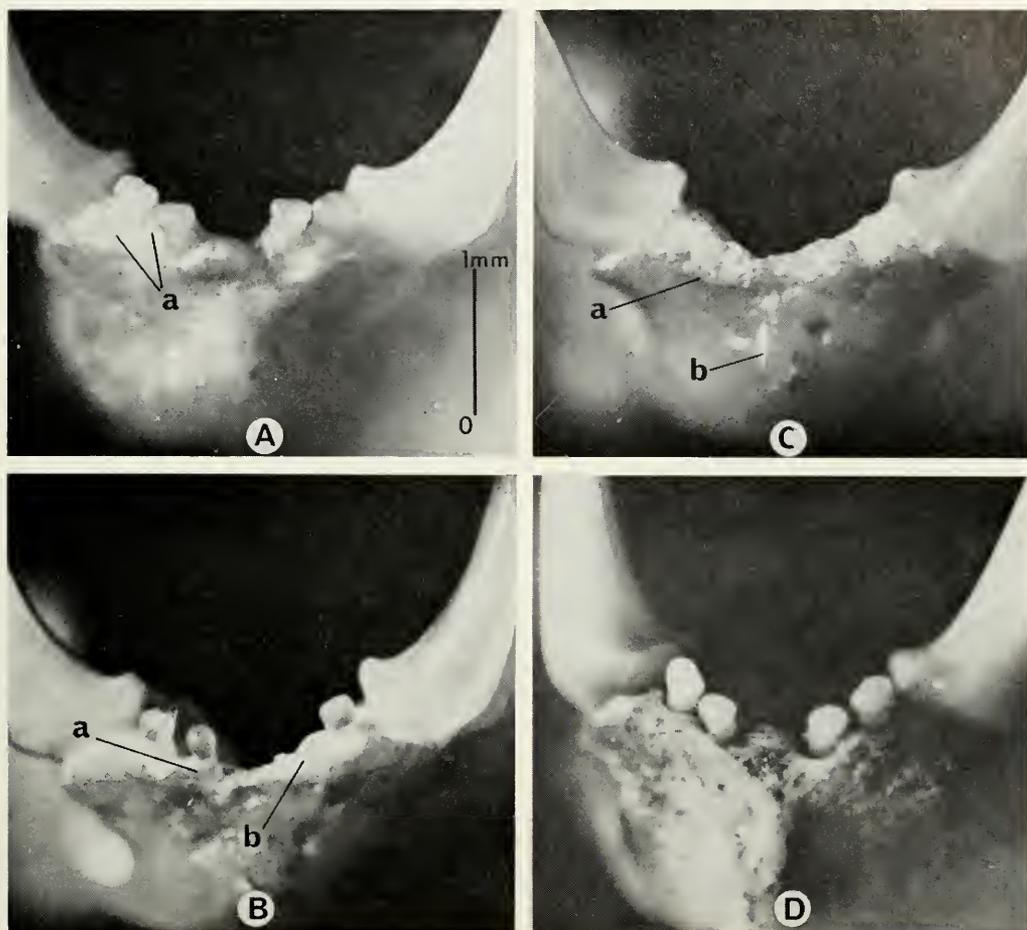


FIG. 27.—(A) Normal, relatively young individual of *Leptonycteris sanborni* having in place all four lower incisors but with slight resorption (a) of alveolar bone; (B) older individual of same species lacking one incisor (b) and having advanced alveolar resorption (a); (C) an old individual of *L. sanborni* lacking all lower incisors and having a build-up of alveolar bone (a) and well-developed site of muscle attachment (b); (D) normal adult of *Leptonycteris nivalis* for comparison.

larger than for *nivalis*, the upper inner incisors often are lost (3.57 in males). None of the differences in incidence between sexes in *sanborni* was found to be significant, but the difference in incidence of loss of the upper second premolar (P4) in males of *nivalis* and of *sanborni* is significant ($P \leq .01$). This difference is due to the fact that *sanborni* is free of periodontal destruction due to mites (see chapter on pathology). The lower incisors in *sanborni* are lost with unusually high frequency (Table 14). The difference in incidence of loss of

these teeth between the two species is highly significant ($P \leq .01$). In *sanborni* the lower incisors are relatively small (Fig. 27). In the course of age related morphological changes, the alveolar bone that supports the lower incisors is resorbed and reconstructed. Changes in the bony support weaken the teeth and, in conjunction with normal attrition, often result in loss of individual teeth. Interestingly enough, the second incisors are not lost as frequently as are the inner teeth (15.10 and 29.55, respectively, in males). Hoffmeister and

Goodpaster (1954:58) also have studied the loss of lower incisors in specimens of *sanborni* and stated that the "degenerative" loss of incisors in life probably "enables the bat to protrude the tongue more easily and naturally increases the normal space or diastema which is present between the [outer] incisors." The remaining lower teeth in *sanborni* are lost much less frequently than are the incisors (Table 14); even so, when males of this species are compared with males of *nivalis*, the incidence of loss of premolars and molars is significantly greater ($P \leq .05$) in *sanborni*.

Lichonycteris Thomas

There are two nominal species of long-nosed bats of the genus *Lichonycteris*; *obscura* is known from Nicaragua, Costa Rica, Panamá, and Surinam (Hall and Kelson, 1959:123; Husson, 1962:135; Handley, 1966a:764), and *degener* is known from Brazil (Cabrera, 1958:73). Bats of this genus are small, brownish in color, and have relatively short muzzles. The short tail barely penetrates the unreduced interfemoral membrane.

The feeding habits of these bats are poorly known and mostly based on inference. Goodwin (1946:315) has stated that *obscura* probably feeds on nectar, judging from its "weak teeth" and absence of lower incisors. He (*loc. cit.*) further speculated that this species "plays an important part in the fertilization of the night-blooming plants."

Miller (1907:143-144) has described the dentition of *Lichonycteris* in moderate detail but incorrectly reported that the W-pattern of the molars was obsolete because of the great reduction of the styles and commissures. Actually, the styles of the molars are enlarged rather than reduced, and it is the paracone that is small and sometimes lacking. Miller (*loc. cit.*) thought that dentition indicated that *Lichonycteris* is most closely related to *Leptonycteris*. As I point out in the summary of this chapter and in the discussion, however, the two genera are not closely related. In-

stead, *Lichonycteris* is related most closely to *Hylonycteris*. Goodwin (1942:131) also thought that the molars of *Lichonycteris obscura* lacked a W-shaped pattern but Handley (1966a:85) characterized the teeth as having a "nearly normal" W-pattern.

Bats of the genus *Lichonycteris* have only 26 permanent teeth; the dental formula is: i 2/0, c 1/1, p 2/3, m 2/2. This is the least number of permanent teeth in any genus of the subfamily. Overall, the teeth in *Lichonycteris* are moderately reduced in size. Morphological variation was not studied statistically in this genus because of the small sample available.

Upper incisors.—The four upper incisors are small and are not in contact. Instead, they are approximately evenly spaced between the canines. The inner incisors have low, flat crowns and the outer teeth have pointed crowns with strongly oblique edges.

Upper canines.—The upper canines are simple, recurved teeth that lack a longitudinal groove or ridge on the anterior-facing surface. The base of the canine is long and narrow and there is only a trace of a posterior cingular style.

Upper premolars.—The two upper premolars are not in contact and do not fill the space between the canine and first molar. The first premolar (P3) is smaller than the second, its breadth being nearly equal to half its length. The main cone is prominent and has a small postero-lingual shelf. The second premolar (P4) also is about twice as long as it is broad; it has a cingular shelf that begins at the anterior end of the tooth and extends along the lingual side to a point where it becomes broader and forms a postero-lingual shelf.

Upper molars.—The two upper molars are not in contact but neither are they widely separated. The W-shaped ectoloph usually is present, but in some specimens the paracone is lacking or so reduced that the pattern is almost obliterated. The second molar is slightly smaller than the first but is similar

morphologically. The paracone (when present) usually is a low, small cone that is separated from the relatively high labial margin of the stylar shelf by a short paracrista. The mesostyle usually is lacking but in a few specimens a trace can be found on the posterior element of the ectoloph. The metacone is lower than the labial margin of the tooth but about the same height as the metastyle. The protocone is a low, ridge-like cusp, and a well defined hypoconal basin is lacking.

Lower canines.—The lower canines are simple, relatively small teeth that are not recurved. A cingular shelf is present but is greatly reduced.

Lower premolars.—The three lower premolars are not in contact but fill the available space. The first premolar is the smallest and the third is largest. All three teeth are relatively short and broad; the p2 is low and lacks anterior and posterior cingular styles, whereas the p3 and p4 are somewhat higher and have an anterior cingular style and a moderately broad posterior style.

Lower molars.—The two lower molars are almost in contact. The first is larger and differs slightly from the second. The metaconid of m1 is a large, nearly vertical cone and the protoconid is greatly reduced and in some specimens is almost lacking. The paraconid is broad and rounded. The entoconid is a low, ridge-like cusp separated from the labial margin of the talonid by a shallow U-shaped valley. The hypoconid is so reduced that a distinct cusp is lacking. The second lower molar differs from the first in having a larger and more distinct protoconid and a narrow paraconid.

Morphological Variation

Too few specimens from a single locality or adjacent localities were available for an analysis of the dimensional variation in the teeth of either species of *Lichonycteris*. Small series of *obscura* from Panamá and Nicaragua provided an opportunity to survey the striking

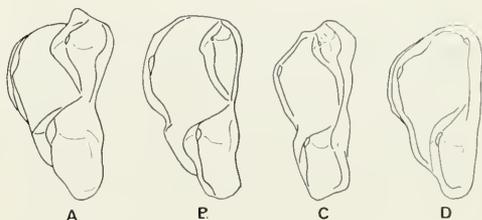


FIG. 28.—Individual variation in the morphology of the first upper molar in *Lichonycteris obscura*: A—most primitive condition, with a large, prominent paracone (KU 106026); B—medium-sized paracone and a trace of a “hypocone” (KU 106025); C—paracone reduced to a small conule, stylar shelf with high, rounded ridge (KU 110785); D—most reduced condition with paracone lacking (USNM 309403). Compare D with the first molar in *Choeronycteris* and *Hylonycteris*.

morphological variation in the upper molars. The upper molars, especially the first one, in this species are more variable in structure than are the molars of any other species in the subfamily. However, most importantly, the molars of *obscura* vary in a way that reveals the pattern of modification seen in the most highly specialized genera of the Glossophaginae in the absence of a fossil record.

Extremes in morphological variation are illustrated in figure 28. In an adult male from Nicaragua (KU 106026) the first upper molar is “primitive” in the sense that the W-pattern is obvious, the paracone and metacone are large and prominent and a small mesostyle is present. The stylar shelf of the anterior element of the ectoloph is slightly lower than the paracone in this specimen but is raised and has a rounded border that can be distinguished easily in occlusal view. Also, there is a small flange on the anterior-facing surface of the tooth at the base of the paracone. Generally, the first molar in this individual resembles a distorted molar of *Lonchophylla* or *Anoura*. Another adult male from Nicaragua (KU 106025) has a W-shaped ectoloph but the paracone is considerably smaller than in the preceding specimen. At the site normally occupied by

a hypocone in the molars of many mammals there is a small projection directly posterior to an indentation in the post-protoerista (Fig. 28). In another adult male from Nicaragua (KU 110785), the paracone of the first molar is greatly reduced so that it is nothing more than a low conule situated on the lingual-facing base of the upturned and rounded stylar shelf (Fig. 28). The first molar in this individual is of additional interest because of the high, moderately prominent mesostyle that is part of the posterior element of the ectoloph. The metacone in the tooth is lower than in the two preceding examples and, in fact, is only as high as is the "mesostyle." Extreme reduction of topographic features is seen in a specimen from Panamá (USNM 309403). In this adult female the paracone is lacking and the anterior stylar shelf is prominent. Indeed, there is a distinct wear facet on the stylar shelf (Fig. 28). A mesostyle also is lacking in this specimen and the tooth thus resembles, in all ways, the first upper molars in *Hylonycteris*, *Choeromiscus*, and *Choeronycteris*. Morphological variation in the upper molars of *Lichonycteris* evidently is not geographical because all conditions illustrated and discussed here can be found in the series from Panamá. It is possible, of course, that additional specimens and large series will eventually reveal geographic trends in structure.

The second molar varies in essentially the same way as does the first and in a given specimen generally resembles the first molar. The lower molars in all species of the Glossophaginae are more or less similar; those of *Lichonycteris* are variable but not to the extremes seen in the upper molars.

Dental Abnormalities

Among the 15 specimens of this rare genus available for examination, there were two that had supernumerary upper premolars. Thus, although there is no way to determine the incidence of dental abnormalities in nature in the species

of *Lichonycteris*, the pattern of developmental variations could prove to be much the same as it is in the other genera of the subfamily.

Hyperdontia

An adult male (USNM 331258) of *obscura* from Panamá was found to have an extra tooth directly anterior to the upper first premolar on the right side. The small supernumerary tooth is about 20 per cent the size of the first premolar, which appears to be normal. The extra tooth differs from the P3, in addition to size, in having but a single root that is set in its own alveolus, but it resembles the P3 in overall coronal configuration. It is likely that the extra tooth is an atavistic P2. The remainder of the dental arcade was normal.

In an adult female (AMNH 95485) of *degener* from Brazil there is an extra tooth located directly posterior to the upper canine on the right side. The abnormal tooth is separated from the P3 by a small gap, and is about 25 per cent its size. The P3 appears normal in all ways. As in the above specimen, the extra tooth in this individual probably is an atavistic P2 because it has a single root and resembles the P3 in coronal morphology, although it is relatively lower-crowned. The remainder of the dental arcade in this specimen was normal.

Loss of Teeth in Life

In the small sample studied, one specimen of *degener* had lost the lower canine and the second and third premolars on the right side.

Hylonycteris Thomas

The single known species of this genus, *Hylonycteris underwoodi*, occurs at least in Jalisco, Oaxaca, Veracruz, Guatemala, Costa Rica, and Panamá (Hall and Kelson, 1959:121; Davis and Carter, 1962:69; Phillips and Jones, 1971; Carter *et al.*, 1966:493; Handley, 1966b:764). *Hylonycteris underwoodi*

is a small, delicate bat that is drab brownish or almost blackish in color. The muzzle is moderately long, and the tip of the short tail extends through the dorsal surface of the interfemoral membrane. In external appearance, bats of this species strongly resemble *Lichonycteris obscura*.

The feeding habits of *Hylonycteris underwoodi* are essentially unknown. Goodwin (1946:314) described the species as being a "flower-visiting bat," but Hall and Dalquest (1963:229) reported that in a cave inhabited by these long-nosed bats "there were several pits of jobo plums . . . showing that some of this fruit [had been] taken to the cave to be eaten." Walker *et al.* (1964:293) included insects in the probable diet of *H. underwoodi*.

The dentition of *Hylonycteris* was not described by Miller (1907), although he did note that the genus closely resembled *Choeronycteris* in all ways excepting the modification of the pterygoids (*op. cit.*, p. 142). Handley (1966a:85) characterized the dentition of *Hylonycteris* as reduced, with high premolars. In many ways, the teeth of *H. underwoodi* resemble those of some specimens of *Lichonycteris* as well as the dentitions of *Choeroniscus*, *Choeronycteris*, and *Musonycteris* (Table 19).

Hylonycteris underwoodi has only 30 permanent teeth; the dental formula is: i 2/0, c 1/1, p 2/3, m 3/3. Details of morphological variation and dental interactions were not studied.

Upper incisors.—The four upper incisors are small and are not in contact but instead are spaced approximately equally between the upper canines. The inner incisors have flat, broad crowns and the outer incisors, which are the same size as the inners, have pointed crowns with strongly oblique edges.

Upper canines.—The upper canines are simple, narrow teeth that lack a longitudinal groove and ridge on their anterior-facing surface. The inner surface is flat or slightly concave, and the outer surface is rounded. The base of

the canine is long and narrow and there is only a trace of a posterior cingular style.

Upper premolars.—The two upper premolars are not in contact and do not fill the space between the canine and first molar. The first premolar (P3) is slightly smaller than the second; it consists of a main cone with a barely concave lingual surface. The anterior and posterior cingular styles are greatly reduced. The second premolar is similar to the first but has larger anterior and posterior cingular styles. Both premolars lack a postero-lingual shelf.

Upper molars.—The three upper molars are not in contact but are not widely spaced. The third molar is only slightly smaller than the other two and differs only slightly morphologically. All three molars lack a paracone and, therefore, have no trace of the W-shaped ectoloph. The parastyle is a narrow, ridge-like cusp on the antero-labial margin of the molars. The mesostyle is lacking and the metacone is a low, rounded cone. The metastyle is small and located directly posterior to the metacone. The protocone is a low, ridge-like cusp and the hypoconal basin is lacking on all of the upper molars.

Lower canines.—The lower canines, like the uppers, are simple teeth. A cingulum is lacking and the slender tooth is slightly recurved.

Lower premolars.—The three lower premolars are not in contact but nearly fill the available space. The first two are smaller than the third. The first (p2) has a low main crown, a slightly concave lingual surface, and lacks anterior and posterior cingular styles. The second and third premolars have a narrow, trenchant main cone, a small anterior cingular style, and a flattened posterior cingular style.

Lower molars.—The three molars are not crowded and usually not in contact. They are long and narrow and the third, although it is the smallest, has the same morphological features as the other two. The protoconid is low and not at all

prominent and the metaconid is a small, vertical cone. The entoconid is a low, ridge-like cusp separated from an indistinct hypoconid by a shallow U-shaped valley along the longitudinal axis of the talonid.

Dental Abnormalities

A total of 24 specimens of *Hylonycteris underwoodi* was examined by me. In this small sample, none of the specimens had developmental abnormalities and only three had lost teeth in life. A male had lost the third lower molar on the right side and a female had lost the last lower premolar (p4) on the right side. Another female had lost an upper inner incisor as well as the left lower canine in life.

Scleronycteris Thomas

Scleronycteris is a monotypic genus known from two specimens, one from Brazil (see Cabrera, 1958:73) and the other from Venezuela (present data). *Scleronycteris ega* is a small glossophagine that is dark brownish in color and has a moderately elongate muzzle. The short tail protrudes through the middle of the unreduced interfemoral membrane.

Nothing is known about the habits or diet of *S. ega*. In size and external appearance, as well as in dental characteristics, this bat is much like *Hylonycteris*, *Lichonycteris*, and *Choeroniscus*. It would not be surprising, therefore, to learn eventually that *S. ega* feeds on fruit, pollen, and nectar.

The only previous description of the dentition of *Scleronycteris* is that of Thomas (1912:404-405). Unfortunately, the only specimen available in the United States, which I examined, lacks a mandible and consequently my comments regarding the lower teeth are based entirely on the cryptic remarks of Thomas (*loc. cit.*). *Scleronycteris ega* has 30 permanent teeth; the dental formula is: i 2/0, c 1/1, p 2/3, m 3/3. Morphological variation and dental in-

teraction, of course, have not been studied in *Scleronycteris*.

Upper incisors.—The four small upper incisors are not in contact and are more or less evenly spaced between the canines. The inner teeth are peg-like and, although not in contact, are not separated by an especially wide median gap. The outer incisors are about the same size as the inner teeth but have pointed crowns.

Upper canines.—The upper canines are simple teeth that lack a longitudinal groove and ridge on the anterior-facing surface but have a small posterior cingular style.

Upper premolars.—The two upper premolars are not in contact. They are similar in size and morphological characteristics; the main cone is high and pointed and both teeth have small anterior and posterior cingular styles.

Upper molars.—The three upper molars are not in contact, but neither are they widely spaced. The third molar is slightly smaller than the first two but resembles them morphologically. The molars are reduced and lack any trace of a W-shaped ectoloph. The paracone is lacking and the parastyle forms a large, narrow stylar cusp of the antero-labial margin of the molar. Indeed, the parastyle is the highest cusp in this specimen. All of the molars have a large mesostyle and labially-directed bulge at the ectoflexus. The metacone is a fairly large, narrow cone, which on the M3 is set almost lingual to the mesostyle. The metastyle is directly posterior to the metacone on the first two molars but is essentially lacking from the third. The protocone is a low, ridge-like cusp on all three molars. A hypoconal basin is lacking.

Lower canines.—The lower canines have a posterior cingular ledge.

Lower premolars.—The lower premolars are not in contact but are not widely separated. The third is slightly larger than the first two and all are oval in outline.

Lower molars.—The three lower mo-

lars are oval in occlusal outline and probably are not in contact. The talonid is deeply concave.

Platalina Thomas

Platalina is a monotypic genus (*P. genovensium*) known only from Perú (Cabrera, 1958:71; Tuttle, 1970). Specimens of *P. genovensium* are rare; apparently only four have been deposited in museums. This bat is a brownish, medium-sized glossophagine with an elongate muzzle. The tip of the tail extends through the middle of the relatively unreduced interfemoral membrane.

Nothing is known about the natural history of *P. genovensium*, but I assume that, like the other glossophagines, it feeds on nectar, soft fruit, and possibly on pollen.

The dentition was described in the original description (Thomas, 1928) and has been illustrated by Aellen (1965). The species has 34 permanent teeth; its dental formula is: $i\ 2/2$, $c\ 1/1$, $p\ 2/3$, $m\ 3/3$. Morphological variation, dental interaction, and dental abnormalities have not been studied in this rare genus.

Upper incisors.—The four upper incisors are large teeth that are set in a shallow arc, completely filling the space between the canines. The inner incisors are especially large, being about 25 per cent larger than the outer pair. The inner teeth are procumbent, spatulate teeth with broad crowns. The outer incisors, in contrast, are pointed and have strongly oblique crowns.

Upper canines.—The upper canines are narrow teeth that have an almost flat internal surface. A cingulum is lacking except for a moderate posterior cingular style. A longitudinal groove and ridge is lacking from the anterior-facing surface of the canine.

Upper premolars.—The two upper premolars are thin, moderately low-crowned teeth that are not in contact. The two teeth resemble each other but the first (P3) is slightly smaller. Both premolars have trenchant main cones and small anterior and posterior cingu-

lar styles. The second premolar (P4) lacks a postero-lingual cingular shelf.

Upper molars.—The three upper molars are not in contact; the third is slightly smaller than the other two but morphologically all three are similar. Generally, the molars are greatly reduced and lack any trace of a W-shaped ectoloph. The paracone is lacking and the parastyle, which is a high, narrow cusp, is the only high point of the antero-labial margin. The mesostyle is lacking from all three teeth so that the posterior element is reduced to a single, narrow cusp that apparently represents the metacone. This cusp is located on the postero-labial margin of the tooth and is directly posterior to the parastyle. The internal element of the upper molars is greatly reduced, consisting only of a small ledge that extends along the anterior half of the lingual side of the tooth. A high point on the lingual margin apparently represents the protocone. A hypoconal basin is lacking.

Lower incisors.—The four lower incisors are relatively large, high-crowned teeth that are slightly procumbent. The inner pair is slightly larger than the outer pair, but morphologically all four teeth are essentially the same. The lower incisors completely fill the available space and all are in contact.

Lower canines.—The lower canines are simple, slightly recurved teeth that have a narrow posterior cingular shelf.

Lower premolars.—The three lower premolars are not in contact, but neither are they widely spaced. The premolars are about the same size and all are narrow and have relatively low main cones. The first (p2) lacks an anterior cingular style and thus differs from the other two, which have both an anterior and a posterior cingular style.

Lower molars.—The three lower molars are not in contact nor are they widely spaced. These teeth are greatly reduced; all are similar morphologically but the first two are slightly larger than the third. The metaconid is the largest and most prominent cusp; it is located

on the lingual margin of the molar. The protoconid is greatly reduced so that it is nothing more than a ridge-like cusp on the longitudinal axis of the tooth. The paraconid is located directly anterior to the protoconid. The talonid is greatly reduced, is narrow, and lacks a hypoconid. A small, low cusp on the lingual margin may represent the entoconid.

Choeronycteris Tschudi

The single species of the genus, *Choeronycteris mexicana*, occurs from Arizona throughout much of México (including Baja California) to as far south as Guatemala (Hall and Kelson, 1959:120). Hog-nosed bats are drab grayish-brown in color, are medium-sized for glossophagines, and have a long muzzle. The tail is short, and the interfemoral membrane is unreduced.

Choeronycteris mexicana apparently feeds mostly on nectar and pollen (Cockrum and Ordway, 1959:14); several specimens collected in Arizona had yellow pollen in the fur around their faces (Hoffmeister and Goodpaster, 1954:54). Captive individuals of *mexicana* have been reported to lap up juices of grapes and plums but reject the solid parts of these fruits, and made no attempt to chew their food (Walker *et al.*, 1964:290).

Miller (1907:141) has described the dentition of this genus; Handley (1966a:85) summarized it as "reduced" and having high premolars. Miller (*loc. cit.*) mistakenly assumed that the parastyle was absent from the molars in *Choeronycteris*. On the basis of my studies of *Lichonycteris*, I regard the paracone as having been lost and the parastyle not only present but enlarged (see generic account of *Lichonycteris*). Handley (*loc. cit.*) synonymized the genus *Muso-*

nycteris with *Choeronycteris*, but for reasons explained in the next generic account, I consider the two as generically distinct. Overall, the dentition of *Choeronycteris* is reduced and highly specialized. The permanent lower incisors have been lost but the deciduous teeth, ranging from one to four, often persist in adults (although the coronal apex is approximately flush with the alveolar bone).

Choeronycteris mexicana has 30 permanent teeth; the dental formula is: i 2/0, c 1/1, p 2/3, m 3/3.

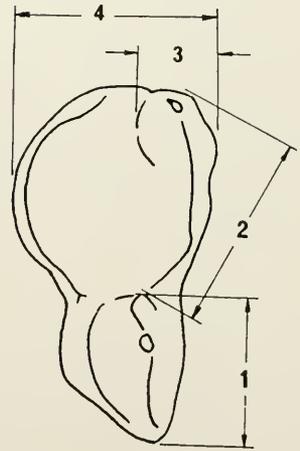
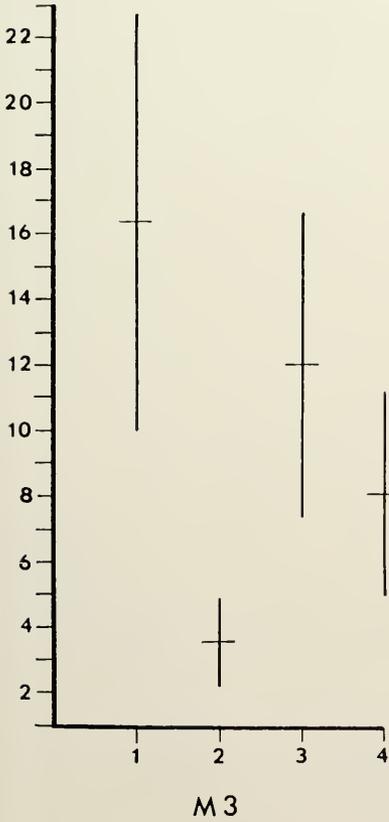
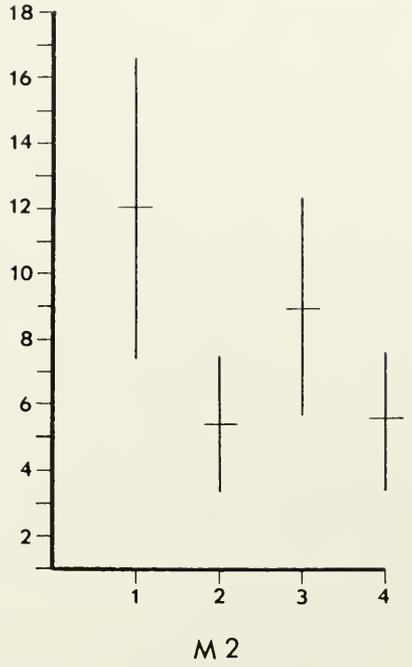
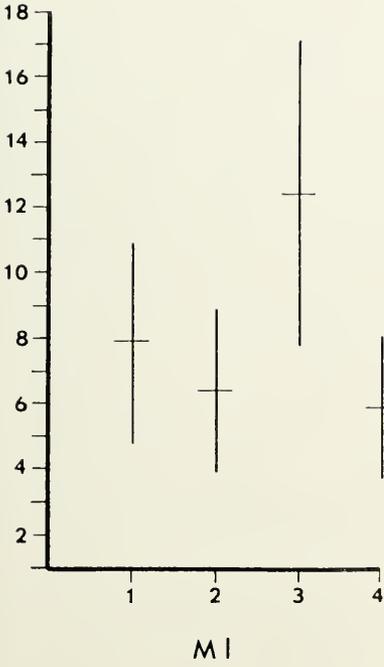
Upper incisors.—The four upper incisors are small teeth that do not fill the space between the canines. The inner incisors are separated, forming a median gap; these teeth have a fairly broad crown and are set so that each is paired with an outer incisor. The outer incisors are about the same size as the inner teeth, but have pointed crowns with an oblique edge.

Upper canines.—The upper canines are stout, nearly vertical teeth that lack a longitudinal groove and ridge on the anterior-facing surface. The canines have a narrow antero-lingual cingulum and small posterior cingular style.

Upper premolars.—The two upper premolars are long, narrow teeth that are widely separated. The two teeth are nearly the same size but differ in that the second has a postero-lingual cingular shelf. The main cone of each tooth is high and trenchant and both have an anterior and posterior cingular style.

Upper molars.—The three upper molars are widely separated. All three are roughly oval in occlusal outline and are so reduced that a W-shaped ectoloph is lacking. The first two are nearly the same size and also closely resemble each other morphologically. The paracone is lacking and the parastyle is a prominent

FIG. 29.—Graphs showing coefficients of variation (horizontal bars) and two standard errors (plotted on ordinate) for measurements of morphological features of upper molars in *Choeronycteris mexicana* (measurement numbers plotted on abscissa). The four different measurements taken on each of the three molars are shown in the inset.



antero-labial style. The mesostyle also is lacking but the metacone is a high, prominent cusp. The metastyle is small and located directly posterior to the metacone. The third molar differs in being slightly smaller than the first two and in lacking a distinct metastyle.

Lower canines.—The lower canines are slender, simple teeth that are tilted laterally. They have but a trace of an antero-lingual and postero-lingual cingular ledge.

Lower premolars.—The lower premolars are not in contact; all three are long and narrow, and are of approximately the same size. The first has a trenchant main cone that is relatively thick at the base and lacks the anterior and posterior cingular styles. The second and third are narrower than the first and have both anterior and posterior cingular styles.

Lower molars.—The three lower molars are widely separated. All three are morphologically similar but the third is somewhat smaller than the first two. The paraconid is on the longitudinal axis of the molar. The metaconid is the highest, most prominent cone and is located beside, or slightly posterior to, the level of the protoconid. The entoconid is a long, low ridge-like cusp and the hypoconid is shorter and more distinct. There usually is a small, posteriorly-directed flange on the posteristid of each of the lower molars.

Morphological Variation

Thirty specimens of *Choeronycteris mexicana* from northern México were used for a study of morphological variation in teeth of bats of this genus. Fourteen specimens from Coahuila and Tamaulipas, México, were used for a statistical analysis of the dimensional variation in the second upper premolars and the upper and lower molars. Coefficients of variation of all measurements are summarized in figures 29 and 30.

The upper incisors in *Choeronycteris* are small and only slightly variable in size and shape. The first premolars,

which are long and narrow, vary only slightly in morphology and size. The second premolars (P4), however, are slightly more variable because of the presence of a small postero-lingual shelf that is narrow in some individuals and fairly broad in others. This variation is expressed in a moderate coefficient of variation (8.19 ± 3.36) for the measurement of width of the premolar.

Variation in morphology of the upper molars in *Choeronycteris* cannot be compared directly with that of the upper molars of *Anoura*, *Glossophaga*, and *Lep-tonycteris*, because of the differences in structure of these teeth in the two groups of genera. Generally, the first upper molar in *Choeronycteris* is a moderately variable tooth, with the width of the parastyle being the most variable feature (CV, 12.43 ± 4.76 , Fig. 29). In some individuals, for example KU 98348 (Fig. 31), the parastyle is fairly broad and nearly vertical, whereas in others the stylar cusp is narrow and tilted labially (KU 98351, Fig. 31). The labial margin of the anterior element is fairly stable (CV, 6.45 ± 2.44), especially in comparison with the width of the parastyle. A definite mesostyle is lacking on the upper molars in *Choeronycteris* and this in part explains why the distance from the base of the metastyle (postcentrocrista) to the antero-labial edge of the tooth is not highly variable. The metacone of the first molar has a small but definite metastyle, which is fairly stable in size and shape. In a few individuals (for example, KU 98351, Fig. 31) the metastyle is slightly larger than in others but the overall consistency of the feature is shown by the relatively low coefficient of variation (7.98 ± 3.02) in comparison with the same measurement on the other molars (Fig. 29). The outline of the lingual half of the first molar varies considerably; in some individuals the lingual side is rounded and in others it is nearly pointed (Fig. 31). The overall breadth of the first molar, however, is the least variable of the four dimensions analyzed (Fig. 29).

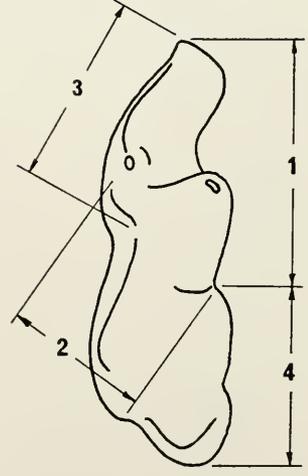
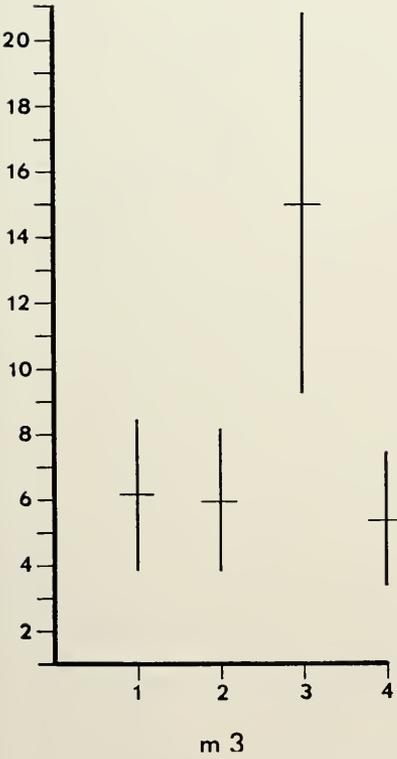
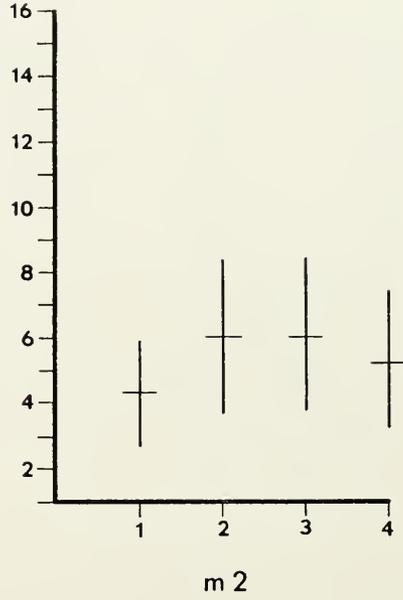
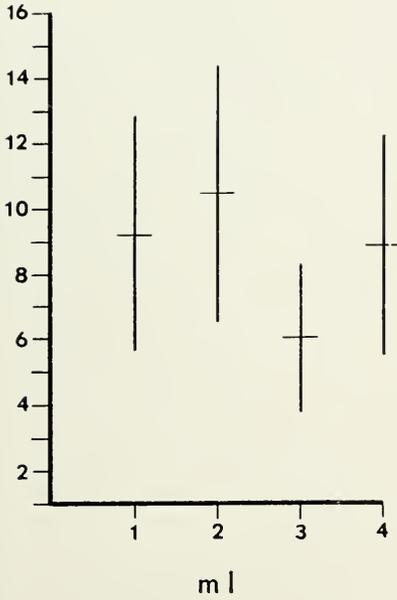
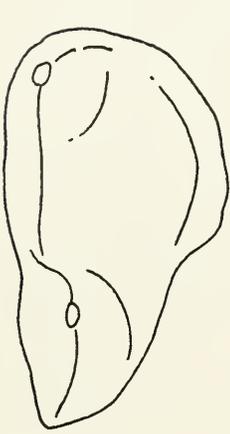
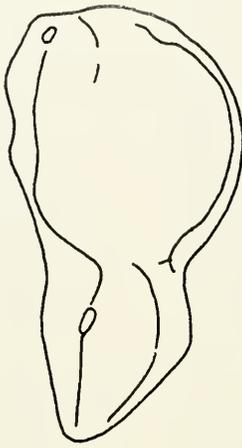


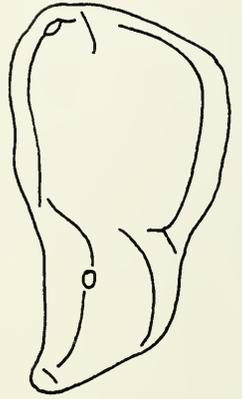
FIG. 30.—Graphs showing coefficients of variation (horizontal bars) and two standard errors (plotted on ordinate) for measurements of morphological features of lower molars in *Choeronycteris mexicana* (measurement numbers are plotted on abscissa). The four different measurements taken on each of the lower molars are shown in the inset.



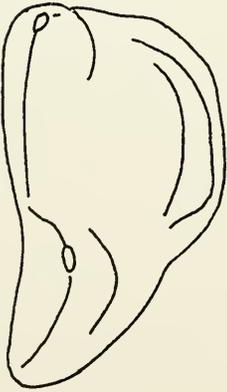
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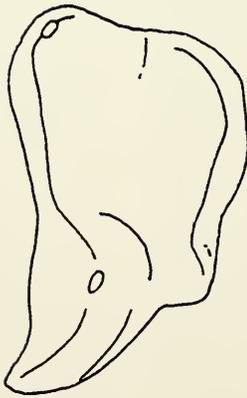
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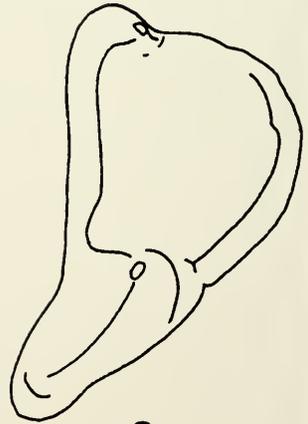
C



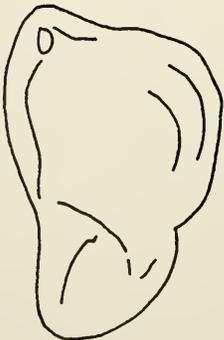
A



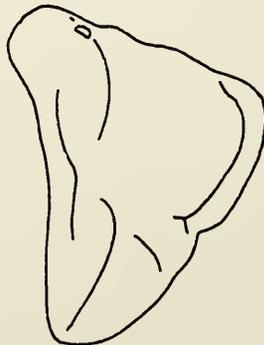
B



C



A



B

The second molar is about as variable as the first, but the greatest variation is in different structures. For example, the width of the parastyle of the second molar is not as variable as in the first (Fig. 29) and the length of the metacone-metastyle is considerably more variable. The position of the parastyle in the second molar does vary considerably, as shown in figure 31; in KU 98349 the paracone is tilted labially, whereas in KU 98348 it is nearly vertical. As in the first molar, the second has a definite metastyle, but unlike the first molar, the metastyle of the second tooth is highly variable in size and shape. In KU 88283 the metastyle is large and strongly twisted labially and in KU 98348, by way of comparison, the metastyle is rounded, relatively short, and nearly directed posteriorly (Fig. 31). The great variation in the metastyle, which overall is nearly always larger than in the first molar, is expressed in a high coefficient of variation (12.08 ± 4.62). As in the first molar, the length of the labial margin from the base of the metacone (postcentrocrista) to the anteriormost end of the tooth is stable, having a relatively low coefficient of variation (5.37 ± 2.03). The lingual portion of the second molar, like that of the first, varies considerably in outline but the overall breadth of the tooth is not especially variable (Fig. 29). The hypoconal basin also is highly variable; in some individuals (for example, KU 98349, Fig. 31), the basin is large and is a prominent feature, whereas in most specimens the postprotocrista connects directly to the base of the metacone or, at most, there is a short, shallow hypoconal basin.

The upper third molars are the most variable of the upper cheekteeth (Fig. 29). The parastyle varies greatly in width (CV, 12.10 ± 4.63) as well as in position. In some individuals (KU 98348,

Fig. 31) the cusp is narrow and nearly vertical but in a few individuals (KU 98395, Fig. 31) the parastyle is broad, tilted slightly, and has a trace of an antero-labial flange. The metacone, which essentially lacks a metastyle, is extremely variable in shape and size. In KU 98395 (Fig. 31), for example, the metacone is slightly elongate, with perhaps a trace of a metastyle, whereas the cone is short and rounded in KU 98348. The great individual variation in the metacone is expressed in an unusually high coefficient of variation (16.34 ± 6.33). As in the first two molars, the shape of the lingual portion of the third molar is highly variable. Furthermore, the overall breadth of the tooth, measured across the widest place, is more variable than in either of the other two molars (Fig. 29).

The lower premolars in *Choeronycteris mexicana* are slightly variable in length and in shape. The first premolars, which usually are curved, are the most variable in size and in curvature as well. The lower molars generally are not highly variable and overall probably are slightly less variable than the upper molars. The first and third lower molars are more variable than the second (Fig. 30). In the first molars, the breadth across the metaconid and protoconid is the most variable measurement (CV, 10.45 ± 3.99). The great individual variation in this feature apparently results from variation in the positions of the metaconid and protoconid as well as from the variation in overall breadth of the base of the tooth. In KU 70704, for example, the metaconid is nearly vertical and the labial margin, in occlusal view, is nearly straight (Fig. 32). In KU 98884, on the other hand, the metaconid is tilted slightly in a lingual direction and the labial margin is rounded (Fig. 32). The paralophid is morphologically variable in the first molar; the

◊

FIG. 31.—Examples of morphological variation in the upper molars of *Choeronycteris mexicana*. Top row (first molar): A, KU 98348; B, KU 98367; C, KU 98351. Middle row (second molar): A, KU 98348; B, KU 98349; C, KU 88283. Bottom row (third molar): A, KU 98348; B, KU 98395.

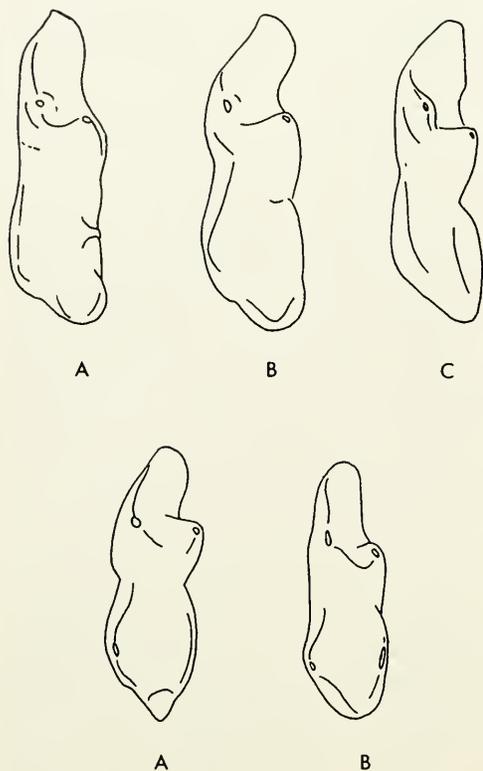


FIG. 32.—Examples of morphological variation in the first and second lower molars of *Choeronycteris mexicana*. Top row (first molar): A, KU 70704; B, KU 98884; C, KU 66412. Bottom row (second molar): A, KU 98884; B, KU 70704.

extent of this variation is illustrated by KU 66412 and KU 70704 (Fig. 32). Although the paralophid is variable in shape, the length is relatively stable ($CV, 6.03 \pm 2.28$). The talonid of the first molar varies considerably in dimension (coefficient of variation of the lingual length is 8.88 ± 3.38) and in morphology as well. The entoconid in some individuals (see KU 70704, Fig. 32) is split into two separate, low, ridge-like cusps, whereas in others it is a single low ridge. The labial margin of the talonid usually is only slightly flared but in a few specimens it extends beyond the labial edge of the trigonid (KU 98884 in Fig. 32). The degree of development of a posterior flange on the post-

crisid varies individually and accounts for the relatively high coefficient of variation in the lingual length of the talonid (Fig. 30).

The second lower molar varies in much the same way as the first, but not nearly to the same degree (Fig. 30). The greatest variation is in the width across the protoconid and metaconid, and in the length of the paralophid ($CV, 6.17 \pm 2.34$ for both). The flange on the postcrisid is not as variable in the second molar as it is in the first and consequently the lingual length of the talonid is not as variable (Fig. 30).

The third lower molar is about as variable as the second in most ways and thus slightly less variable than the first. The main difference, however, is in the length of the paralophid, which is highly variable ($CV, 14.92 \pm 5.76$). This interesting degree of variation apparently results from variation in the position of the protoconid. In the first two molars the protoconid is set slightly anterior to the metaconid, whereas in the third molar the protoconid has shifted posteriorly so that in some individuals it is at the same level as the metaconid. Variation in the position of the protoconid, along an anterior-posterior axis, causes the length of the paralophid to be considerably more variable than usual. The metaconid, in comparison with the protoconid, is fairly stable in position (although in some specimens the metaconid tilts lingually and in others it is vertical) and the length of the meta-crisid is not especially variable ($CV, 6.08 \pm 2.30$). All of the cusps of the talonid are reduced in the third molar, especially in comparison with the larger first molar, and do not seem to be as morphologically variable. The small flange on the postcrisid varies slightly, from being a definite flattened area (KU 98884, Fig. 32) to being indefinite and rounded (KU 70704, Fig. 32), and as a result the length of the lingual margin of the talonid is about as variable as it is in the second molar ($CV, 5.37 \pm 2.03$).

TABLE 15.—Correlation matrix for measurements of the three upper molars in *Choeronycteris mexicana*. Abbreviations for measurements are the same as those given in Table 1. Measurements are illustrated in Fig. 29. Coefficients significant at the alpha level of 0.05 are marked with an asterisk and those significant at the 0.01 level are marked with a double asterisk.

	M 1				M 2				M 3				
	MEC-MTS	MEC-PAS	WIDTH OF PAS	WIDTH OF TOOTH	MEC-MTS	MEC-PAS	WIDTH OF PAS	WIDTH OF TOOTH	MEC-MTS	MEC-PAS	WIDTH OF PAS	WIDTH OF TOOTH	
M 1	1.00												
	MEC-PAS	1.00											
	WIDTH OF PAS	0.42	1.00										
	WIDTH OF TOOTH	0.49	0.56*	1.00									
M 2	MEC-MTS	0.61*	0.33	0.48	1.00								
	MEC-PAS	0.19	0.45	0.36	0.27	1.00							
	WIDTH OF PAS	0.42	0.67**	0.36	0.44	0.35	1.00						
	WIDTH OF TOOTH	0.42	0.87**	0.53	0.71**	0.59*	0.76**	1.00					
M 3	MEC-MTS	0.31	0.03	0.15	0.54*	0.65*	0.22	-0.04	0.25	1.00			
	MEC-PAS	0.20	0.75**	0.24	0.45	0.27	0.56*	0.43	0.60*	0.18	1.00		
	WIDTH OF PAS	0.28	0.76**	0.29	0.43	0.39	0.40	0.60*	0.70**	0.31	0.62*	1.00	
	WIDTH OF TOOTH	0.37	0.28	0.05	0.45	0.72**	0.13	0.48	0.50	0.63*	0.32	0.47	1.00

Dental Interactions

A matrix of Pearson product moment correlation coefficients was prepared using the dimensional data discussed in the previous section. Overall, the coefficients of correlation were low; coefficients above 0.53 are significant at the critical level of 0.05 and those above 0.66 are significant above the 0.01 level. The measurements that were analyzed are illustrated in figures 29 and 30. Unfortunately, the measurements of the upper molars are not directly comparable with those taken on the upper molars of *Anoura*, *Glossophaga*, and *Leptoncycteris* because the reduced molars of *Choeronycteris* lack a W-shaped ectoloph. Furthermore, the molars in *Choeronycteris* are widely spaced.

Within the upper molars, few of the four measurements taken on each tooth are significantly correlated and, furthermore, the inter-tooth patterns are inconsistent (Table 15). In the first molar, the overall width of the tooth is correlated ($P \leq .05$) with the width of the prominent parastyle (r , 0.59) and also with the length of the "anterior element," which is the distance between the base of the metacone and the tip of the parastyle (r , 0.56). The only two significant coefficients of correlation within the M2 also involve the overall width of the tooth; the width is highly correlated ($P \leq .01$) with the length of the anterior element (r , 0.76) as well as with the metacone-metastyle length. The third molar differs in that although the width is correlated with the metacone-metastyle length, the only other significant correlation is between the width of the parastyle and the length of the anterior element (Table 15).

All three upper molars appear to be in the same morphogenetic field. When all combinations of measurements of M1 and M2 are compared, five of 16 have significant coefficients of correlation, whereas when the first molar is compared to M3, only three of 16 combinations are significantly correlated (Table 15). When the second and third molars

are compared, however, six of 16 combinations are significantly correlated. The width of the parastyle of the M1 is the only measurement, of the four taken, that does not correlate with any measurements of M2 or M3. In this regard, it should be noted that of the four measurements of M1 this was by far the most variable (CV , 12.43 ± 4.77). The metacone-metastyle length of the first molar is significantly ($P \leq .05$) correlated with the equivalent measurement of M2 (r , 0.61) but not with that of M3 (r , 0.31). The length of the anterior element (base of the metacone to the tip of the parastyle) is well correlated ($P \leq .01$) with the width of the parastyle and overall width of the second molar (0.67 and 0.87, respectively), and with the length of the anterior element and width of the parastyle of M3. The overall width of the first molar is correlated with the metacone-metastyle length of both M2 and M3 and with the overall width of M2 (Table 15). Interestingly enough, the overall width of the third molar is not correlated with any measured feature of the first molar, the highest coefficient of correlation being only 0.45. The third molar is fairly well correlated with the second molar; for example, the metacone-metastyle length of M2 is significantly correlated with its equivalent measurement on M3 (r , 0.66) as well as with the width of the third molar (r , 0.72). The overall width of the second molar is strongly correlated with both the length of the anterior element and the width of the parastyle (0.60 and 0.70, respectively). In general, therefore, the size of the M2 is correlated with the size of the M1, but only the size of the labial margin of the M3 is correlated with the size of the first molar. The M1 develops and completes its eruptive movements well before the maturation of the third molar (Fig. 10). Thus, the inter-relationship between the three upper molars in *Choeronycteris* can be summarized as follows: 1) the size of the M2 is directly related to the size of the M1, which undergoes odontogenesis slightly before

TABLE 16.—Correlation matrix for measurements of the three lower molars in *Choeronycteris mexicana*. Abbreviations for measurements are the same as those given in Table 2. Measurements are illustrated in Fig. 30. Coefficients significant at the alpha level of 0.05 are marked with an asterisk and those significant at the 0.01 level are marked with a double asterisk.

	m 1				m 2				m 3							
	PAD-MTD	MTD-POD	POD-PAD	TALONID												
m 1	1.00	0.37	1.00													
		0.34	0.14	1.00												
		-0.24	0.27	0.01	1.00											
m 2	0.07	-0.17	-0.27	0.15	1.00											
	0.56*	0.49	0.39	0.00	0.03	1.00										
	-0.14	-0.44	0.17	-0.24	0.12	-0.11	1.00									
	0.43	0.01	0.06	0.01	0.42	0.45	0.24	1.00								
m 3	0.28	-0.02	0.12	0.45	0.67**	0.42	0.24	0.68**	1.00							
	0.47	0.82**	0.04	0.19	0.18	0.47	-0.13	0.26	0.33	1.00						
	-0.14	-0.27	0.08	-0.03	0.45	0.15	0.47	-0.03	0.48	0.02	1.00					
	0.22	0.26	0.15	-0.01	0.24	0.52	0.01	0.18	0.44	0.59*	0.45	1.00				

the former, and 2) the size of the M3 is related more directly to the overall size of the M2 than to that of the M1, probably because the first molar is almost in the functional eruptive phase before amelogenesis of the third molar takes place.

The lower molars are remarkable because within the first and second teeth none of the measured features are correlated (Table 16). Within the m3, however, the length of the talonid has a significant ($P \leq .05$) correlation with the width of the trigonid (metaconid-protocoid width). Inter-tooth relationships are equally weak; the m1 has but one significant coefficient of correlation with each of the other two lower molars and the m2 and m3 have two significant coefficients of correlation (out of a possibility of 16). The length of the trigonid (paraconid-metaconid) of the first lower molar is correlated with the width of the trigonid of the second ($r, 0.56$) and the width of the trigonid of m1 is well correlated ($P \leq .01$) with the width of the trigonid of m3 ($r, 0.82$). The paraconid-metaconid length of the m3 is significantly correlated with both the equivalent measurement of m2 ($r, 0.67$) and the length of the talonid of the second molar ($r, 0.68$). When considering these weak inter-tooth dimensional relationships, two factors must be borne in mind. First, the lower molars in *Choeronycteris* are not in contact and even during development are not especially crowded; second, the lower molars generally are highly variable teeth (see previous section and Fig. 30).

The inter-relationships between the upper and lower molars also are highly unusual. Indeed, significant coefficients of correlation are so few in number that the upper and lower teeth possibly actually are independent units and thus are in separate morphogenetic fields. As can be seen in the matrix in table 17, there are only three significant coefficients of correlation (out of 144 combinations) when all measurements are compared. Interestingly enough, the

only significant relationships do not follow any particular pattern; for example, the paraconid-metaconid length of the m2 is negatively correlated ($r, -0.57$) with the overall width of the M2, and the paraconid-metaconid length and the width of the trigonid (metaconid-protocoid) of the m1 are positively correlated with the overall width of the third upper molar (Table 17).

In summary, size of the lower molars essentially is independent of size of the upper molars, and, among the lower molars, the teeth are almost independent in development. In the upper molars, however, the dimensions of the individual teeth are inter-related. Lack of correlation between the upper and lower teeth is possible only because of the incomplete and possibly insignificant amount of occlusion (Fig. 47).

Dental Abnormalities

In the 143 adults of *Choeronycteris mexicana* examined, no instances of hypodontia were found and only one specimen with partial anodontia, resulting from dental agenesis, was noted. Occasionally, however, specimens of adults were found to have retained the deciduous upper canines, and, as in other glossophagines, there was a moderate incidence of loss of teeth in life.

Dental Agenesis

In one specimen, an adult male from Colima (AMNH 188392), there was no trace of an upper left first incisor. The surface of the bone at the site normally occupied by this tooth was smooth and transillumination revealed no sign of an alveolar crypt. This specimen was abnormal in another way; the left second lower molar lacked a metaconid and two teeth had been lost or partially lost in life. The incidence of agenesis in males of *C. mexicana* thus is 1.64 and in both sexes combined is 0.70.

In the course of examination of histological preparations of juveniles of *C. mexicana*, it was discovered that permanent lower incisors, although typically

TABLE 17.—Matrix of coefficients of correlation for upper and lower molars in *Choeronycteris mexicana*. The lower molars are plotted across the top; measurements compared are those illustrated in Figs. 29 and 30. Coefficients significant at the alpha level of 0.05 are marked with an asterisk and those significant at the 0.01 level are marked with a double asterisk.

	m 1				m 2				m 3			
	PAD-MTD	MTD-POD	POD-PAD	TALONID	PAD-MTD	MTD-POD	POD-PAD	TALONID	PAD-MTD	MTD-POD	POD-PAD	TALONID
M 1												
MEC-MTS	0.27	0.10	0.50	0.27	-0.40	0.12	0.05	-0.11	0.08	-0.01	-0.07	-0.02
MEC-PAS	0.21	-0.10	0.32	-0.37	-0.49	0.15	0.43	-0.18	-0.12	0.02	0.29	0.31
WIDTH OF PAS	-0.02	0.05	-0.15	0.38	-0.42	-0.10	-0.03	-0.11	0.07	0.07	-0.07	-0.07
WIDTH OF TOOTH	0.21	0.18	0.04	0.17	-0.33	0.28	-0.04	0.14	0.21	0.26	-0.03	0.45
M 2												
MEC-MTS	0.29	0.47	0.36	0.34	-0.48	0.46	-0.36	0.08	0.15	0.33	-0.15	0.36
MEC-PAS	0.34	-0.04	-0.03	-0.47	-0.26	0.37	0.33	0.18	-0.05	0.00	0.14	-0.04
WIDTH OF PAS	0.41	0.38	0.35	-0.10	-0.48	0.05	0.30	-0.04	-0.13	0.46	-0.17	0.13
WIDTH OF TOOTH	0.40	0.10	0.32	-0.18	-0.57*	0.19	0.17	0.01	-0.04	0.16	-0.01	0.23
M 3												
MEC-MTS	0.50	0.35	-0.05	0.08	0.07	0.50	-0.40	0.37	0.35	0.33	0.04	0.30
MEC-PAS	0.22	0.21	0.08	-0.30	-0.40	0.34	0.08	-0.36	-0.24	0.12	0.24	0.20
WIDTH OF PAS	0.30	0.23	0.23	-0.32	-0.28	0.18	0.24	-0.18	-0.02	0.38	0.46	0.44
WIDTH OF TOOTH	0.62*	0.68**	0.33	-0.15	-0.45	0.50	-0.46	0.06	-0.17	0.53	-0.35	0.32

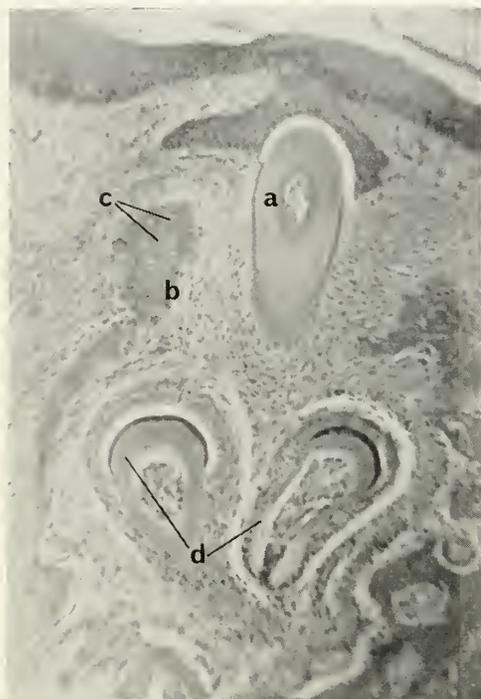


FIG. 33.—Longitudinal section through anterior part of mandible of a juvenile individual of *Choeronycteris* showing a deciduous incisor (a), partially resorbed alveolar bone (b), osteoclasts (c), and two “permanent” lower incisors (d). Stained with hematoxylin and eosin.

lacking in adults, do form but do not erupt. In the microscopic view in figure 33, a deciduous incisor can be seen directly above the two fully formed permanent incisors. Alveolar bone was being actively resorbed in the area adjacent to the deciduous tooth. The two permanent teeth are shown at high magnification in figure 34. The ameloblasts are squared rather than columnar (compare with Fig. 9) and have a large, centrally located nucleus; possibly, this configuration indicates that the enamel on the two teeth was mature. On the other hand, the ameloblasts could have been abnormal. In the tooth on the left in figure 34, there is a space between the enamel (which was not decalcified in preparation) and the bases of the ameloblasts. This space is an artifact of preparation and is not seen in the other tooth. The pulp cavities of both permanent

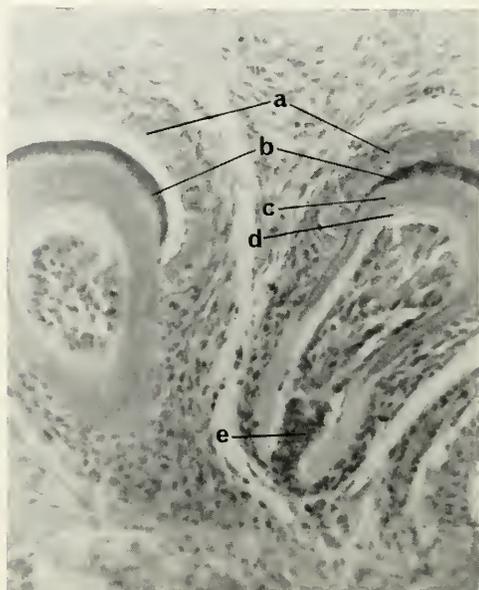


FIG. 34.—Highly magnified view of two unerupted permanent teeth shown in Figure 33. Note the squared ameloblasts with large nuclei (a), apparently mature enamel (b), dentin (c), and predentin (d), and a cluster of osteoclasts at the apex of the root of one of the two teeth (e). Stained with hematoxylin and eosin.

lower incisors obviously are abnormal (Fig. 34); both contain odontoblasts and fibroblasts as well. At the apex of the root of the tooth on the right, there is a cluster of cells that appear to be osteoclasts. The presence of these cells might mean that the permanent teeth are destroyed by this process.

Incomplete Shedding

As was mentioned in the chapter on deciduous teeth, occasionally the upper deciduous canines in *Choeronycteris* are not shed. In three adult males examined by me, both deciduous upper canines were in place between the canine and first premolar and not in contact with either tooth. The deciduous teeth are well rooted and show no signs of partial resorption. The teeth are so short, however, that it is doubtful they extended through the gingivum and thus they probably were totally nonfunctional. The incidence in males was 4.92 and in both

TABLE 18.—Comparative incidence of loss of teeth in life in males and females of *Choeronycteris mexicana*. Total numbers of teeth, given at bottom of table, were used to calculate the percentages.

Teeth	Male	Female	Teeth	Male	Female
Upper			Lower		
I1	0.82	3.66	c	0.82	0
I2	2.46	4.88	p2	0.82	0
C	0	0	p3	0	0
P3	0	0	p4	0.82	0
P4	0.82	0	m1	0.82	0
M1	0	0.61	m2	1.64	0
M2	1.64	0.61	m3	0.82	0.61
M3	0	0			
Totals	122	164		122	164

sexes combined (as there is no reason to think that this phenomenon is peculiar to males) was 2.10. Apparently the growth of the jaws is rapid enough that if the deciduous canines have not been shed during the eruptive movements of the permanent teeth they will be retained because of lack of contact or proximity with either the permanent canines or first premolars.

Loss of Teeth in Life

Loss of teeth in life in *Choeronycteris* is summarized in table 18. In the fairly small sample studied there was no significant difference between the sexes. As in most other glossophagine bats, the upper incisors frequently are lost in life in *Choeronycteris*; the second incisors apparently are lost most frequently (Table 18). The cheekteeth are subject to a moderate incidence of erosion (see chapter on pathology) and not infrequently specimens were examined in which a portion of a molar was partially eroded.

Musonycteris Schaldach and McLaughlin

Only a few specimens of the one species, *Musonycteris harrisoni*, of this recently named genus have been collected. All of the localities of record are in Colima and Guerrero, México; (Schaldach and McLaughlin, 1960:8;

Goodwin, 1969:70). Banana bats are medium-sized, among the glossophagines, and are drab grayish-brown in color. They have a strikingly long muzzle, a short tail, and a generally unreduced interfemoral membrane.

In the original description of *Musonycteris harrisoni*, Schaldach and McLaughlin (1960:3) did not present a detailed analysis of the dentition, although they did note that the "cheek teeth [are] delicately formed with much reduction of lingual elements." Handley (1966a:85) considered *Musonycteris* to be a synonym of *Choeronycteris* because he thought that the two differed only in that the former had a "strikingly elongated rostrum and associated modifications in proportions." In my opinion, however, the two genera differ in several fundamental ways. For example, the basicranial regions are considerably different and the third upper molars of *Musonycteris*, in comparison with those in *Choeronycteris*, are considerably less reduced and have a large, prominent metastyle. In view of the generally subtle differences among species of the Glossophaginae, those between *Musonycteris* and *Choeronycteris* are of generic value.

The feeding habits of *M. harrisoni* are unknown but by inference it is thought that this species feeds on nectar of banana flowers (Schaldach and McLaughlin, 1960:6). The extremely long rostrum and greatly reduced dentition

supports the hypothesis that these bats primarily feed on nectar.

The rostrum of *Musonycteris harrisoni* is greatly elongated and consequently the reduced teeth are widely spaced. Unlike many of the other glossophagines, including *Choeronycteris*, the third upper molar in *M. harrisoni* is relatively unreduced. In *Musonycteris* there are 30 permanent teeth; the dental formula is: $i\ 2/0$, $c\ 1/1$, $p\ 2/3$, $m\ 3/3$.

Upper incisors.—The four upper incisors are relatively small teeth that are not in contact; there is a small gap between the inner incisors. The first incisors have a flat, broad crown that is oval in occlusal outline. The outer incisors are slightly larger and have a pointed crown and strongly oblique edge.

Upper canines.—The canines are narrow, nearly vertical teeth that lack a longitudinal groove and ridge on the anterior-facing surface. There is a small posterior cingular style but a cingulum otherwise is lacking.

Upper premolars.—The two upper premolars are not in contact; instead, they are widely spaced between the canine and first molar. Both premolars are long and narrow and of essentially the same size and morphology. The trenchant main cone is relatively low and the anterior and posterior cingular styles are small.

Upper molars.—The three upper molars are widely spaced; all three are about the same in size and morphology. The paracone is lacking and the parastyle is a large, prominent antero-labial style. The mesostyle is nearly indistinguishable and thus could be considered lacking. The metacone is prominent but not as large or as high as the parastyle. The metastyle is directly posterior, or slightly labial, to the metacone. The protocone is a low, ridge-like cusp, and a hypoconal basin is lacking.

Lower canines.—The lower canines are simple teeth that are slightly recurved. They have a narrow postero-lingual cingular ledge but a cingulum otherwise is lacking.

Lower premolars.—The three lower premolars are widely spaced; all three are approximately the same size but the first (p2) differs morphologically from the other two. The p2 is the broadest of the premolars and has a slightly convex lingual surface, a low main cone, and a small posterior cingular style; an anterior style is lacking. The second and third premolars (p3 and p4) are narrower than the first and have higher main cones as well as anterior and posterior cingular styles.

Lower molars.—The three lower molars are widely spaced; all are long and narrow. The m1 is the largest and the m3 the smallest. The third molar is somewhat reduced in size and morphology. On all three teeth the paraconid is upturned and has a small accessory flange on the anterior-facing surface. The metaconid and protoconid are high, prominent cusps that are of about the same size. The entoconid is a high, prominent ridge-like cusp, whereas the hypoconid is a low, rounded one. There is a small, posteriorly-directed flange on the posteristid.

Choeroniscus Thomas

Five species of these slender-nosed bats currently are recognized (Handley, 1966a:85). *Choeroniscus godmani* occurs from northwestern México into Central America, *periosus* is known from Colombia, *inca* is known from Perú and Ecuador, *minor* is recorded from the Guianas, and *intermedius* is known from Perú, Venezuela, Guayana, and Trinidad (Cabrera, 1958:72-73; Hall and Kelson, 1959:120-121; Jones, 1964:510-511; Handley, 1966a:84; Tuttle, 1970). Bats of the genus *Choeroniscus* are small, delicate glossophagines that are drab grayish-brown in color, have a moderately long muzzle, and a relatively long tail that barely penetrates the dorsal surface of the unreduced interfemoral membrane.

Goodwin (1946:313) described the extremely long tongue of *Choeroniscus godmani*, which is covered with numer-

ous thread-like papillae that form a brush adapted for reaching nectar at the base of the corolla in large flowers. The diet of bats of the genus *Choeroniscus* probably includes a fair variety of items, however, because pollen, fragments of coleopterous insects, and possibly crystallized honey or fruit juices were found in the stomach of an *intermedius* from Trinidad (Goodwin and Greenhall, 1961: 248).

The genus *Choeroniscus* is poorly known because only a few specimens are available for study, and many of these are from widely scattered places. *Choeroniscus* is closely related to *Choeronycteris* and until recently there was some doubt as to its generic validity (Handley, 1966a:84). In addition to major differences in proportion of the length of rostrum to overall size, these two genera differ morphologically in several ways, especially in the degree of specialization of the basicranial region of the skull. As in other glossophagine genera, there are only subtle differences in dentition between the nominal species of *Choeroniscus*. Handley (1966a:84-85) has presented a moderately detailed description of the dentition of *C. periosus*, which in many ways can be applied to the other species as well. All species of *Choeroniscus* have 30 permanent teeth; the dental formula is: $i\ 2/0, c\ 1/1, p\ 2/3, m\ 3/3$.

Upper incisors.—The four upper incisors are small teeth that are not in contact; the teeth of the inner pair are separated by a medium gap. The first incisors have a low, broad crown, whereas the outer teeth, which are about the same size, have a pointed crown and an oblique edge.

Upper canines.—The canines are thin, simple teeth that are nearly vertical and lack a longitudinal ridge and groove on the anterior-facing surface. The internal surface of the canines is concave. A cingulum is lacking.

Upper premolars.—The two upper premolars are small, thin teeth that are not in contact but neither are they widely separated. Both teeth are the same

size and have small anterior and posterior cingular styles.

Upper molars.—The three upper molars are not crowded. The third is smaller than the first two but all are similar morphologically. The paracone is lacking and the parastyle is prominent. The W-shaped ectoloph is obliterated. The mesostyle is barely distinguishable and could be considered lacking. The metacone is prominent but the metastyle is reduced on all of the molars. The protocone is low and ridge-like and the hypoconal basin is lacking.

Lower canines.—The canines are slender, recurved teeth that have but a trace of a postero-lingual cingulum.

Lower premolars.—The three lower premolars are not in contact but even so are not widely separated. All three are about the same size and are similar morphologically. The first premolar (p2) lacks a distinct anterior cingular style but has a broad posterior style, whereas the second and third premolars have both an anterior and posterior cingular style.

Lower molars.—The lower molars are not in contact. The third is only slightly smaller than the other two; morphologically, all three are similar. The paraconid is located near the labial margin of the molar and the metaconid and protoconid are moderate in size with the former being slightly posterior to the level of the latter. The entoconid is a low, ridge-like cusp and the hypoconid is inconspicuous.

Dental Abnormalities

Too few specimens of the species of *Choeroniscus* were examined to make an adequate appraisal of the kinds and incidence of dental abnormalities that occur in nature. In the 31 specimens studied, however, several did exhibit interesting abnormalities and are described below.

Hyperdontia

In an adult female (AMNH 140471) of *Choeroniscus minor* from Guayana

there are abnormal second lower premolars (p3). The tooth on the left is partially split in the middle as the result of incomplete dichotomy that apparently occurred during morpho-differentiation. The main cone is partially separated (to the level of the alveolus) and there is a median root. The anterior half of the tooth appears to be normal in that it is equal in size to the anterior portion of a normal p3 and has the anterior lingular style. The posterior half of the abnormal tooth also is of normal size and structure. In the second premolar on the right side the "split" is in the anterior style. The posterior half of this tooth and the main cone appear to be normal. Anterior to the split style there is another lingular style. In all other ways, this specimen was normal.

In an adult male of *Choeroniscus godmani* (AMNH 131765) from Costa Rica there is an extra molariform tooth on the right side, anterior to the normal first lower molar. Because the supernumerary tooth is set directly behind the last premolar (p4), all of the molars, which appear to be normal, are moved farther posteriorly than are those on the left side of the jaw. The extra tooth is the same size as a normal first molar and has many of the same features, except that a "paraconid" is lacking and the cusps are less distinct than on a normal first molar. The most likely explanation for the presence of the supernumerary tooth is that it resulted from a double initiation of the first molar but for one reason or another did not develop fully (perhaps because of the crowding from the last premolar). The remainder of the dental arcade in this specimen was normal.

In another specimen, an adult male of *Choeroniscus inca* (AMNH 67626) from Ecuador, there are extra upper premolars on the left and right sides directly behind the canines and anterior to the first premolars (P3). The extra teeth are smaller than a normal P3, being only about 40 per cent its size, and probably are atavistic teeth representing perma-

nent P2. The supernumerary tooth on the right is slightly larger than the one on the left and appears to have an anterior and posterior root, whereas the one on the left has but one root. Morphologically, however, both of the extra teeth are otherwise much the same. Interestingly enough, Husson (1962:134) reported that in the holotype of *C. minor*, a specimen from Trinidad, there is a small, extra tooth located on the left side between the upper canine and first premolar. Because the extra tooth was widely separated from the canine and P3, Husson thought that it might be a persistent deciduous premolar. Although I have not examined this specimen, it seems likely that the extra tooth either is an atavistic permanent P2 or the deciduous P2, which probably is found in *Choeroniscus* just as it is in the other glossophagines thus far studied.

Loss of Teeth in Life

Although my sample is too small to warrant analysis of the incidence of loss of individual teeth in life, it is worthwhile to note that in the six of 31 specimens that had lost teeth in life, the upper incisors were the teeth most frequently involved. It is probable that the pattern of exfoliation of teeth due to erosion and other factors is generally the same in *Choeroniscus* as it is in a closely related genus like *Choeronycteris*.

COMPARISONS OF GLOSSOPHAGINE DENTITIONS

At first glance, the genera comprising the subfamily Glossophaginae present a rather confusing array of dental characteristics that seem to be randomly intermixed. However, this is not the case, because several trends are discernible upon careful examination. Convergent evolution has resulted in a group of species whose genetic relationships often are obscured by apparent, but highly superficial, similarities. This fact, above all others, must be borne in mind in considering the importance of similarities

TABLE 19.—Schematic summary of similarities and differences in the upper dentitions of the 13 genera of the Glossophaginae. Genera grouped in a column are most alike; genera enclosed in a bracket are basically similar. The groupings do not necessarily reflect relationships because of convergence within the subfamily. See text for discussion.

TEETH	GENERA			
Upper incisors	ANOURA CHOERONYCTERIS CHOERONISCUS MUSONYCTERIS	HYLONYCTERIS LICHONYCTERIS SCLERONYCTERIS	LONCHOPHYLLA LIONYCTERIS GLOSSOPHAGA PLATALINA	MONOPHYLLUS LEPTONYCTERIS
	CHOERONISCUS CHOERONYCTERIS MUSONYCTERIS LICHONYCTERIS HYLONYCTERIS PLATALINA SCLERONYCTERIS		LONCHOPHYLLA LIONYCTERIS GLOSSOPHAGA	ANOURA MONOPHYLLUS LEPTONYCTERIS
Upper canines	CHOERONISCUS CHOERONYCTERIS MUSONYCTERIS LICHONYCTERIS HYLONYCTERIS PLATALINA SCLERONYCTERIS		LONCHOPHYLLA LIONYCTERIS GLOSSOPHAGA	ANOURA MONOPHYLLUS LEPTONYCTERIS
	CHOERONISCUS CHOERONYCTERIS MUSONYCTERIS PLATALINA	HYLONYCTERIS LICHONYCTERIS	LONCHOPHYLLA GLOSSOPHAGA MONOPHYLLUS LEPTONYCTERIS	ANOURA
Upper premolars	CHOERONISCUS CHOERONYCTERIS MUSONYCTERIS PLATALINA		LONCHOPHYLLA GLOSSOPHAGA MONOPHYLLUS LEPTONYCTERIS	ANOURA
	CHOERONISCUS CHOERONYCTERIS MUSONYCTERIS HYLONYCTERIS PLATALINA	SCLERONYCTERIS	LICHONYCTERIS	MONOPHYLLUS GLOSSOPHAGA LEPTONYCTERIS
First upper molar	MUSONYCTERIS CHOERONYCTERIS HYLONYCTERIS	CHOERONISCUS LICHONYCTERIS PLATALINA SCLERONYCTERIS	LIONYCTERIS ANOURA MONOPHYLLUS LEPTONYCTERIS	LONCHOPHYLLA
	MUSONYCTERIS CHOERONYCTERIS HYLONYCTERIS	CHOERONISCUS LICHONYCTERIS PLATALINA SCLERONYCTERIS	LIONYCTERIS ANOURA MONOPHYLLUS LEPTONYCTERIS	LONCHOPHYLLA
Last upper molar (M2 or M3)	MUSONYCTERIS CHOERONYCTERIS HYLONYCTERIS	CHOERONISCUS LICHONYCTERIS PLATALINA SCLERONYCTERIS	LIONYCTERIS ANOURA MONOPHYLLUS LEPTONYCTERIS	LONCHOPHYLLA
	MUSONYCTERIS CHOERONYCTERIS HYLONYCTERIS	CHOERONISCUS LICHONYCTERIS PLATALINA SCLERONYCTERIS	LIONYCTERIS ANOURA MONOPHYLLUS LEPTONYCTERIS	LONCHOPHYLLA

and differences of glossophagine dentitions.

The first and second upper incisors differ morphologically from each other in all genera. Upper incisors of any genus fall into one of two basic groups—reduced or large (Table 19). *Glossophaga*, *Platalina*, *Lonchophylla*, and *Lionycteris* show the least amount of reduction. In each of these genera the inner incisors are notably larger than the other teeth and have fairly broad, only slightly oblique, cutting edges. In contrast, the outer incisors are pointed and are strongly oblique; in *Platalina*, *Lonchophylla*, and *Lionycteris* the inner incisors are much longer than in *Glossophaga*. Two other genera, *Monophyllus* and *Leptonycteris*, also have relatively unreduced upper incisors; in these genera the inner incisors are essentially the same size as the teeth of the outer pair. The upper incisors, especially the inner pair, are greatly reduced in the remaining seven genera. In *Anoura*, *Choeronycteris*, *Musonycteris*, and *Choeroniscus*, the inner incisors are small, almost peg-like teeth that are widely separated by a median gap and usually are slanted toward, and sometimes contact, the second incisors. The latter are morphologically similar to those found in the glossophagine genera having unreduced upper incisors but are much smaller. In *Scleronycteris*, *Hylonycteris*, and *Lichonycteris* the upper incisors are reduced and the inner and outer teeth are about the same size. The inner incisors, however, are not separated by an especially wide median gap.

The upper canines have two basic configurations (Table 19). In *Anoura*, *Monophyllus*, *Leptonycteris*, *Lonchophylla*, *Lionycteris*, and *Glossophaga*, the canines are fairly large, stout teeth with a posterior cingular style and, usually, an anterior cingular style and a lingual cingular shelf. There is a fairly well-defined longitudinal groove and associated ridge on the anterior-facing surface of the canine in the first three of these genera. In *Platalina*, *Scleronycteris*, *Hylonycteris*, *Lichonycteris*, *Choe-*

roniscus, *Choeronycteris*, and *Musonycteris*, the upper canines are slim teeth, reduced in size, that essentially lack any cingular development (although there is a slight trace of a posterior cingular style in the last two genera).

The upper premolars vary in number as well as in configuration; three permanent upper premolars (P2, P3, P4) are found in *Anoura* but only two (P3, P4) in the remaining genera. In *Platalina*, *Choeronycteris*, *Musonycteris*, and *Choeroniscus*, the two upper premolars are long, thin teeth that resemble each other morphologically. In *Lonchophylla*, *Lionycteris*, *Glossophaga*, *Leptonycteris*, and *Monophyllus*, the first premolar is a fairly narrow, simple tooth with a trenchant main cone and small anterior and posterior styles, whereas the last premolar (P4) has all these characteristics plus a postero-lingual shelf. The upper premolars of *Glossophaga* differ slightly from this pattern in that they are relatively broader. The upper premolars of *Anoura* have the same general configuration as those in the group of genera just listed except that a permanent P2, which usually is a simple, peg-like tooth, also is present. The upper premolars in *Hylonycteris* are similar to those of *Lichonycteris*, although the former genus has somewhat smaller premolars. In both genera the first premolar is a short and relatively broad tooth having a trenchant main cone but essentially lacking anterior and posterior styles. The second premolar also is broad and short but in *Lichonycteris* it has a postero-lingual shelf as well as small anterior and posterior styles. The postero-lingual shelf is lacking in *Hylonycteris*. The two upper premolars in *Scleronycteris* and *Lionycteris* present yet another morphological configuration; P3 and P4 are structurally similar, both consisting of a high, trenchant main cone (about 50% of height of canines in *Lionycteris*) that is as broad as it is long at the base. Both premolars have a moderate postero-lingual shelf.

The upper molars in the glossopha-

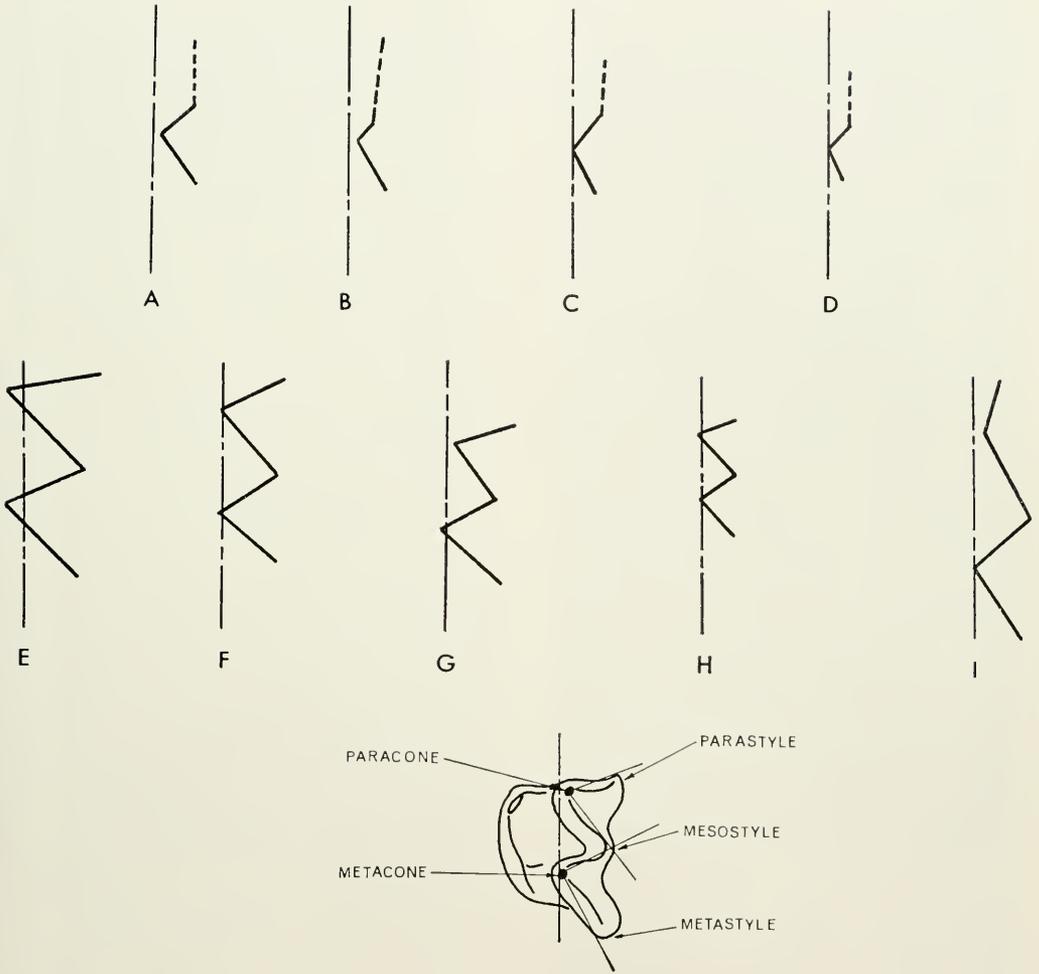


FIG. 35.—Diagrammatic comparison of modification of the first upper molar in nine glossophagine genera. The heavy center line is the longitudinal axis; morphological features are labeled in the example at the bottom. (A) *Choeronycteris*—note the loss of the W-shaped ectoloph through modification of the anterior element; (B) *Musonycteris*; (C) *Choeromiscus*; (D) *Hylonycteris*; (E) *Lonchophylla*—the “primitive” condition and distinct W-shaped ectoloph; (F) *Anoura*; (G) *Glossophaga*; (H) *Monophyllus*; (I) *Leptonycteris*—note the extreme modification in which the parastyle has shifted toward the longitudinal axis.

gines are especially interesting and serve to break the subfamily into several groups (Table 19) having minor differences. Basically, however, there are two groups—one having a W-shaped ectoloph and the other lacking it. Two genera (*Leptonycteris* and *Lichonycteris*) have but two molars, whereas all others have three. In the group of genera having the more primitive W-shaped ectoloph, there are several genera in which

the anterior and posterior elements of the ectoloph contribute equally to form the mesostyle and there are three genera in which the mesostyle is part of the posterior element alone. In three genera (*Lonchophylla*, *Lionycteris*, and *Anoura*), the W-shaped ectoloph is prominent and high-crowned. In *Lonchophylla*, the paracone and metacone of the first two molars are set slightly lingual to the midline of the tooth, whereas this is the

case only in the second molar in *Anoura* and *Lionycteris*. In the latter two genera, the paracone of the first molar has been shifted labially so that it is slightly to the right of the longitudinal axis of the tooth and the W-pattern is distorted (Fig. 35). The mesostyle in all three genera is part of the posterior element of the ectoloph; it is most prominent in *Lonchophylla* and *Anoura*. The W-shaped ectoloph is distinct in *Glossophaga* and *Monophyllus* but slightly distorted in *Leptonycteris*. In all these genera, the molars have lower crowns than do those of the three preceding genera. The ectolophs of the first and second molars are similar in *Glossophaga* and *Monophyllus*; the paracone and metacone of the second molars are set approximately on the longitudinal axis of the teeth, whereas in the first molar in both genera they are located on the labial side of the midline (Fig. 35). In *Leptonycteris*, which has only two upper molars, only the first has the typical ectoloph because the second is reduced in much the same way as the third molar in the other genera. In the first molar of *Leptonycteris*, the paracone is located slightly to the labial side of the longitudinal axis of the tooth and the parastyle is shifted toward the midline, causing distortion of the anterior triangle of the W-pattern (Fig. 35). The last upper molar (either M2 or M3) in five of the six genera having the more primitive ectoloph is morphologically reduced and because the metastyle is lacking, the W-pattern has been lost. *Lionycteris* is the single exception among this group of genera; in this genus the third molar, although smaller than the first two, retains the metastyle and thus has a typical ectoloph (Table 19).

The first upper molar in *Lichonycteris* is so variable that structural configurations seen in the few available specimens resemble those of the group just described (with a primitive W-shaped ectoloph) as well as that found in the following group (loss of the W-shaped ectoloph and paracone). *Licho-*

nycteris furthermore is one of the two genera having only two upper and two lower molars; the second upper molar in this genus is structurally similar to the M1 (although slightly smaller in overall size) rather than morphologically reduced as in *Leptonycteris*. A trace of a mesostyle sometimes is seen in specimens of *Lichonycteris*; when present, this style is formed entirely by the posterior element of the ectoloph, as it also is in *Lonchophylla*, *Lionycteris*, and *Anoura*.

The second general grouping of glossophagines, based on morphological features of the upper molars, includes the genera *Scleronycteris*, *Platalina*, *Hylonycteris*, *Choeroniscus*, *Choeronycteris*, and *Musonycteris* (Table 19). The W-shaped ectoloph has been obliterated in all of these genera; the paracone is lacking and the remaining stylar shelf and parastyle is greatly enlarged (Fig. 35). A distinct mesostyle also is lacking in all of these genera except *Scleronycteris* (in which the mesostyle is enlarged) and the metacone, which usually is the most prominent cone, is located on, or slightly labial to, the midline. The degree of reduction of the last molar varies in this group. In *Hylonycteris* and *Choeronycteris* the metastyle of the last molar (M3) is lacking or is reduced in comparison to the first two molars; in *Choeronycteris*, *Scleronycteris*, and *Platalina* the third molar closely resembles the first two. *Musonycteris* differs from the others in that the metastyle of the third molar actually is larger than it is on the other two molars.

As expected, the pattern of the lower dentitions corresponds well with that of the upper teeth. The presence or absence of lower incisors, for example, matches the reduced or unreduced conditions of the upper incisors. Permanent lower incisors thus are lacking in those genera having greatly reduced upper incisors (*Anoura*, *Lichonycteris*, *Scleronycteris*, *Hylonycteris*, *Choeroniscus*, *Choeronycteris*, and *Musonycteris*). In *Platalina*, *Lonchophylla*, and *Lionycteris*

the four lower incisors are large, robust teeth. The lower incisors in *Glossophaga* are smaller and less robust and lack the trifold crowns characteristic of those of *Lonchophylla* and *Lionycteris*, but even so usually are relatively larger than the lower incisors of either *Leptonycteris* or *Monophyllus*.

There are two basic configurations of lower canines, which essentially match those of the upper canines; in *Anoura*, *Lonchophylla*, *Lionycteris*, *Glossophaga*, *Monophyllus*, and *Leptonycteris*, the lower canines are stout, relatively large, and have a moderate to well-developed cingulum, whereas in the remaining genera the canines are slim and lack a prominent, wide base and cingula.

Three permanent lower premolars are found in all of the glossophagine genera. As was pointed out in the generic account, details of the lower premolars and molars of the genus *Scleronycteris* are unknown to me. In *Musonycteris*, *Choeronycteris*, and *Choeroniscus*, all three premolars are long, thin, and essentially the same size. The second and third teeth greatly resemble one another; both have a trenchant main cone and prominent, upturned anterior and posterior styles. The first premolar in these genera differs slightly from the other two in that the anterior end is nearly as high as the tip of the main cone. In *Hylonycteris* and *Lichonycteris*, the three lower premolars generally resemble each other morphologically; all three are short and relatively broad teeth with a low, thick main cone. In both genera, the first lower premolar clearly is the smallest and the third is the largest. The lower premolars of *Platalina*, *Lonchophylla*, *Anoura*, *Monophyllus*, *Glossophaga*, and *Leptonycteris* are much the same in their basic pattern. There are minor differences, however, which are noteworthy. In *Glossophaga*, for example, the three premolars are all about the same size but the main cones are not much higher than the remainder of the

occlusal edge and the teeth are relatively broad. In *Monophyllus* and *Leptonycteris*, on the other hand, the first premolar (p2) is 15 to 20 per cent larger than the second and third teeth, which are narrow and have prominent, trenchant main cones and anterior and posterior styles. The lower premolars in the remaining genera (*Anoura*, *Platalina*, and *Lonchophylla*) are broader. The lower premolars of *Lionycteris* differ considerably from those of the other genera; all three teeth are similar (although p3 and p4 are slightly larger than p2) and have the appearance of small canines. These premolars consist essentially of an extremely high main cone (about 75 per cent the height of the lower canines) with a moderate base. Each lower premolar has a small anterior and posterior style.

The lower molars are remarkably similar in all of the genera. In *Musonycteris* and in *Choeronycteris* the molars are long and thin and there is a small flange on the posteristid, directly behind the entoconid. This flange is present but small in *Choeroniscus*. In each of these three genera the entoconid is a short (anterior-posterior) but distinct ridge-like cusp. The lower molars in *Platalina*, *Hylonycteris*, and *Lichonycteris* also are long and narrow, but the entoconid is a long, low ridge and the protoconid is low and greatly reduced. The lower molars of *Lonchophylla*, *Lionycteris*, *Anoura*, and *Monophyllus* are much alike. In all four genera the paraconid projects sharply in an anterior direction and the hypoconid is flared labially. *Leptonycteris* follows this general pattern but the molars are longer and narrower. *Glossophaga* differs slightly from each of these genera in having relatively shorter, bulkier molars in which the protoconid is located near the longitudinal axis of the teeth and the hypoconid is not greatly flared. The entoconid is a long, low ridge in all six genera.

PATHOLOGICAL CONDITIONS OF THE ORAL CAVITY

Incidences and kinds of oral diseases found in populations of free-living, non-human, mammals have not been studied in detail, although Colyer (1936), Hall (1940; 1945), Phillips and Jones (1969; 1970), and Phillips *et al.* (1969) among others have more or less touched on the subject. Captive mammals of several species, however, play a significant role in experimental studies of many pathological conditions that are common to man and other mammals. Laboratory strains of the Norway rat, *Rattus norvegicus*, for example, have been used extensively in investigations of the genetics of dental caries (Hunt and Hoppert, 1939; 1944; and many other papers). Because the basic biochemical, physiochemical, and physical factors that interact to cause dental caries apparently are comparable in all mammals, such studies are directly applicable to man (see König, 1965:87). Recently, it was discovered that a species of South American marmoset (*Hapale jacchus*) meets the requirements for use in interdisciplinary studies of the biology of the periodontum in health and disease. Periodontal disorders in this primate closely resemble those of man (Levy, 1966).

Heretofore, essentially nothing was known about the kinds of pathological conditions found in the oral cavities of glossophagine bats. Only a few of the many potential abnormal conditions are discussed herein. The subject, therefore, remains open to additional investigations. Furthermore, the results of the present study were limited by the mediocre condition of materials preserved in alcohol (insofar as histological work is concerned), by the general unavailability of fresh tissues, and by the necessity of using cleaned skulls alone in the diagnosis of disease and in the recognition of disorders that usually affect soft as well as hard tissues.

PERIODONTAL DISEASES

Periodontal diseases, which involve infection and inflammation of the gingi-

vae and periodontal tissues, and often lead to destruction of alveolar bone and dental tissue, are a major cause of loss of teeth in many kinds of mammals, including man (Colyer, 1936:652; Fullmer, 1966:180). The variety of etiological factors associated with periodontitis, which is one of the most common periodontal diseases, include: 1) microorganisms; 2) calculus; 3) oral hygiene; 4) vitamin insufficiencies; and 5) irregular teeth (Fullmer, 1966:180). The role of malnutrition, especially protein deprivation, is unclear but studies have indicated that healing of gingival wounds is retarded in animals living on protein-free diets (Sweeney, 1964:66-67). Certain enzymes (possibly kallikrein, for example) apparently play a role as etiological factors or mediators of periodontal diseases, but techniques of value for studying this aspect only recently have been devised (Narrod and Braunbery, 1964:219; Fullmer, 1966:181).

Common periodontal diseases are rare in all genera of glossophagine bats, and generally are found only in old individuals. This conclusion is subject to the limitation that in specimens available as cleaned skulls, recession of alveolar bone, presence of spongy bone, or actual localized lesions are the only indicators of periodontitis. There is no way, of course, to recognize the occurrence of simple gingivitis that did not result in at least some destruction of hard tissues in such specimens. Furthermore, examination of specimens stored in alcohol does not elucidate the matter because color and swelling associated with infection are lost. One example of the few instances of periodontitis found in several of the more than 2400 specimens examined by me, is in an adult male of *Glossophaga alticola* (KU 28399) from Guerrero, México, and is illustrated in figure 36. In this individual, there is a severe lesion localized at the lower right first molar. The lesion extends approximately 1.00 mm along the posterior root,

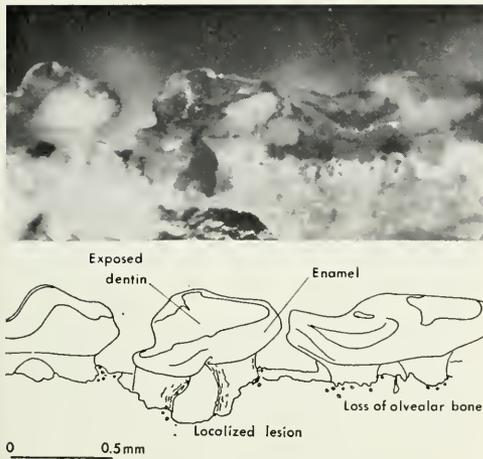


FIG. 36.—Periodontitis in an old adult male of *Glossophaga alticola* (KU 28399). The severe, localized lesion is at the base of the second molar.

thus completely exposing it, and approximately 0.25 mm along the anterior root, leaving the apex completely covered with alveolar bone. The thin cementoid layer, divested of periodontal ligaments, is rugose and partially resorbed. This is typical of periodontitis, although it is unknown why alveolar bone is resorbed before the hard dental tissues. Studies have indicated that the presence of pericemental fibers might retard the destruction of teeth, in comparison with adjacent bone (Reichborn-Kjennerud, 1963:314). Extreme coronal destruction is apparent in the specimen illustrated (Fig. 36); the dentin, which is stained brown, is widely exposed and most of the talonid of the first molar is missing. Generalized recession of the alveolar crest can be seen adjacent to the lesion. The coronal destruction undoubtedly resulted from a combination of factors, including attrition and erosion; the remaining teeth in this individual are greatly worn but still more nearly normal than is the first molar. The similarity of the localized lesion and dental destruction in this specimen of *G. alticola* and that caused by periodontitis in primates is striking (see Levy, 1966:233).

Some of the potential etiological fac-

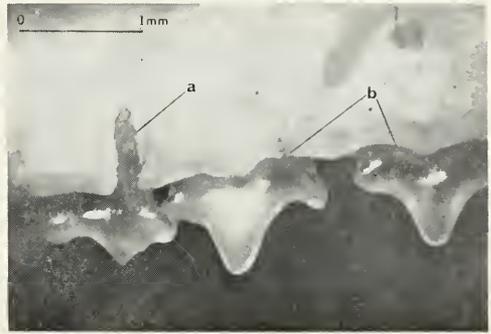


FIG. 37.—Localized rarefying osteitis, exposing the antero-labial root of the upper first molar in an adult male of *Leptonycteris sanborni* (KU 59608); a, lesion; b, normal alveolar bone of the first and second premolars.

tors in periodontitis apparently are lacking in the glossophagine bats, thus accounting for a low incidence of this particular periodontal disorder. Calculus, which probably is of primary importance in periodontitis (Fullmer, 1966:180; Levy, 1966:233-234), was not found on teeth of glossophagine bats. Furthermore, judging from specimens stored in alcohol, food does not tend to accumulate between individual teeth or between the gingivae and either the enamel or the cementum. Vitamin deficiencies and malnutrition probably occur in free-living mammals like glossophagine bats (although the subject has not really been studied) but manifestations of such inadequacies probably are generalized and involve the entire skeletal system to the point where the individual would be unable to survive at all.

A localized rarefying osteitis that is extremely common in all genera of glossophagine bats, but is not a disease in the strict sense, is illustrated in figure 37. This condition, which is seen in most kinds of small mammals, is often confused with periodontitis by mammalogists and thus is discussed in some detail here. In the example shown, an adult male of *Leptonycteris sanborni* (KU 59608) from Jalisco, México, about 0.75 mm of the alveolar crest of the maxillary bone adjacent to the antero-labial root of the first molar, has been completely

resorbed. In comparison with loss of bone resulting from periodontitis (Fig. 36), it can be seen that the non-diseased bone is relatively thick and smooth, and that the edge of the lesion is regular rather than thin, pitted, and irregular as in the lesion resulting from a periodontal disease. The labial surface of one or more roots of the upper molars and the apex of the roots of the last upper molars are at least partially exposed in nearly 100 per cent of adult long-nosed bats (*Leptonycteris*) and the condition is essentially as common in all other genera of glossophagines. Functional stresses and thinness of maxillary bone probably are the primary factors in alveolar resorption of this kind. Reichborn-Kjennerud (1963:315) has discussed the mechanisms that result in alveolar resorption when functional stress from mastication increases beyond the limit of compensatory response. In glossophagines, resorption is found at sites where lateral drift or dorsally-directed stress causes greatest pressure against the alveolar bone. Judging from the more than 2400 specimens examined in this study, rarefying osteitis of this sort does not advance beyond the stage illustrated (Fig. 37) or result in loss of teeth.

An unusual periodontal disease, known so far only in glossophagine bats, has been described recently by Phillips *et al.* (1969). In this disorder, the major etiological factor is the presence of protonymphs of mites of at least two species of the genus *Radfordiella* (Macronyssidae) in the oral mucosa of certain species (Fig. 38). The mites penetrate the gingivae at the epithelial attachment to the lingual surface of upper premolars and molars. The resultant pathological condition, which includes destruction of soft and hard tissues, frequently leads to exfoliation of teeth in life. The mites are so highly host specific that the presence or absence of the periodontal disorder is a remarkable artificial "taxonomic" characteristic that can be used to identify some glossophagine species. For example, in two of the

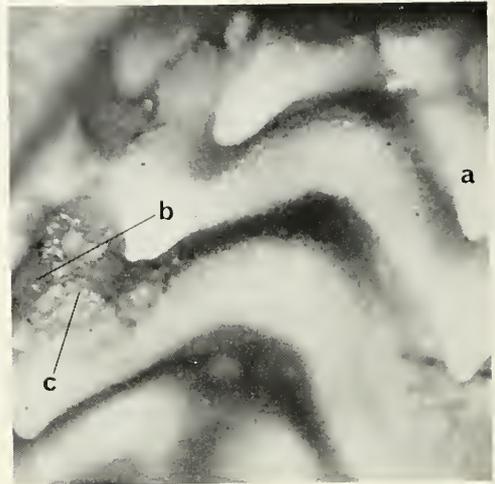


FIG. 38.—Palate of a specimen of *Leptonycteris nivalis* showing palatal ridges (a), the upper right first premolar (b), and a cluster of more than 20 oral mites (c). Photograph through courtesy of Frank J. Radovsky.

three species of *Leptonycteris* (*sanborni* and *nivalis*), which are sympatric over a broad area on the North American mainland, macronyssid mites are found only in the oral submucosa of *nivalis*.

Until recently, no species of mites of the suborder Mesostigmata were known from the oral cavity of a mammal and of the Macronyssidae, only *Draconyssus belgicae*, recovered from the nasal passage of a lizard, was known from an internal cavity (Phillips *et al.*, 1969). In the other suborders of Acarina, species of *Stomatodex* (Trombidiformes) are specific to the buccal mucosa of bats; males and immature stages of *Chironyssus* and some species of *Nycteridocoptes* (Sarcoptiformes) have been recovered frequently from the mucosa of the oral cavities of bats (Fain, 1959, 1960; Fain and Aellen, 1961). Many of the parasitic trombidiform and sarcoptiform mites are extremely small and live continuously in close association with the tissues of the host and thus it is not surprising that species of these two groups previously have been found in oral tissues. Generally, members of Mesostigmata are more robust and agile and consequently less often are tissue parasites.

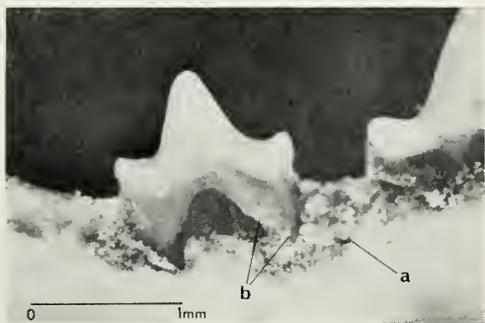


FIG. 39.—Palatal view of upper left premolar (P3) of an adult of *Leptonycteris nivalis* (KU 98411) showing extensive palatal lesion (a) and destruction of the posterior root of the tooth (b) as a result of infestation by oral mites.

Tissue reactions to infestations of ectoparasites are poorly known, although there have been several detailed studies of skin reactions to mites, which indicates an increasing interest among parasitologists (see, for example, Lavoipierre *et al.*, 1967 and Lavoipierre and Rajamanickam, 1968). The reactions of the soft and hard oral tissues to the presence of protonymphs of species of *Radfordiella* are of special interest for several reasons, which can be summarized as follows: 1) tissue reactions to ectoparasites are as yet little known; 2) the presence or absence of oral mites is highly host specific at the species level and therefore of potential systematic importance, and; 3) the epidemiology and histochemistry of a variety of periodontal disorders currently are being studied, and thus can be compared to this new periodontal disease in which macronyssid mites are the pathogens and therefore the primary etiological factor.

To date, specimens of protonymphs of at least two species of *Radfordiella* have been recovered from specimens of *Leptonycteris nivalis* and *Anoura geoffroyi* from México. Judging from the presence of palatal lesions that are a typical response to infestations, the mites also occur in *Monophyllus redmani* in the Greater Antilles. Adult mites have not yet been found, although fur of bats stored in alcohol has been examined. The

other known species of *Radfordiella* have been collected from the pelage of vampire bats (*Desmodus*), short-tailed bats (*Carollia*), mustached bats (*Pteronotus*), and mastiff bats (*Molossus*). Radovsky (1967:158) noted that *Molossus* probably is not a natural host.

The pathological conditions resulting from infestations of mites in the oral mucosa include: 1) general resorption of bone of the hard palate and alveolus at the site of infection (Fig. 39); 2) destruction of periodontal ligaments supporting the teeth; 3) resorption of cementum and dentin of teeth adjacent to the infection, and; 4) loss of teeth in severe cases. Generally speaking, therefore, the effects of oral mites somewhat parallel those of typical periodontitis. Normal oral epithelium and connective tissue are compared to that of an infected site in figure 40. Palatal and alveolar lesions are of special interest because they can be recognized readily in cleaned skulls and thereby the incidence and geographic distribution of mite-caused periodontal disease can be studied using materials stored in museums. In *Leptonycteris nivalis*, palatal lesions usually are found on the lingual side of the upper first premolars (P3), but in severe infestations lesions also are found along the lingual surface of the second premolars and molars as well (Fig. 39); lesions never have been found adjacent to upper canines and incisors. Palatal and alveolar lesions typically extend the full length of the tooth and they sometimes are as much as 1.0 mm long (anterior-posterior length) and nearly 0.5 mm deep. The edges of the palatal lesions are smooth and rounded but the sides and bottom are pitted and irregular. In severe cases, the maxillary sinus is exposed and the extremely thin epithelial lining of the sinus, which essentially is indistinguishable from the periosteum of the surrounding bone, thus becomes contiguous with the connective tissue of the submucosa (Fig. 40). Such exposure of the maxillary sinus, in conjunction with adjacent infection, can

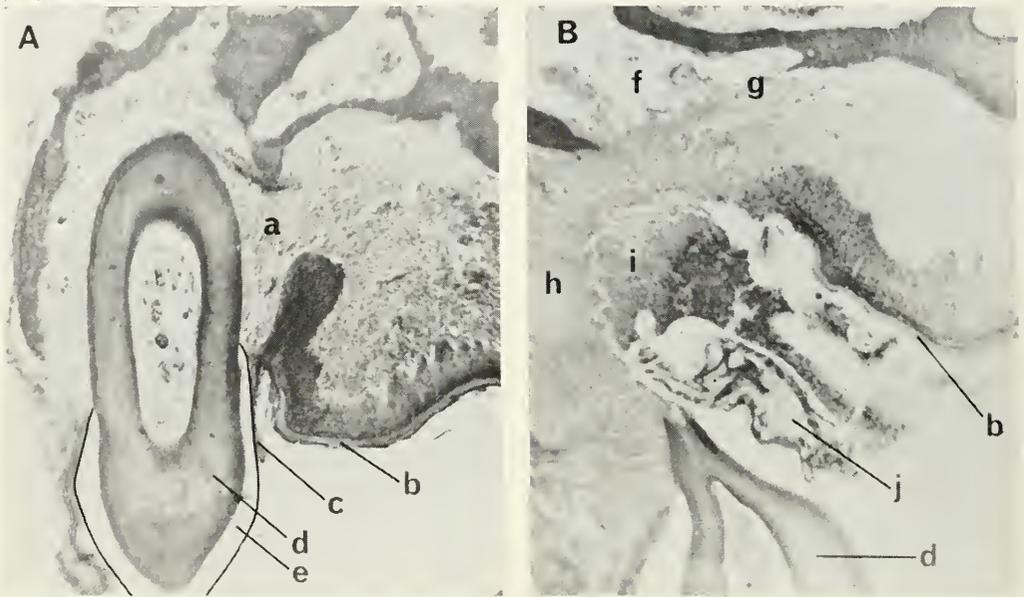


FIG. 40.—Histological views of a normal upper premolar and associated tissues (A) and of an infection resulting from an infestation of oral mites adjacent to the first upper premolar (B) in *Leptoncyteris nivalis*. Lower case letters denote: a, normal connective tissue; b, keratinous outer layer of oral epithelium; c, epithelial attachment to the enamel; d, dentin; e, enamel (decalcified in preparation and drawn in with ink); f, exposed maxillary sinus; g, area of resorbed floor of maxillary sinus; h, loose, partially destroyed connective tissue; i, necrotic tissue and inflammatory cells; j, longitudinal section through mite.

cause drainage and pain in humans (Kitchin and Edwards, 1966:344, 350); the effect on bats is unknown but presumably is not very deleterious, because mite-related periodontal infection is extremely common in some glossophagine species (nearly 100 per cent in *Leptoncyteris nivalis*). In glossophagine bats the normal maxillary sinus is filled with loose connective tissue that supports numerous venioles and arterioles. Judging from histological comparisons, at the sites of infection and resorption of the floor of the sinus, the loose connective tissue partially is destroyed and consequently many of the small vessels are lost (Fig. 40).

Palatal lesions in *Monophyllus redmani* closely resemble those found in *Leptoncyteris nivalis*. In *Anoura geoffroyi*, on the other hand, the lesions are almost always found around the cervical region of the first upper premolar, which is P2 in this species, but nowhere else.

Lesions in *Anoura* are not as extensive as those found in species of the other two genera, probably indicating that on the average, individuals of *A. geoffroyi* have less severe infestations of mites, a conclusion that is supported by examination of specimens stored in alcohol. Resorption of palatal and alveolar bone, which produces the lesions characteristic of mite-caused periodontal disease, probably results from localized circulatory disturbances. Increase in amount of blood transported to the site of periodontal infection alters the level and quality of transudate supplied to the bone, a condition that can lead to resorption (Reichborn-Kjennerud, 1963:300). In histological preparations, it can be seen that venioles at the sites of infestation appear to be dilated. A similar resorption of bone as a result of infestations of nasal mites (Halarachnidae) has been reported by Kenyon *et al.* (1965:960). In their study, destruction

of the turbinals left a nearly unobstructed void from the external nares to the posterior nasal passages in sea otters.

The effects of protonymphs of species of *Radfordiella* on connective tissue have not yet been studied in adequate detail. The following remarks are descriptive and based on basic histological examination. As in typical periodontitis, the non-mineralized connective tissue is extensively involved in mite-caused infections and periodontal ligaments that normally connect the cementum with supporting alveolar bone as well as with other teeth, are lost (Fullmer, 1966:180-181). The affected periodontal tissue lacks ligaments and has a loose, somewhat edematous, appearance. The similarity of appearance of the infected periodontal tissue with the appearance of connective tissue altered to allow passage of erupting permanent teeth is striking (see chapter on Development of Dentition). Protonymphs initially enter the gingiva at the site of the epithelial attachment to the cervix of the lingual surface of the tooth rather than through the hard keratinous layer of the oral epithelium (Figs. 38, 40). The oral epithelium thus is separated from the tooth and pushed away leaving a shallow pocket. Unlike gingivitis, in which calcified bacterial plaques are a primary etiological factor (see Levy, 1966:226-227), mite-caused infections do not result in edematous epithelium and furthermore, the epithelium apparently does not proliferate toward the apex of the root. Although hyperkeratosis is one epithelial reaction to external infestations of certain ectoparasites (Lavoipierre *et al.*, 1967:10; Lavoipierre and Rajamanickam, 1968), it has not been found in conjunction with infestations of oral mites. The pocket of periodontal infection caused by oral mites is densely packed with inflammatory cells and necrotic tissue remnants as well as excretions from the protonymphs, which may number more than 30 per site of infection (Fig. 40).

Resorption of dental tissue at infected sites is slower and less extensive than is

destruction of the alveolar and palatal bone. Dental resorption is typical of several periodontal disorders, including periodontitis and, especially, hyperplastic gingivitis (Reichborn-Kjennerud, 1963:312). In both of these pathological conditions, circulatory disturbances are thought to be responsible. Dental destruction at sites infested by oral mites is greatest at the apex of adjacent roots, but some loss of the cementum layer along the lingual surface of the roots can be seen grossly as well as histologically (Fig. 39). Centrifugal resorption of dental tissues in mite-caused periodontal disorders has essentially the same histological appearance as resorption during shedding of deciduous teeth. The similarity of both the resorption and the general destruction of the periodontal tissue gives rise to the possibility that some of the same mechanisms are involved. Release of certain enzymes could be responsible for the breakdown of non-mineralized connective tissue and this in turn might cause osteoclasts to differentiate from the loose connective tissue (see Aisenburg, 1966:320). Destruction of non-mineralized connective tissue in conjunction with resorption of roots frequently leads to loss of teeth in life. Incidence of loss of one or more upper premolars in *Leptonycteris nivalis* was 13.6 per cent (11 of 81 adults); in *Anoura geoffroyi*, in which the upper first premolar is a small, single rooted tooth, the incidence of loss of one or more teeth was higher, being 20.4 per cent (43 of 211 adults from México). On the other hand, incidence of palatal and alveolar lesions (which can be taken as indicators of incidence of infestation) is slightly lower in *Anoura geoffroyi* than in *Leptonycteris nivalis*.

The distribution and incidence of mite infestations is of as much interest as the associated pathology and, in fact, in some ways perhaps more so. The life cycle of the mites remains generally unknown because only the protonymphs as yet are available for study. This is not surprising because macronyssid pro-

tonymphs feed continuously over a period of several days without leaving their host, whereas the quick-feeding adults engage in a few minutes and generally are nidicolous (Radovsky, 1967). In the genus *Leptoncyteris* only the species *L. nivalis* is parasitized by oral mites. This species is sympatric (to the point of sharing the same caves) with *L. sanborni* and the two kinds are morphologically similar to the extent that there has been taxonomic confusion about their relationships. In a total of 111 specimens (cleaned skulls) of *L. nivalis* from Texas, and from the Mexican states of Nuevo León, Coahuila, Michoacán, Jalisco, Hidalgo, Guerrero, México, and Morelos, all adults from all places, except Texas (only four of 14 individuals), exhibited palatal and alveolar lesions. For comparative purposes, 431 specimens of *L. sanborni* from Arizona and México also were examined; none had lesions in the palate or alveolus. Also, lesions were not found in specimens of *L. curasoeae* from Margarita Island, off the northern coast of South America. In the genus *Anoura*, lesions were found in specimens of *A. geoffroyi*, of which more than 230 were examined, but not in specimens of *A. cultrata* from Panamá or in specimens of *A. caudifer* from South America. Judging from the occurrence of lesions in *A. geoffroyi*, the incidence of infestation is geographically variable in that there is a considerably lower incidence in specimens from Panamá and South America than in specimens from Guatemala and México. Unfortunately, an artifact may have been introduced into these data through misidentification, because subsequent to my analysis of available specimens, two new species of *Anoura*, one from Costa Rica (*A. werckleae*) and one from Perú (*A. brevirostrum*), were named; possibly specimens of these species were present in my samples. In *Monophyllus*, the third genus known to be parasitized by macronyssid oral mites, the protonymphs are highly host specific; the mites are found

only in *M. redmani* and not in *M. plethodon*. The occurrence of the mites corresponds exactly to the taxonomic arrangement suggested by Schwartz and Jones (1967). Although specimens of both species of *Monophyllus* are fairly uncommon in collections, the available material indicates that the occurrence of mite-caused pathology is geographically variable within the species *M. redmani*. For example, lesions were found in nearly all (15 of 16) specimens from Cuba, but in only 17.6 per cent of 17 specimens from Jamaica, and 33.3 per cent of 39 specimens from Puerto Rico.

All aspects of mite-caused periodontal disease need additional study. For example, fresh specimens of bats will enable histochemical studies of the pathological process and study of the life cycles of the parasites will be necessary for an analysis of the epidemiology of infestation. The high degree of host specificity at the specific level will remain a taxonomic curiosity until the biochemical and epidemiological factors can be studied.

DENTAL CARIES

Dental caries make up a complex disease in which many etiological factors interact to cause destruction of dental tissues. Basically, three factorial parameters—microflora, substrate (including diet), and characteristics of the host (especially its teeth)—are interrelated in the production of carious lesions (Keyes and Jordan, 1963:263). The disease has been reported from a variety of free-living mammals (for examples, see Colyer, 1936:597-629; Hall, 1940:119; 1945), but apparently is uncommon in microchiropteran bats (Phillips and Jones, 1969, 1970). For example, in 1508 specimens of bats of three families (Emballonuridae, Noctilionidae, and Chilonycteridae), only one individual, an adult male *Mormoops megalophylla*, had carious lesions (Phillips and Jones, 1969: 519). In the subfamily Phyllostomatinae, however, a species of spear-nosed bat, *Phyllostomus hastatus*, is highly prone

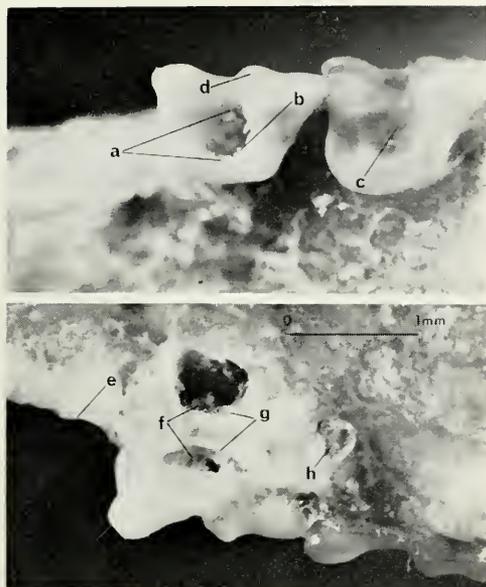


FIG. 41.—Dental caries in the first upper molar of an adult female of *Anoura geoffroyi* (KU 110105); occlusal view in upper photograph, labial view in lower one. Symbols, as follows, denote: a, area of carious lesion; b, exposed dentin; c, normal, non-carious, second molar; e, slightly resorbed area from which upper premolars were exfoliated in life; f, partially resorbed antero-labial root; g, localized lesions; h, rarefying osteitis.

to development of acute dental caries. Interestingly enough, this is the only species in the genus, indeed, in the family Phyllostomatidae, in which the disease thus far is known. Several potential endogenous factors, including topographic dental features and tiny fissures in the enamel and dentin, have been implicated in pathogenesis of the disease in this species (Phillips and Jones, 1970). Judging from specimens seen by me, dental caries is extremely rare in glossophagine bats. It must be noted, however, that recognition of carious lesions is limited to teeth remaining in place in preserved specimens; when specimens examined had lost one or more teeth in life (other than through loss resulting from mite-caused periodontal destruction) it was always possible that the coronal surface had been carious and thus the tooth had been fractured and

shed. One example of dental caries was found in an adult male *Glossophaga soricina* (KU 39503) from Sinaloa, México. In this individual, carious lesions were found in the basin of the talonid of the first lower right and left molars. In the tooth on the right side, the lesion was large and the pulp exposed, whereas in the other tooth the lesion was shallow and small. Several teeth had been lost in life and extensive attrition had greatly reduced the coronal surfaces of the remaining teeth.

Another example of dental caries, in an adult female of *Anoura geoffroyi* (KU 110105) from Grenada in the Lesser Antilles, is shown in figure 41. This individual was nearly completely edentulous, the upper and lower premolars, several molars, and canines, having been lost in life. The left upper first molar was the only carious tooth of those few remaining; a large lesion had exposed most of the lingual half of the tooth. The antero-labial root was almost completely resorbed and the surface of the maxilla adjacent to the apex of this root and the alveolar margin also had been extensively resorbed. It is possible, of course, that the teeth lost in life had been carious but there is no means of establishing this fact.

The reasons why dental caries are uncommon in most bats are unknown. As has been pointed out elsewhere (Keyes and Jordan, 1963:263; Dirks, 1965:66-67; Darling, 1965:149; Phillips and Jones, 1970) it is difficult, if not impossible, to establish that lack of caries, especially in free-living mammals, is the result of immunity. If genetic resistance is not the case, however, one would assume that etiological factors are absent.

ATTRITION AND EROSION

Teeth of many kinds of mammals are subject to partial or total destruction from causes other than periodontal diseases and dental caries. Sognaes (1963: 92-93) has tabulated the dento-alveolar aspects of hard tissue destruction and in addition to the above two pathological

conditions, has listed: 1) attrition (from mastication and general or localized trauma); 2) resorption from external causes, such as trauma; and 3) erosion-abrasion, caused by exogenous and endogenous chemical agents, mechanical factors, and idiopathic conditions.

Attrition, of course, is a normal characteristic in which the anatomical crowns of teeth are lowered with age. Abnormal or irregular attrition is not uncommon in mammals; indeed, many species seem especially prone to this condition (Colyer, 1936:630-634; Barnicoat, 1963). In a study of excessive and unusual attrition of lower incisors of sheep, it was suggested that some enzymes (proteinases) and acids in conjunction with tough foods played a significant role (Barnicoat, 1963:169). Mammalogists long have been inclined to rate degree of attrition in different specimens for use as a means of determination of relative age; a pertinent example is that of Christian's (1956) use of attrition as one means of classifying big brown bats (*Eptesicus fuscus*) according to age. He (1956:71) stated that ". . . dentin is laid down in annular rings and that . . . a wide band of dentin is deposited during summer months followed by a dense zone during the periods of hibernation . . . these rings . . . offer an exact method for aging." In glossophagines, which of course do not hibernate, additional dentin apparently is not deposited except in response to some abnormal condition such as severe attrition. It is possible that the bands of dentin seen in *Eptesicus* also are in part a response to attrition, since Christian (1956:71) himself noted that the rings conformed to age based on tooth wear. Deposition of reparative dentin in traumatized teeth is well documented (Bevelander, 1966). Furthermore, it is known now that in hibernation the process of calcification is disturbed and the number of interglobular spaces in the dentin increases, thus considerably altering its appearance (Mayer and Bernick, 1963:287-289).

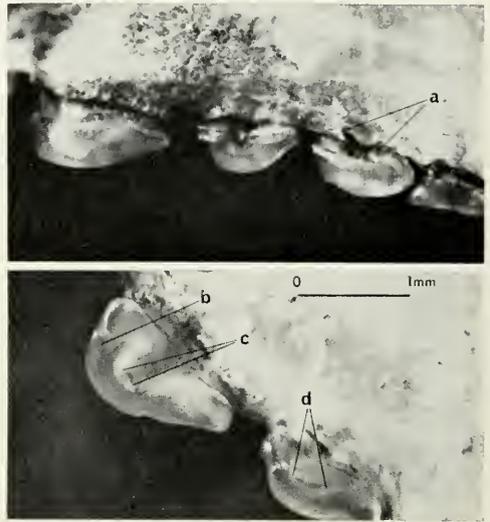


FIG. 42.—Labial and occlusal views of extreme attrition of upper teeth in an old adult male of *Glossophaga alticola* (KU 28399); a, area of slight resorption of alveolar bone; b, smooth, exposed dentin (compare with Figure 36); c and d, pulp cavities filled with compensatory dentin.

Specimens with severe abnormal attrition are rare in collections of glossophagine bats. Normally, certain teeth and tooth elements are more subject to attrition than are others; for example, in genera having relatively large upper incisors and lower canines with broad postero-lingual cingula (such as *Glossophaga*) there is a tendency for considerable attrition of the posterior-facing surface of the outer incisors. In the genus *Leptonycteris*, the metaconid of the first lower molar commonly is worn more greatly than are elements of the other teeth. In old individuals of all genera, and particularly in those lacking one or more teeth, most of the remaining teeth are greatly worn. For example, in the specimen of *Glossophaga alticola* illustrated in figure 42, an old adult male, the crowns of most of the teeth, including the canines, have been flattened due to extensive attrition. The coronal portion of the pulp cavities, which can be seen fairly well by means of transillumination, have been filled with layers of reparative

dentin, which is a typical compensatory response (Bevelander, 1966:144-145).

In an adult male of *Choeronycteris mexicana* (AMNH 188329) from Colima, the lower left third premolar (p4) had been lost in life and the anterior half (trigonid) of the lower right second molar had been eroded away. Furthermore, the lower left second molar was structurally abnormal in that it completely lacked a metaconid. Compensatory attrition in this individual had resulted in extreme wear on the upper left first molar. Extensive compensatory attrition in this species is interesting because of the little use apparently made by chewing according to the report of Walker *et al.* (1964:290). In yet another example, an adult male of *Leptonycteris sanborni* from Jalisco, the upper right first incisor, second premolar, and first and second molars had been completely lost. Lack of these teeth had resulted in extensive attrition to the upper teeth on the left side and to the lower canines and right and left first premolars. Furthermore, the talonid of the lower left second molar had been eroded away and the roots of this tooth had been almost completely resorbed so that the remaining portion of crown (trigonid) essentially was disconnected from the roots.

Localized, abnormal attrition of teeth of glossophagines in conjunction with other factors, leads to loss of teeth in life. The mechanisms of loss that can be initiated by attrition are discussed in the following paragraphs.

Several kinds of abnormal erosion of dental tissue that have been reported can be classified as due to chemical causes without concurrent abrasion, due to chemical causes in conjunction with abrasion, and due to idiopathic factors (Sognaes, 1963:99, 101). A wide variety of factors have been implicated in abrasive or chemical erosion, or both, in man; examples include acids, fruit drinks, natural juices, and general hydrogen ion concentration (Stafne and Lovestedt, 1946; Elsbury, 1952; Gortner and Kenigsberg, 1952; Halloway *et al.*, 1958). Den-

tal erosions caused by these factors appear as diffuse dissolutions, in contrast with the fairly distinctive patterns that are typical of idiopathic erosion. Lesions of atypical (idiopathic) erosion often are found on the labial or lingual cervical surfaces of teeth and have the appearance of smooth gouges. Recent studies have indicated that three events may be involved in the pathogenesis of idiopathic erosion: 1) primary or secondary absence of the protective salivary coating; 2) drainage of minerals by some agent present or introduced to the oral environment; and 3) destruction of decalcified surfaces through biochemical and biophysical influences or simple mechanical friction (Sognaes, 1963: 148).

In the generic accounts, I have pointed out the high incidence of loss of teeth in life in glossophagine bats. In addition to the two factors already discussed in this chapter (high incidence of loss at sites of periodontal destruction due to mites and generalized resorption of boney support), certain teeth, especially incisors and premolars, often are lost due to erosion in conjunction with attrition and abrasion. Another author (Herskovitz, 1949:438) has attributed loss of teeth in glossophagines (particularly in *Glossophaga*) to some kind of violence, such as voracious attacks on fruit containing hard pits. Herskovitz (*loc. cit.*) opined, probably correctly, that teeth of glossophagines are ". . . weak and frequently defective." Idiopathic erosion, as outlined above, has not been found in any specimens of glossophagines examined by me. Instead of localized lesions, the erosion of teeth in these bats is characterized by a generalized area of dissolution (Figs. 43, 44). Erosion often begins at sites of wear facets but soon spreads over the surface of the tooth into areas not subject to attrition.

In the example shown in figure 43, the left lower molar of a specimen of *Glossophaga soricina* (an adult female) is partially eroded and there is a broad area of exposed dentin connecting the

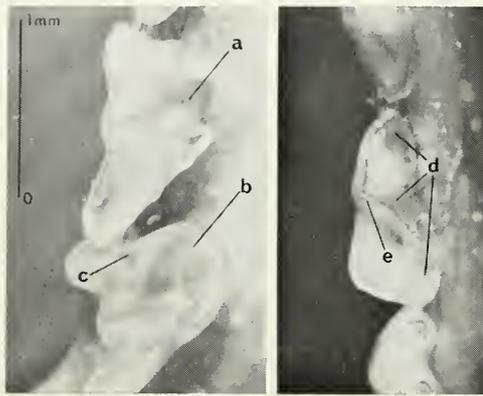


FIG. 43.—Occlusal view of upper first molar (left) and lower first molar (right) of an adult female of *Glossophaga soricina* (KU 102337) illustrating extreme erosion of lingual half of molar (a), normal molar (b), normal attrition of paracone (c), exposed dentin due to erosion of first molar (d), and enamel (e).

paraconid, protoconid, and metaconid. The exposed dentin is relatively smooth and stained pale brown. Dentin also is exposed at the entoconid, but this exposure had not yet spread beyond that typical of moderate to severe attrition. The last lower premolar, half of which can be seen anterior to the first molar, was essentially unworn and although the second and third molars had typical wear facets, generalized erosion either was lacking or was not obvious. The lower cheekteeth on the right side exhibit attrition and erosion that parallels that seen on the left side. More than half of the lingual portion of the right and left first upper molars were destroyed; the second and third upper molars are slightly worn but no evidence of erosion can be seen. When the strength of a tooth is sufficiently decreased through diffuse dissolution, the coronal portion often is fractured (probably from mastication) and the fragments shed. In the example shown in figure 44, an adult male of *Anoura geoffroyi*, the anterior three-fourths of the lower left third premolar had been lost in life. The remainder of the dental arcade of this specimen is normal and attrition of individual teeth minimal. In the partially destroyed

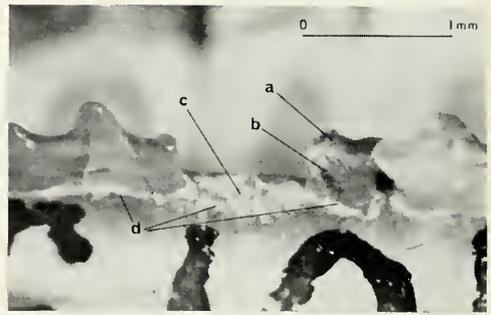


FIG. 44.—Labial view of extensive erosion of last lower premolar in an adult male of *Anoura geoffroyi* (KU 61017); a, enamel; b, exposed, rough dentin; c, site of anterior root of premolar; d, relatively normal, unresorbed alveolar bone.

tooth, a cross-section of the dentin in the posterior heel was broadly exposed; the dentinal surface is relatively smooth although some tiny, nearly microscopic pits can be seen. The anterior root of this tooth is in place, having been separated from the crown below the cervical region. The alveolar bone was not resorbed and although the surface is rough, it appears to be essentially normal.

In the genus *Leptonycteris* there is an extremely high incidence of erosion initiated at the base of the metacone of the last upper molar (M2). There is a shallow depression at this site (hypocanal basin); usually, the enamel is lost and the small area of stained dentin can be seen. Although the incidence is high, the loss of this tooth in life as a result of fracturing following extensive dissolution is not especially great (Table 14).

The incidence of tooth loss due to erosion is high in most species of glossophagine bats. Significant differences in the incidence of the disorder between sexes, species, and genera, have been noted in the generic accounts. Usually, erosion is localized in one or two teeth; often occluding teeth are destroyed. Complete loss of individual teeth does not necessarily result in compensatory attrition; for example, in the specimen of *Anoura geoffroyi* illustrated in figure 44, a lower premolar has been nearly de-

stroyed by erosion and the remainder of the tooth probably was nonfunctional, but the remaining teeth were completely normal. Detailed analysis of the pathogenesis of erosion of glossophagine teeth will be the subject of a later study but some mechanisms that undoubtedly are involved should be considered here. The initiation of lesions could result from the following factors: 1) a localized loss of protective organic coating of saliva; 2) normal attrition exposing abnormally soft (incompletely calcified) dentin; 3) abnormally rapid attrition due to soft dentin. The last factor deserves future consideration primarily because of the work of Adamczewska-Andrzejewska (1966: 55), who found that in a shrew (*Sorex araneus*) the "hardness of the dentine varies in series from different years . . . [and has] . . . a significant effect on the rate of wear of the teeth." This author

further stated (*op. cit.*:66) that ". . . differences in wear of the teeth may be due to variations in hardness of the dentine itself, without the participation of the enamel." This particular mechanism could explain the exposure of dentin through abnormally rapid attrition of individual teeth in specimens of glossophagines. A variety of factors could account for the diffuse dissolution of dental tissue that follows exposure. Abrasion by the tongue or lips or food particles in conjunction with the chemical action of acids from soft tropical fruits, which constitute a large proportion of the diet of glossophagines, probably are important factors in overall destruction of the crown (see Stafne and Lovstedt, 1947; Holloway *et al.*, 1958). The crown thus weakened could easily fracture and be lost, leaving only the roots of the tooth in place.

RELATIONSHIPS AMONG GLOSSOPHAGINE BATS

The 13 nominal genera of glossophagine bats can be divided into two basic groups that suggest either a polyphyletic origin of what has been considered a single subfamily of phyllostomatid bats or, at least, that a single ancestral kind gave rise to the two branches early in the evolutionary history of these bats. Evidence for the basic dichotomy comes mainly from four sources: 1) analysis of karyotypes and karyotypic variation; 2) analysis of immunological reactions of blood sera; 3) noteworthy morphological differences in the basicranial region of the skull; and 4) differences in the characteristics of the upper deciduous incisors.

Baker (1967:426) studied chromosomes of representatives of *Glossophaga*, *Leptonycteris*, *Anoura*, *Choeronycteris*, and *Choeroniscus*, and concluded that the diversity of karyotypes indicated that the subfamily was "an artificial grouping of species evolving to a nectar-feeding way of life from two or more independent lines." *Leptonycteris* and *Glossophaga* were shown to have identical karyo-

types that strongly resembled those of three phyllostomatine genera (*Phyllostomus*, *Trachops*, and *Macrotus*), whereas *Choeronycteris* and *Choeroniscus*, which have different diploid numbers (16 and 19, respectively), were allied by Baker (*op. cit.*:420-422) with *Carollia*. The genus *Anoura* was not placed in either grouping, however, because in fundamental number and in X and Y elements it was found to resemble *Glossophaga* and *Leptonycteris*, whereas in morphology of some individual chromosomes it resembled *Choeronycteris* and *Choeroniscus* (*op. cit.*:423). In contrast to these cytological data, Gerber (1968) reported, on the basis of immunologic and electrophoretic comparisons, that *Choeronycteris* is more closely related to *Phyllostomus* than to *Anoura*, *Leptonycteris*, and *Glossophaga*. The latter three genera were thought to be most closely related to *Carollia*, *Artibeus*, and *Sturnira*. The only apparent area of agreement between the serological and cytological analyses, therefore, is that the subfamily Glossophaginae in-

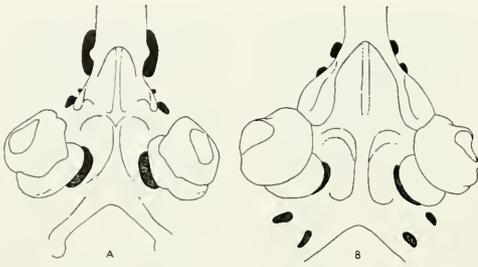


FIG. 45.—Comparison of the basiscranial region of *Glossophaga soricina* (A) and *Choeronycteris mexicana* (B). These two species are representative of the two groups discussed in text.

cludes two basically different kinds of bats, one exemplified by *Choeronycteris* and the other by *Glossophaga*.

The basic basiscranial differences that support the division of the glossophagines into two groups are illustrated in figure 45. In *Choeronycteris*, *Choeroniscus*, and *Musonycteris*, the pterygoid wings are greatly modified structures that curl inward toward the longitudinal axis of the cranium. The pterygoids in all three genera are expanded at the base so that they have an inflated appearance and, in some species at least, are in contact with the mandibular fossa and auditory bulla. The pterygoids differ within the other group of genera (*Glossophaga*, *Monophyllus*, *Leptonycteris*, *Anoura*, *Lonchophylla*, *Lionycteris*, *Lichonycteris*, *Hylonycteris*, *Scleronycteris*, *Platylina*) but are similar to the extent that all these genera can be distinguished easily from the *Choeronycteris* group. In the *Glossophaga* group, the pterygoids are relatively unmodified and resemble those of most other phyllostomatids. The pterygoids generally are nearly vertical or tilted slightly in a lateral direction, and are not inflated or expanded at the base (Fig. 45). In ventral aspect the pterygoid wings do not curl toward the longitudinal axis of the skull, but instead are either not turned at all or are turned outward (laterally). Handley (1966a:85) examined several genera of glossophagines and characterized the pterygoids as "normal" (*Lichonycteris*

or "slightly specialized" (*Hylonycteris*), as compared with "specialized" (*Choeronycteris*), and "greatly specialized" (*Choeroniscus*).

The deciduous dentitions of bats have not been used, heretofore, for determining taxonomic relationships even though several persons have pointed out their potential as conservative characters (Leche, 1875, 1877, 1878; Friant, 1963). Unfortunately, to date only three genera of glossophagines (*Glossophaga*, *Leptonycteris*, and *Choeronycteris*) have been available for study and comparison. Interestingly enough, however, these three show a basic difference that deserves consideration here. In *Choeronycteris* the inner upper deciduous incisors are small, recurved teeth that taper to a fine point, whereas in *Glossophaga* and *Leptonycteris* these teeth are forked (Figs. 4-6). When compared to the other phyllostomatids in which the deciduous dentitions have been described, *Choeronycteris* resembles *Phyllostomus*, *Mimon*, *Tonatia*, *Chrotopterus*, and *Carollia*, whereas *Glossophaga* and *Leptonycteris* resemble *Macrotus*, *Artibeus*, and *Ametrida*. Perhaps it is not surprising that the phyllostomatine genera listed here also fall into two groups because Walton (1967:55) recently pointed out differences between *Phyllostomus* and *Macrotus* on the basis of features of the post-cranial skeleton. With the exception of recognition of a basic dichotomy in the glossophagines, none of the currently available data can be utilized in formulation of a reasonable explanation of the relationships among the above-listed phyllostomatid bats because the cytological, serological, and dental comparisons provide contradictory results. Thus, the only pertinent systematic conclusion, upheld by all available evidence, is that the subfamily Glossophaginae is comprised of two groups of genera—the *Choeronycteris* group and the *Glossophaga* group.

Baker (1967:426) stated that if relationships suggested by his cytological studies were valid, "then the subfamily

Glossophaginae as now recognized [would be] an unnatural assemblage and . . . not valid." Although his data clearly support the basic dichotomy in the subfamily, which is shown by other characters as well, there is no reason, in my opinion, to consider the subfamily "invalid." Although one might logically separate the Glossophaginae into two tribes, establishment of a new subfamily, at a time when there is so much conflicting evidence regarding relationships within the entire family, would confuse the issues. Tribal names would perhaps be useful, but in the absence of an understanding of the evolution of the Phyllostomatidae they would constitute nothing more than a "stop-gap" measure because eventual establishment of a new subfamily might indeed be the best way to elucidate the relationships. Furthermore, results of current studies of comparative anatomy and histology of tongues and morphometric analysis of cranial features of glossophagine bats and other phyllostomatids are not yet available, but could add to the difficulty by suggesting relationships not discussed here (J. R. Winkleman, personal communication, 1969). I have decided, for the purposes of this report, to consider the Glossophaginae as comprising simply two groups of genera that have several basic differences.

EVOLUTIONARY MECHANISMS AND DENTAL INTERACTION

Before outlining the possible pathways and trends in the evolution of the dentitions of glossophagine bats, it is necessary to consider first the evolutionary mechanisms that operate in the selection of particular dental configurations.

Loss of certain permanent teeth is one characteristic shared by all of the glossophagines. Several mechanisms potentially are involved in such a loss and although some mammalian taxonomists seem to believe that teeth simply "become smaller and eventually disappear," the actual factors may be more interest-

ing and certainly more complex. The pattern of "loss" of permanent teeth can in some instances be deciphered (in the absence of a fossil record) by the presence of unreplaced deciduous teeth. Few workers have emphasized the fact that species of several chiropteran genera have unreplaced deciduous teeth; some workers have overlooked this fact altogether. Inconsistencies between the number of deciduous teeth and the number of permanent teeth are not restricted to the Chiroptera; Berkovitz (1968:448) recently discussed the phylogenetic implications of four upper deciduous incisors in ferrets (*Mustela putorius*), which have only three permanent incisors. In one glossophagine, *Choeronycteris mexicana*, which usually retains some of its four lower deciduous incisors in adulthood, histological studies have revealed that permanent incisors form but do not erupt. Thus, in this species at least, the permanent lower incisors have not really been "lost." The mechanism involved in this instance is unknown; it could be a matter of a single mutation that causes local biochemical alteration and destruction of partially developed permanent teeth at a time when they are in an advanced stage of morphogenesis. In this regard, it is of interest that Grewal (1962) found that teeth are in fact initiated and begin to develop normally until approximately the sixth day post-partum, when they begin to regress in certain strains of laboratory mice (*Mus musculus*) in which the third molars are congenitally lacking.

Further consideration of the mechanism(s) that causes permanent teeth to fail to develop fully and erupt, even though their morphogenesis is normally initiated, raises the question of whether or not several permanent teeth in the glossophagines, especially the P2, have been lost completely in the sense that morphogenesis is not initiated. The high incidence of what I consider to be atavistic P2's indicates that in populations of species of many genera, the potential

for development of these teeth still is present. Krutzsch (1953:265) doubted that "supernumerary" teeth in rodents had any phylogenetic significance, as had been suggested by Johnson (1952:70). Sheppe (1964:35), who studied supernumerary teeth in *Peromyscus*, stated that "the atavistic theory seems unlikely on genetic grounds." Sheppe (*loc. cit.*) based his argument on the fact that in mammals "there may be an excess number of any kind of tooth, including canines [and that] since there was never more than one canine a second one could not represent one that had been lost." This argument, of course, cannot be refuted. Even so, at least in the glossophagine bats, supernumerary teeth resulting from double initiation or from some abnormality during differentiation generally can be recognized because 1) they are morphological duplicates of another tooth, or 2) they actually are a part of another tooth (Figs. 20 and 25). The theory that the small, single-rooted, permanent teeth formed between the P3 and canine in many species of glossophagine bats most likely represent the permanent P2's, and thus are atavistic teeth, also is supported by the fact that in the three genera in which the deciduous teeth have been studied (*Glossophaga*, *Leptonycteris*, and *Choronycteris*), there is a deciduous upper P2. Additional evidence was presented in the generic account of *Glossophaga*; atavistic P2's were studied histologically in a specimen that had been preserved in alcohol.

Sheppe (1964:35) has stated that "in the evolutionary history of a tooth there is a time when it occurs in almost all individuals. If for some reason the genes necessary for its development begin to be lost by the population the tooth will appear less and less frequently and eventually it will be quite rare. . . . Eventually all genetic basis for the tooth will be lost and the tooth will disappear from the population. If a tooth later appears in the same place it will be because of either a new mutation or some develop-

mental accident without genetic basis." Kurtén (1963:11) has discussed the loss and "return" of the m2 in the evolution of certain felids; he pointed out that the return of a tooth could have been the product of activation of the field of molarization, which presupposed that the genotype for m2 had never been lost although the tooth had been lacking. A route to "loss" of certain permanent teeth is suggested by the pattern seen in the glossophagines. A mutation that causes regression of a developing permanent tooth through some local biochemical alteration could account for its apparent absence in a given species, and reversal of the same mutation could allow for its occasional appearance. The occurrence of P2's in the species of glossophagines thought to lack them is extremely low, judging from the incidence in the 2400 specimens examined by me. If selection favors adjustments in the alveolar bone it is altogether possible that a permanent tooth could be lacking in all individuals of a species even though, in theory at least, its genetic basis is retained. Discussion of the evolutionary mechanisms involved in loss of teeth and of the existence of atavistic teeth is limited by semantics because it could be fairly said that the permanent P2 has not really been "lost" in a given species of glossophagine if it is found rarely in a population.

Gould and Garwood (1969:276) recently have succinctly pointed out and discussed the demise of the "simplistic myth" that tied genes to characters by direct and complete causation. As a consequence, analysis of dental patterns in terms of morphological integration can be especially useful in devising concepts of how dentitions have evolved (Olson and Miller, 1958; Kurtén, 1963). Another evolutionary concept that recently has come under reconsideration (and which is especially pertinent to any discussion of mechanisms in the evolution of teeth) is the previously held theory that populational response to directional selection results in a decrease in genetic and

phenotypic variation. Guthrie (1965), in a study of variation in the molars of living and extinct species of *Microtus*, and Bader and Lehmann (1965), in a study of phenotypic variation in the width of molars in *Mus musculus*, obtained data that indicate that the magnitude of genetic variability may be reflected in the level of phenotypic variability and that phenotypic variation increases when characters are undergoing rapid evolution.

The patterns of morphological and dimensional variation in the molars of *Glossophaga soricina*, *Leptonycteris sanborni*, *Anoura geoffroyi*, and *Choeronycteris mexicana* were reviewed in the generic accounts. The last molar in the first three genera, although morphologically reduced, was no more variable than the first two and, in fact, overall was slightly less variable. The most striking pattern seen in the variation in the upper molars in the first three species is in the relatively great amount of variation centered around the paracone and parastyle, particularly in the M1 (Figs. 11, 16, and 23). In *Anoura*, *Glossophaga*, and *Leptonycteris*, the first upper molar is large and certainly in no way vestigial, but its anterior element is highly variable. The pattern of high coefficients of variation for the paracone-parastyle length in M1 and M2 in three different genera in which the molars have a W-shaped ectoloph is noteworthy for two interrelated reasons: 1) the remarkable uniformity of the pattern of variation in these distinct genera; and 2) the fact that in several other genera of glossophagines the paracone has been lost, or has become part of the high antero-labial margin that I consider to be the parastyle. The strongest evidence for this trend is found in specimens of *Lichonycteris obscura* in which all conditions can be found; some specimens have a paracone and others either have a small paracone that is located near the labial margin or completely lack a paracone (Fig. 28). Although evidence that selective pressures are operating on

the anterior element of the upper molars in these genera is only circumstantial, these data are most interesting when considered in terms of Guthrie's (1965) conclusion that variation increases in evolving characters. In the glossophagines, selection probably is for reduction in complexity of coronal morphology, whereas in Guthrie's study (*loc. cit.*) selection was for increase in complexity.

In the *Glossophaga* group, the lower molars morphologically are more uniform than are the upper molars, although the lower teeth are different enough to be useful in identification of the genera (and sometimes species). It is noteworthy, therefore, that in terms of dimensional variation, the lower molars of *Glossophaga soricina*, *Leptonycteris sanborni*, and *Anoura geoffroyi*, are considerably less variable, overall, than are the upper molars (Figs. 12, 17, and 23). The sites and degree of dimensional variation in the teeth of species of these genera, and of *Choeronycteris mexicana* as well, are not related clearly to either time of development and eruption or to degree of reduction. Thus, in *Glossophaga*, for example, the third upper molar is morphologically reduced and develops and erupts well after the first molar (Fig. 10) but is not significantly more variable.

The size and shape of different teeth in a molar series are not independent, and in the evolution of a particular dentition all individual teeth comprise a more or less integrated system. Olson and Miller (1958) apparently were the first to demonstrate high correlation between functionally related morphological features. Correlations between measurements of certain features are the direct result of an ontogenetic relationship (see Van Valen, 1965:349) and, because the crowns of teeth do not continue to grow subsequent to completion of development prior to eruption, studies of correlation between coronal features of different teeth are especially interesting in terms of morphogenetic integration (see Van Valen, 1962, and Gould and

Garwood, 1969). The production of matrices of coefficients of correlation for measurements of upper and lower molars in *Glossophaga*, *Leptonycteris*, *Anoura*, and *Choeronycteris* (see generic accounts) was the simplest approach to the problem of dental interaction. For the purposes of this report, individual correlations were used in the detection and analysis of patterns. Admittedly, as has been pointed out by Wallace and Bader (1967) and Gould and Garwood (1969), a multivariate factor analysis probably would have yielded a better elucidation of morphogenetic fields. Such an analysis will be presented in a later paper.

Analysis of dental interactions is facilitated by knowledge of the sequence of odontogenesis and eruption of permanent teeth. Consequently, data for *Glossophaga*, *Leptonycteris*, and *Choeronycteris*, are more easily interpreted than are those for *Anoura*. In the model suggested for dental integration in *Glossophaga soricina*, time of odontogenesis was thought to play a crucial role in the interactions. Weak negative coefficients of correlation indicated that the size of the trigonid of m3 was limited by the length of the talonid of m2. This interaction, if real, would probably be a result of spatial limitation. This is especially logical when one considers the sequence of development in *Glossophaga* (Fig. 10), because the m1 and m2 develop and erupt together, well ahead of the third molar. Relative time of dentinogenesis, spatial limitations imposed by bone, and presence of other teeth have been shown to influence greatly the size of the last upper and lower molars in *Mus musculus* (Gaunt, 1964).

Width rather than length of molar teeth has been the most important dimension in many species in which dental interactions have been studied. For example, Wallace (1968:375) found that in *Mus musculus* the most powerful field operative in the system of dental integration (intra-jaw) acted principally on width. Similarly, Van Valen (1962:272)

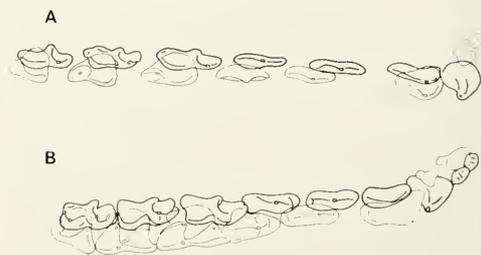


FIG. 46.—Diagram showing extremes in pattern of occlusion in the Glossophaginae: A, *Choeronycteris mexicana*; B, *Lonchophylla robusta*.

found that control of tooth width in *Peromyscus* seemed more important than control of length. Sych (1966) found essentially the same pattern in two genera of leporids (*Lepus* and *Oryctolagus*).

In the glossophagines, overall width of the upper molars *per se* was a dimension used only in *Choeronycteris mexicana*. In the lower molars of all four genera, however, a width measurement (across the metaconid and protoconid) was taken as well as were three slightly different measurements of length—length of the talonid, paraconid-metaconid length, and paraconid-protoconid length. Among the lower molars of *Anoura*, six of 21 significant ($P \leq .05$) coefficients of correlation (28.6%) involved the width (Table 2); in *Glossophaga*, six of 11 (54.5%) involved the width dimension (Table 6); in *Leptonycteris*, two of nine (22.2%) involved the width (Table 12); and in *Choeronycteris*, three of five (60.0%) involved the measurement of width (Table 16). In these bats, therefore, width of lower molars is not under a stricter system of control than is length. In this regard it is instructive to compare the occlusal patterns of glossophagines with those of rodents. In *Peromyscus*, crowns of the upper and lower molars occlude directly, whereas in a glossophagine bat the entire crown of individual upper molars does not occlude directly with the entire crown of an individual lower molar (see Fig. 46); furthermore, the molars are offset laterally as well as antero-posteriorly.

TABLE 20.—Per cent significant ($P \leq .05$) individual coefficients of correlation for all measurements of molars in four genera of glossophagine bats. See generic accounts for correlation matrices.

Genera	Upper molars	Lower molars	Upper and lower molars
<i>Anoura</i>	19.2 (23/120)	31.8 (21/66)	13.5 (26/192)
<i>Glossophaga</i>	20.0 (24/130)	16.7 (11/66)	10.4 (20/192)
<i>Leptonycteris</i>	22.2 (10/45)	32.1 (9/28)	22.5 (18/80)
<i>Choeronycteris</i>	28.7 (19/66)	7.6 (5/66)	2.1 (3/144)

Kurtén (1953) and Sych (1966) have shown that the patterns of dental integration can be different in species having teeth that are morphologically similar. Percentage of significant ($P \leq .05$) coefficients of correlation for all combinations of measurements of coronal features of molars of four genera of glossophagines are given in table 20. If percentage of significant correlations can be taken as one indication of degree of dental interaction, it can be clearly seen that, although the patterns are different for each of the species, there are definite trends in integration. Unfortunately, the sequence of odontogenesis and eruption is unknown for *Anoura geoffroyi* and it is difficult to appraise fully the level of integration in terms of its relationship to development. In this species, the level of intra-mandibular integration apparently is greater than is the level of intra-maxillary integration. The three upper and three lower molars in *Anoura geoffroyi* all are relatively large, robust teeth that are in linear contact and there is no obvious disparity between the upper and lower molars in amount of overall dimensional variability (Figs. 11 and 12). The percentage of significant ($P \leq .05$) inter-jaw coefficients of correlation (out of a total of 192 combinations) is only 13.5 (Table 20). The strongest relationship in the system of inter-jaw integration is between M1 and the lower molars because 8.9 per cent (17 of 192) of the combinations involve the M1. It is of special interest that there are no significant negative inter-jaw correlations. In the absence of data on odontogenesis in *A. geoffroyi*, it only can be assumed that the first upper and lower

molars develop first and set the stage for the remaining molars.

In *Glossophaga soricina* the pattern of morphogenetic integration differs strongly from that of *Anoura geoffroyi*, even though both species have three upper and lower molars that morphologically are relatively unreduced. The level of integration among the dimensions of the lower molars in *G. soricina* (16.7% of the coefficients were significant) is less than the level among the upper molars (20% of the coefficients were significant). The lower molars overall are slightly less variable than the upper molars in this species (Figs. 16, 17). The sequence of morphogenesis of the lower molars is different from that of the upper molars; m1 and m2 develop and erupt as a unit well in advance of the m3, whereas among the upper molars the development and eruption of the individual teeth is spaced equally (Fig. 10). In the model developed to show the pattern of morphogenetic integration in the lower molars, overall size of the m1 is strongly correlated with size of the m3. Length of the talonid of m2 was thought to have negative interaction with length of the trigonid of m3 as a result of spatial restriction imposed on the m3 before onset of dentinogenesis. In evolutionary terms, it is possible that selection for increase in size of certain teeth has indirectly caused the loss of smaller adjacent teeth (Kurtén, 1967: 819). With this in mind, the importance of negative interaction becomes clear. The level of inter-jaw integration is relatively low in *G. soricina* (10.4% of 192 coefficients were significant), and involves a total of six significant negative

interactions. The size of the m3 (dimensions of length and width) is most subject to negative integration, particularly with the third upper molar (see matrix in table 7). These two teeth develop and attain the functional eruptive stage coincidentally. Negative interaction among molars has been found in other mammals; Van Valen (1962:274) termed it "intraembryonic compensation," and Garn *et al.* (1966:55) referred to it as "reciprocal variation in odontogenesis." It is unclear whether or not the negative interaction between upper and lower third molars in *Glossophaga soricina* is the result of a direct relationship or their relationships with the other molars in their respective jaws.

Morphogenetic integration is strongest in *Leptonycteris sanborni*, a species in which the third upper and lower molars are lacking and the M2 is morphologically reduced (Table 20). The level of integration is 32.1 per cent among the lower molars as compared with 22.2 per cent for the upper molars. Overall, the lower molars are considerably less variable than the upper molars (Fig. 22), and neither of them is reduced. Not surprisingly, the level of integration of the upper and lower molars is higher (28.5%) in *Leptonycteris* than in any of the other three genera studied (Table 20) and, in comparison with *Glossophaga*, there were no significant negative interactions in the inter-jaw comparisons.

The dental characteristics of *Choeronycteris mexicana* differ greatly from those of *Anoura*, *Glossophaga*, and *Leptonycteris*. The molar teeth in the former species are morphologically reduced and are widely spaced so that occlusion is minimal (Fig. 46). The level of morphogenetic integration is relatively high among the upper molars (28.7% incidence of significant coefficients of correlation), which is interesting in view of their characteristics and overall high variability (Fig. 29). The three lower molars, which develop and attain the functional eruptive phase at almost equal intervals (Fig. 10), are essentially inde-

pendent units because the level of integration is extremely low (7.6%). Consequently, the inter-jaw integration is almost lacking; only 2.1 per cent of 144 combinations in the correlation matrix were significant ($P \leq .05$). A high level of morphogenetic integration of upper and lower teeth probably would not be necessary in a species having minimal occlusion. Gould and Garwood (1969:294), in their discussion of independence of lengths of the M3 and m3 in *Peromyscus*, *Oryzomys*, and *Nesophontes*, point out the "intriguing phylogenetic implication" that dimensional independence of a tooth could permit independent evolution. These authors suggested that this may have been the case in the striking ontogenetic enlargement of the M3 in capybaras (*Hydrochoerus*) and wart-hogs (*Phacochoerus*). In the case of *Choeronycteris* one wonders whether or not relative independence between upper and lower molars allowed the uniform reduction of the ectoloph and loss of the paracone in the upper molars. Although this may have been the case, the lower molars, which essentially are independent morphogenetic units, are not appreciably altered from the basic morphological configuration found in others of the Glossophaginae.

In the four species of glossophagine bats just discussed, no mention was made of teeth other than molars. This should not be construed as evidence that only the molar teeth are involved in morphogenetic fields. Relationships between molars and anterior teeth, such as premolars, in glossophagines is an area that should be analyzed in the future. Butler (1939) thought that molarization of posterior premolars might have been the result of influence of the molars.

The controlling forces in morphogenetic fields are in part unknown; several authors have attributed correlations to a single factor such as common function or enzymatic or hormonal organizers (Schour, 1934; White, 1959; Van Valen,

1966b). Some dimensional relationships among molars in various species of glossophagine bats clearly are the product of mechanical interaction. This especially is true in the case of molars that undergo dentinogenesis well after the preceding tooth in a spatially limited environment. Genetic-based integration seems most likely when the first upper and lower molars are highly integrated. If these teeth "set the stage," as it were, they in turn could influence the dimensional characteristics of the other molars within their respective jaws. The relatively great negative interaction between the upper and lower third molars in *Glossophaga soricina* is of special interest, however, because of their lack of physical contact and because of their respective relationships with adjacent teeth. Van Valen (1966b:428, 430) has discussed an instance in *Rattus* in which growth rates of teeth in different jaws possibly were regulated by some vascular or neural factor. This matter remains open to additional research.

ORAL DISEASE AND ABNORMALITIES

The relationships of oral diseases and congenital dental abnormalities to the evolution of mammals are unknown and for the most part as yet unstudied. One example of a specifically restricted acute dental disease in phyllostomatid bats has been discussed elsewhere (Phillips and Jones, 1970). In the glossophagines, loss of teeth in life, probably in large measure as the result of erosion, is common. Basically, the high incidence of destruction and loss of teeth must be taken as an indication of their lack of importance to survival of the individual because some structural factors as well as dietary factors probably are involved. Incidences of loss of teeth in life as well as the kind of teeth lost have been shown to differ significantly between species and between sexes within species. The frequent loss of upper and lower incisors, in those species that have both, fits well with the overall tendency in many gen-

era toward reduction of the dentition. In *Leptonycteris sanborni* and *nivalis*, where incidence of loss of lower incisors differs significantly ($P \leq .05$) between the species, not all of the factors are known but certainly include 1) the possibly defective nature of the dental tissues in the lower incisors of *sanborni*, 2) the apparently continuous remodeling of the alveolar bone in conjunction with development of muscle attachments in *sanborni*, and 3) the diminutive size of the teeth themselves.

The cause of significant sexual differences in the incidence of loss of teeth in life found in *Anoura*, *Glossophaga*, and *Monophyllus* is not apparent, but if the differences are real and not simply artifacts of sampling technique, one would suppose that some endocrine factors are involved.

Dental agenesis, hyperdontia, and incomplete duplication are relatively common in *Glossophaga soricina* and *Leptonycteris sanborni*, but are as yet unknown in *Anoura geoffroyi*, even though a fairly large sample of the latter was examined. Dental agenesis is the most difficult of the above-listed abnormalities to study and analyze, because determination of the incidence is largely subjective when one deals with specimens of small mammals that have tiny teeth and that frequently were taken under difficult collecting conditions and later cleaned of flesh in a museum laboratory. Nevertheless, some instances of this anomaly are obvious enough to warrant consideration. Overall, upper and lower incisors most frequently are lacking due to apparent agenesis. This is not surprising considering their small size and lack of functional importance. In *Glossophaga soricina*, the upper and lower third molars occasionally are lacking (Table 8). Examination of specimens having partial anodontia as a result of agenesis did not reveal any concurrent abnormalities (such as small or weak teeth) in the dental arcade. When the last molars are congenitally absent in man, by way of contrast, the remaining

molars tend to be both smaller and to develop later (Garn *et al.*, 1963). Congenitally missing teeth, especially the small upper premolars in many vesper-tillionids, have drawn some attention from previous authors (Mumford, 1963, and Frum, 1946, for example), which is not surprising considering the frequent use of teeth in taxonomy. In the glossophagine bats the pattern of anodontia is not useful in taxonomy and not likely to cause any difficulties in identification.

The occurrence of supernumerary and partially duplicated teeth was found to be highest in *Glossophaga soricina* and *Leptonycteris sanborni*. In *G. soricina* the incidence of duplication of lower incisors was significantly greater ($P \leq .01$) in males than in females thus indicating the possibility of sex-linkage. Unilateral and bilateral duplication of lower incisors in *Mus musculus* has been shown to be a recessive trait of an as yet unknown linkage (Danforth, 1958). Supernumerary first upper premolars (P3) have been found in *G. soricina* and *L. sanborni*, but not in any of the more than 360 specimens of *Anoura geoffroyi* examined. In *Anoura* the P2 is present, although relatively small and peg-like, whereas in the other two genera this tooth is lacking and, furthermore, the two remaining premolars (P3 and P4) are uncrowded. It is noteworthy that specimens having supernumerary teeth were found to have otherwise normal dental arcades, thus indicating that the mutation(s) that caused the double initiation or partial dichotomy in the differentiation stage apparently was not especially deleterious.

RELATIONSHIPS AMONG THE GLOSSOPHAGINAE

Similarities and dissimilarities in the dentitions of glossophagine bats were discussed and summarized in the final section of the generic accounts.

The subfamily Glossophaginae comprises 13 nominal genera belonging to two basic groups that I have referred to as the *Glossophaga* group and the *Choe-*

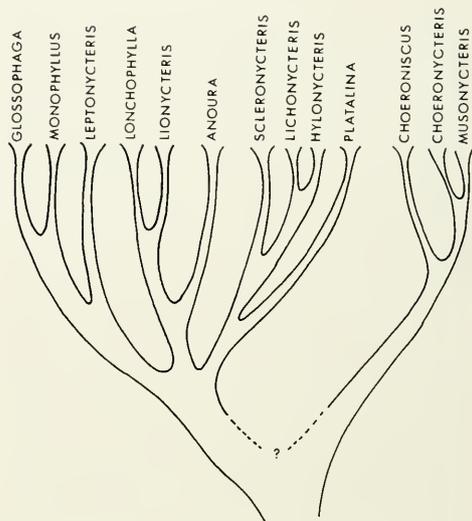


FIG. 47.—Relationships among the nominal genera of Glossophaginae based on an analysis of dentition as well as cytological, serological, and basicranial characteristics.

ronycteris group. The general relationships in the subfamily, insofar as they can be determined in the absence of a fossil record, are illustrated in figure 47. The subgroups of genera within the *Glossophaga* group can be distinguished on the basis of their molar teeth. The ancestral condition that gave rise to the *Glossophaga* group of genera is unknown but a prototype would probably have had the following characteristics: muzzle not elongate; P2 present; upper molars large and high-crowned teeth having a W-shaped ectoloph, prominent cones and commissures, and possibly a hypocone; mesostyle probably formed as part of the posterior element; third upper molars unreduced in size or complexity; four large and well-rooted lower incisors; four upper incisors, of which the inner pair differed from the outer pair.

Three types of molar configuration have evolved in the *Glossophaga* groups. In *Anoura*, *Lonchophylla*, and *Lionycteris*, the upper molars are relatively primitive (Fig. 48); the mesostyle is a large, prominent cusp on the posterior element of the W-shaped ectoloph. The paracone is large although variable in

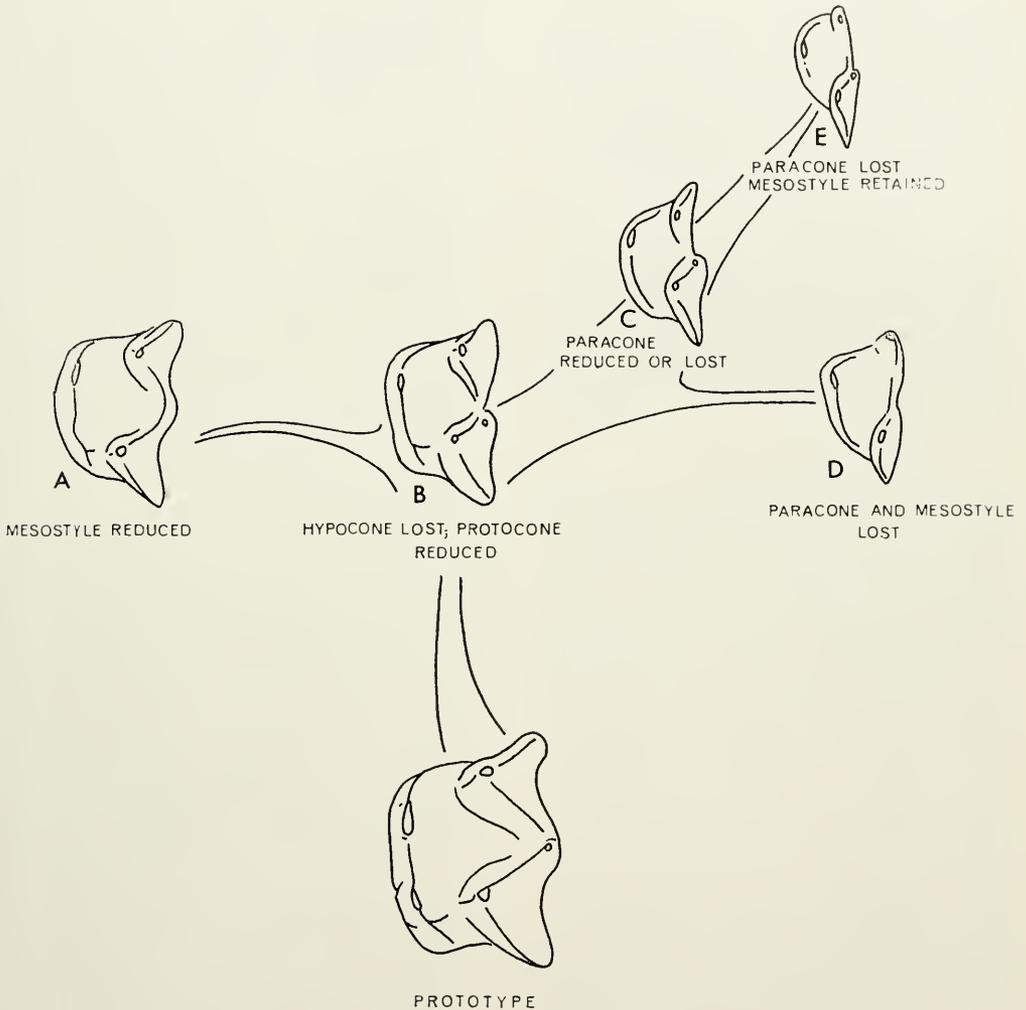


FIG. 48.— Diagrammatic representation of possible evolutionary relationships among the *Glossophaga* group of genera, based on the coronal configuration of the upper molars. A, *Glossophaga*, *Leptonycteris*, *Monophyllus*; B, *Anoura*, *Lonchophylla*, *Lionycteris*; C, *Lichonycteris*, *Scleronycteris*; D, *Hylonycteris*; E, *Platalina*.

position. Development of a moderately high ridge along the labial margin is a modification seen in the upper molars of all three genera. The canine and post-canine dentition in *Anoura* is primitive but the upper incisors are highly specialized, the inner pair having been reduced greatly in size and separated by a median gap (Fig. 49). Permanent lower incisors are lacking. The genus is polytypic and has as great a geographic range as any of the other glossophagines. *Lonchophylla*, which primarily is South

and Central American in distribution, is the least specialized of the three genera in that, although the permanent P2 is lacking, all of the teeth are primitive. Indeed, the lower incisors are large and have trifold crowns. *Lionycteris*, which insofar as known is monotypic and restricted to South America, is a highly specialized relative of *Lonchophylla* in which the incisors and premolars have become greatly enlarged in height.

Adaptive radiation has not been spectacular in the subgroup comprised of

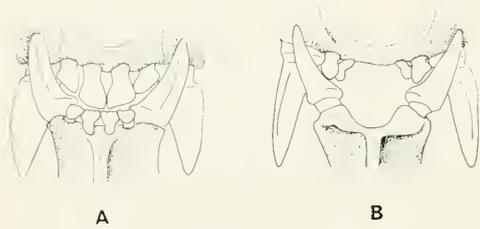


FIG. 49.—Extremes in arrangement of the upper and lower incisors in the Glossophaginae: A, *Lonchophylla robusta* with large upper inner incisors and large, trifid lower incisors; B, *Anoura geoffroyi* with greatly reduced upper inner incisors and no permanent lower incisors, leaving a nearly round opening for passage of the long tongue.

Glossophaga, *Monophyllus*, and *Leptonycteris*. In all three genera the P2 is lacking, the muzzle is only slightly elongate, and the upper molars have been reduced in two main ways: 1) the crowns are lower than in the more primitive molars; and 2) the mesostyle is reduced and is formed at the site where the precentrocrista and postcentrocrista meet. In terms of evolution toward a fruit- and nectar-feeding mode of life, *Leptonycteris* is most advanced. The third upper and lower molars have been lost and the M2 reduced and the lower incisors are small. With regard to loss of the M3 and m3 in *Leptonycteris*, it is interesting to note that there is a notable incidence of agenesis of these teeth in *Glossophaga soricina* (Table 8). *Glossophaga* and *Monophyllus* are distinct genera but are clearly related. It is likely that the precursor of *Monophyllus*, or perhaps even a species of the genus as currently defined, became isolated in the Antilles, where the genus is endemic. *Glossophaga* appears to be the most primitive of this group of genera; the teeth overall are more robust and the species are known to include meat and insects along with fruit in their diet. In the Lesser Antilles, the available data indicate that *Glossophaga* and *Monophyllus* compete and generally do not occur sympatrically (Jones and Phillips, 1969). It is likely that their eco-

logical requirements overlap. Inclusion of *Glossophaga* and *Leptonycteris* in a lineage separate from *Anoura* is of additional interest when considered in terms of cytological studies (Baker, 1967:324).

The genera comprising the third lineage are the most highly modified members of the *Glossophaga* group. I have allied this lineage to that including *Anoura* because in the genera in which a mesostyle has not been lost it is a prominent feature of the posterior element (Figs. 47 and 48). *Platalina* is a South American offshoot in which the rostrum became greatly elongate and the cheekteeth reduced in size and complexity. The upper and lower incisors, however, were enlarged from what must have been the primitive condition. This monotypic genus has no close relative among the living glossophagines and represents a highly specialized independent branch of the lineage (Fig. 47). In the other genera (*Scletonycteris*, *Lichonycteris*, and *Hylonycteris*) the lower incisors were lost and the upper incisors greatly reduced in size and equally spaced between the canines. In *Scletonycteris*, which is a monotypic South American genus, the molars are partially reduced but retain a large, prominent mesostyle (Fig. 48). The premolars are high-crowned and in this respect resemble those of *Lioncycteris*. *Lichonycteris* and *Hylonycteris* are related genera whose ranges overlap in Central America. The upper molars in the former genus are of special interest because, even though the M3 has been lost, the first and second molars present us with an indication of the intermediate stage of evolution. The mesostyle is present but reduced (it is part of the posterior element) and the paracone is highly variable, being present but small in some specimens and completely lacking in others (Figs. 28 and 48).

The *Choeronycteris* group of glossophagines includes *Choeronycteris*, *Choeronicus*, and *Musonycteris*. The teeth are greatly reduced in size and complexity in all three genera, the para-

cone and mesostyle have been lost from the upper molars, permanent lower incisors are lacking, and the upper incisors are small and the inner pair are separated by a gap. Because none of the genera is intermediate in dental configuration, it is difficult to suggest an ancestral condition. It is most likely, however, that the ancestor of this group was essentially the same as that described for the *Glossophaga* group. The genus *Choeroniscus* comprises species of small-sized bats that are highly specialized; the evolutionary trend has been toward convergence with *Lichonycteris*,

Hylonycteris, and *Scleronycteris*. *Choeronycteris* and *Musonycteris* are closely related genera (considered congeneric by Handley, 1966a) in which an extremely long rostrum and greatly reduced dentition have been developed. It is interesting that of these two monotypic genera, *Choeronycteris* is known only from the southwestern United States, México, and Guatemala, whereas *Musonycteris* is restricted to southern and western México. *Platalina*, which in many ways converges with these genera, is known only from northwestern South America.

SPECIMENS EXAMINED

Following is the number of specimens, and the countries in which they were collected, for the material examined in the study of permanent dentition. Genera, species, and countries are listed alphabetically.

Anoura caudifer.—Brazil 17, Colombia 8, Ecuador 4, Perú 18, Venezuela 3.

Anoura cultrata.—Panamá 13.

Anoura geoffroyi.—Bolivia 1, Colombia 26, Ecuador 1, Grenada 20, Guatemala 8, México 215, Panamá 24, Perú 23, Trinidad 2, Venezuela 44.

Choeroniscus godmani.—Costa Rica 4, México 6, Nicaragua 2.

Choeroniscus intermedius.—Trinidad 3, Venezuela 10.

Choeroniscus inca.—Ecuador 2, Guayana 1, Perú 1.

Choeroniscus minor.—Guayana 2.

Choeronycteris mexicana.—Guatemala 1, México 160, United States 7.

Glossophaga alticola.—Costa Rica 2, El Salvador 1, Guatemala 8, Honduras 5, México 95, Nicaragua 30.

Glossophaga commissarisi.—Costa Rica 11,

Guatemala 2, Honduras 5, México 32, Nicaragua 25, Panamá 28.

Glossophaga soricina.—Costa Rica 12, El Salvador 3, Guatemala 11, México 690, Nicaragua 102.

Hylonycteris underwoodi.—México 18, Panamá 5.

Leptonycteris nivalis.—México 97, United States 14.

Leptonycteris sanborni.—México 429, United States 2.

Lichonycteris degener.—Brazil 2.

Lichonycteris obscura.—Costa Rica 2, Nicaragua 3, Panamá 8.

Lionycteris spurrelli.—Brazil 19, Guayana 1, Panamá 1, Venezuela 4.

Lonchophylla hesperia.—Perú 1.

Lonchophylla mordax.—Brazil 3, Panamá 10.

Lonchophylla robusta.—Colombia 4, Costa Rica 13, Panamá 14.

Lonchophylla thomasi.—Brazil 4.

Monophyllus plethodon.—Dominica 16, St. Lucia 14, St. Vincent 1.

Monophyllus redmani.—Cuba 16, Haiti 3, Jamaica 17, Puerto Rico 39.

Musonycteris harrisoni.—México 1.

Platalina genovensium.—Perú 1.

Scleronycteris ega.—Venezuela 1.

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