

Evolutionary Trends of Chiropteran Dentitions

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INTRODUCTION

The paleontologist's obsession with teeth may be a cause for wonder to the neo-mammalogist accustomed to utilizing knowledge of habits as well as the whole suite of physical characters when evaluating an animal. The occasional more-or-less complete fossil skeleton is most welcome, but more often only isolated skeletal elements are recovered. Teeth being constructed of relatively hard and resistant material are more readily preserved and usually reflect dietary habits and relationships better than other isolated elements. Horizontal classification faces a real possibility that two groups with a common ancestor have greatly diverged in their dietary habits and consequent tooth-pattern. The primary problem in vertical classification lies in the fact that in the distant past a large group of related forms shared the same dental patterns, but only one gave rise to the modern group under study, while others left no descendants at all. Moreover, after the basic eutherian pattern was established, additional cusps, such as the hypocone, were added in the same position independently by different groups at different times. Furthermore, suggesting formal lineages by evaluation of contemporary forms can be misleading, although such studies have their value.

Very few cave deposits predate the Pleistocene, and forest faunal elements are extremely rare as fossils. As caves and forests are the primary habitats of chiropterans, they have the poorest fossil record of any major group, even though they are second only to rodents in numbers of living forms. Working with what we have seems preferable to begging the whole question. By a careful examination of the dentitions of modern forms and the few available pre-Pleistocene fossils, one can plot the probable route each type has taken to arrive at the dentition it possesses. Using taxonomic units as representatives of stages in dental evolution seems preferable to numbering hypothetical stages. Even if the procession of stages is not 100% accurate, in most cases such an exercise can *eliminate* certain types of dentitions from the ancestry of others.

I wish to dedicate this contribution to Dr. S. W. Geiser, Professor Emeritus, Department of Biology, Southern Methodist University, on his eightieth birthday; for his constant aid and encouragement through the years.

PRE-CHIROPTERAN EUTHERIAN DENTAL EVOLUTION

It should be reiterated that the use of taxonomic units as examples (as shown by the prefix *e.g.*) does not suggest an actual ancestor-descendant relationship of the genera. It suggests rather that the later genera had passed through a stage in which their dentition was much like the former example.

Too often the dentist, physical anthropologist, or student of some other essentially modern mammalian group will learn, and use, the proper nomenclature of the cusps without really understanding the evolution of the pattern. Unless one has this understanding, he loses all perspective of the morphological relationships of the teeth of all therian mammals. The literature on origin and evolution of the mammalian tooth pattern is extensive. Although the evolution from the tritubercular type has been well established for many years, the origin of this tooth form has been entirely speculative until within the past few years. Butler (1941) was pretty well on target in his views of the origin and early evolution of the therian molar pattern. We now have actual examples of some of his hypothetical intermediate forms. Not only are these intermediate in form between molars of extinct orders and primitive members of living orders, but the new material is chronologically intermediate as well.

One of the most fascinating facts in paleontology is that tooth patterns of shrews, rats, cats, bears, horses, camels, man and *bats* can be traced back through time to a single type of dentition.

Dryolestid pantotheres are suggested in the older literature as the probable Jurassic predecessors of mammals of metatherian-eutherian grade. More recently, however, it has become apparent that the actual ancestors of marsupials and placentals (which include 99% of the living mammals) were more like the symmetriodonts of late Triassic and Jurassic. Kermack *et al.* (1968) reported tooth and jaw fragments from late Triassic fissure-fills in England, and proposed the name *Kuehneotherium* (Fig. 1, A). These teeth are very like Jurassic symmetriodonts but are less symmetrical in their cusp arrangement. The upper molars form a scalene triangle in occlusal view. The largest cusp which is centered over the lingual angle of the triangle is the paracone. The paracone is considered the primary cusp, homologous with the reptilian cone. A sharpened crest extends from the paracone anterolabially to join a smaller cusp (stylocone). This cusp in turn is connected by a lower crest to the parastyle which is anterior and just slightly lingual. Another crest, extending postero-labially from the paracone contains the second largest cusp (metacone) midway, and the metastyle at the postero-labial corner of the tooth. This is essentially

like the pattern of the most primitive placentals and marsupials, except there is no protocone. There is, however, a strong lingual cingulum which could easily give rise to a more normal protocone. The lower molars also present a scalene triangle in occlusal view, although slightly more compressed transversely. The central and tallest cusp (protoconid) is labial instead of lingual and is connected by crests anteriorly to the paraconid and posteriorly to the metaconid. Although not so compressed antero-posteriorly, this is essentially the trigonid of therians. The talonid is small and contains but a single cusp. Mills (1964), using a composite of *Peramus* and *Amphitherium*, suggests intermediate steps between something like *Kuehneotherium* and dentitions of metatherian-eutherian grade. The only steps necessary for the intermediate stage is the enlargement of the labial cingulum of the upper molars, forming an incipient protocone which would occlude with an enlarged but still unicuspid talonid of the lower molars. There is also a slight antero-posterior compression of the trigonid.

The first mammal we can definitely consider of metatherian-eutherian grade is *Aegialodon* from the Neocomian (lowest Cretaceous) of England (Kermack *et al.*, 1965). The form is known only by a single lower molariform tooth. It differs from *Amphitherium* mainly in the modern aspect of the talonid, which is basined and contains hypoconid, hypoconulid, and entoconid. The *crista obliqua*, however, joins the trigonid at the metaconid rather than at trigonid mid-width. In this the tooth is more like *Amphitherium*. Without additional knowledge of the form we have at least three possibilities as to affinity: marsupial, placental or stem stock from which both took origin.

Sometime between late Jurassic and mid-Cretaceous the metatherian-eutherian stem evolved and diverged into marsupials and placentals. Prior to this all mammals had non-prismatic dental enamel (Moss). The oldest demonstrated prismatic enamel occurs in specimens from the Albian (mid-Cretaceous) of Texas, and therians after that time apparently maintain that trait. Patterson (1956) and Slaughter (1965) have reported mammals of metatherian-eutherian grade from the Texas Albian; and more recently, Slaughter (1968b) has distinguished didelphid marsupials from deposits of the same age in north-central Texas. More important to our discussion, however, is the recovery from the same deposits of premolars which are submolariform (Slaughter, 1968a). Triassic and Jurassic mammals had up to seven molars in addition to the four premolars. The maximum number of molars in marsupials is four and there has been no attempt to molarize premolars. The maximum number of true molars is three in placentals, but very early in their history a trend developed toward the molarization

of the posterior premolars. A brief résumé of the progressive molarization of these premolars is important in demonstrating just what the primitive condition is in bats. Taking as a starting point a dentition with four simple premolars and three typical molars, the first apparent step was the addition of a protocone to the ultimate upper premolar (P4). Initially the protocone was not tall enough to occlude with the incipient talonid of the opposing tooth (p4) as do molar protocones. Instead, the protocone was inclined posteriorly (opisthoclinal) to occlude with the much taller trigonid of m1. This condition has been labeled Stage I (Slaughter, 1968a). Stage II involves the addition of an opisthoclinal protocone to P3; this occludes with a new trigonid formed by the addition of a metaconid to p4. At the same time the protocone of P4 enlarges and shifts its occlusion to the talonid of p4; it thus serves the same purpose as do the protocones of the molars. The most primitive members of all eutherian orders is at Stage II of premolar molarization and this stage was reached by mid-Cretaceous. Many artiodactyls have extended molarization to P2-p3 and perissodactyls even to P1-p2. Carnivora, most Insectivora, Rodentia, Primates, and Microchiroptera never extended molarization beyond the primitive Stage II (P3-p4). However, there has been considerable demolarization from Stage II in some groups (*e.g.*, shrews, dogs, cats, and bats).

It is now rather apparent that the genus *Pappotherium* described from the same Albian deposits (Slaughter, 1965) is eutherian and, considering the evidence of isolated molariform premolars, may have been at Stage II. This form makes a perfect prototype to all subsequent placental dentitions (Fig. 1, B). Three distinct morphologic trends proceed from this basic placental form. In the rarest of these, which is termed "zalambodont," the paracone migrates lingually, increasing the shear length at the expense of the grinding area furnished by the protoconal and talonid basins (*e.g.*, potamogales, solenodonts, etc.). A second trend involves the migration of the paracone and metacone labially at the expense of the labial shelf (tritubercular). This course was taken by the ancestors of erinaceoids, carnivores, rodents, primates, and ungulates. In the third, and most important to our discussion, the paracone and metacone remain at about the transverse mid-width of the tooth (dilambodont). The significant change in form from the primitive is the development of the W-shaped ectoloph, which nearly doubles the shear surface with no loss of grinding surface. This was accomplished by the deepening of the notch between the paracone and metacone almost to the tooth's labial border, and the addition of the mesostyle at the juncture of the post-paracrista and pre-metacrista. The talonid cusps of placental mammals not having exaggerated W-shaped ectolophs are

essentially equidistant (Fig. 1, D). The development of the W-shaped ectoloph creates a need for the hypoconulid of the lower molars to reach further between the primary cusps above, and this requires lingual displacement of the hypoconulid much closer to the entoconid. The degree of "twinning" of the hypoconulid to the entoconid is related to the length of the antero-lingual face of the metacone above (Slaughter, 1968b). It is long enough to cause twinning in didelphid marsupials, owing to the increase in size of the metacone beyond that of the paracone. In tupaiids, shrews, and many insectivorous bats the length of the anterolingual face of the metacone and consequent twinning of the hypoconulid and entoconid is due to the deepening of the notch between the paracone and metacone (Fig. 1, C). In extreme cases the notch remains deep and the metacone exceeds the size of the paracone as well. When this happens, there is no room for hypoconulids even if they are twinned. At first the hypoconulid is lost as a cusp, but its former position is evident as an inflection of the post-cristid. In more advanced cases the post-cristid joins directly to the entoconid without the inflection.

GENERAL CHARACTERS OF CHIROPTERAN TEETH

Milk dentition.—As in most placental mammals all but one of the permanent premolars have deciduous predecessors. However, rather than being similar to the permanent set they are slender, spike-like, and often slightly hooked at their distal ends. The megachiropteran milk teeth are more simple than those of microchiropterans in that there are no accessory cusps (Fig. 2, G). One or two lateral cusps, somewhat lower than the primary one, are usually present on the milk teeth of the latter (Fig. 2, F). The most often stated use for the hooked milk teeth is to allow the young to cling to the mother's fur in lieu of grasping forefeet. Spillman (1927) reported that while milk teeth are present in prenatal rhinolophids, they are resorbed before birth. This may offer further evidence that the hooked milk teeth are indeed used for clinging, for rhinolophids have unique dummy teats not connected to the mammary glands, which the young grasp, and therefore would have less need for the "clinging" milk teeth.

Of great interest is the fact that the Eocene form, *Archaeonycteris* (clearly a microchiropteran), has a molariform dp4, typical of the ultimate milk tooth of any other order of therian mammals. This would seem to indicate that the development of the "clinging" milk teeth occurred after Megachiroptera-Microchiroptera divergence, and that both suborders developed this unique mechanism independently.

Incisors.—Many bats retain the maximum number of lower incisors

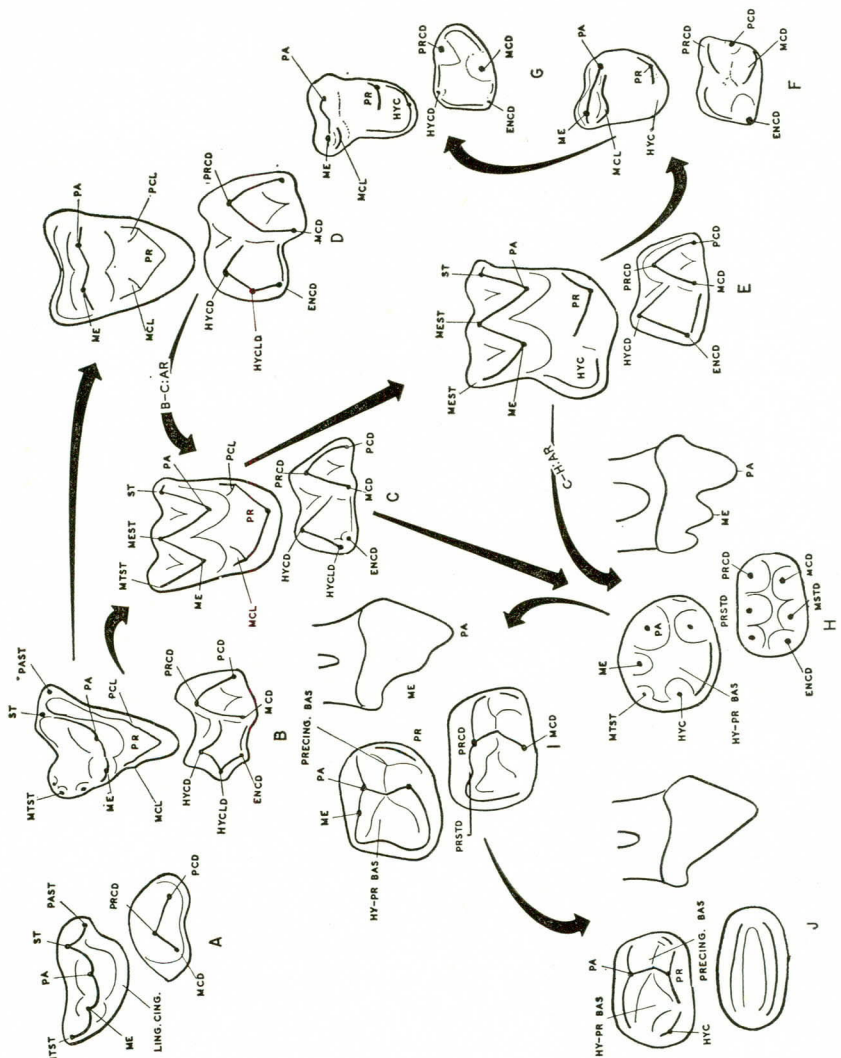


FIG. 1. Diagram showing suggested molar patterns through which certain primitive mammals and chiropterans have passed. Cusp nomenclature used in text; ENCD, ectoconid; HYC, hypocone; HYCD, hypoconid; HYCLD, hypoconulid; HY-PR BAS, hypo-protoconal basin; LING CING, lingual cingulum; MCD, metaconid; MCL, metaconule; ME, metacone; MSTD, metastylid; PA, paracone; PAST, parastyle; PCD, paraconid; PCL, paraconule; PR, protocone; PRCD, protoconid; PRECING BAS, precingular basin; PRSTD, protostylid; ST, stylocone.

B-C:AR, route alternate to that of B-C

C-H:AR, route alternate to that of C-H

(3) but there is no known form, fossil or living, that retains all three above. There has been considerable speculation as to which of the original upper three has been lost. Andersen (1912), Thomas (1908), and others have suggested that the missing upper incisor is the outermost (I3), as indicated by the upper pre-canine diastema which receives the lower canine when the two dentitions are occluded. Miller (1907) believed it to be the inner incisor (I1). He reasons that the tendency toward reduction of the premaxillary bones, which frequently become detached one from another would select against I1. Miller's idea is most seductive when one examines a vespertilionid, but the inner remaining incisor is usually somewhat larger than the outer one even in forms having contact between the premaxillae. For this reason I find Andersen's position more reasonable. The vast majority of bats, both megachiropteran and microchiropteran, have either trifold or bifid lower incisors (Fig. 2, B). If the cuspid nature of these teeth were related to the feeding mechanism it seems strange that the form would be retained in almost all groups, regardless of their widely divergent dietary habits. It seems probable that they may be used in grooming the fur, or perhaps useful for extracting ectoparasites.

Canines.—While the canines of most bats remain rather tall and trenchant, they are usually somewhat more complex than those of primitive insectivores. A well developed cingulum is very often present in microchiropterans, especially in insectivorous forms. The canines of Old World fruit bats are usually smooth to the base. Even in New World bats the internal cingulum tends to develop more into a basined shelf, and the external cingulum is usually weak. I suspect that the development of a cingulum serves as a guard, protecting the peridental tissue from damage by fragmented insect exoskeletons.

Premolars.—Although the basic placental number of premolars in each jaw is four, there is no known bat with more than three. The most widely accepted identification of the missing premolar is P1-p1 (Miller, 1907), although there is little evidence that this is the case. Thomas (1908) is emphatically against this, and his candidates for the missing premolars are P2 and p2. This is indicated, he believed, by the diastema behind the most anterior premolar in *Lonchoglossa*, and others, and by an extra tooth in this position in a specimen of *Pteropus scapulatus*, which he presumed to be an atavistic P2. Some authors have gone so far as to number the premolars P1-P3 stating it is merely for convenience. I reject this latter view as there can be no doubt the ultimate premolar is p4 because of the occasional presence of a metaconid. While Thomas's argument is credible, numbering premolars "P1-P3-P4" is clumsy, and I fear would mislead some readers as to which tooth is

referred to. I, therefore, prefer Miller's identification in absence of firm evidence to the contrary.

Although the earliest bat, *Icaronycteris*, is at Stage II in the molari- zation of its premolars, in later forms there has been a widespread trend toward reducing the number of premolars and simplifying the most anterior of those remaining. Among the Microchiroptera almost all have some development of cingula. New World fruit bats utilize lingual cingula as a part of the pulverizing mechanism. Insectivorous forms have strong cingula which probably serve to guard the peridontal tissue from fragmented insect exoskeletons during mastication. Old World fruit bats have no development of cingula on the premolars.

Molars.—Other than the lingual migration or loss of the hypoconulid of the lower molars, the insectivorous bats maintain an essentially primitive tribosphenic dentition of the dilambdodont type. Upper molars usually have well developed hypocones or basal lingual cingula and labial cingula on the lower molars. These probably perform the same guard service as the cingula of the canines and premolars (deflection of exoskeletal fragments from accidental insertion into the alveoli). The fact that megachiropterans do not develop such cingula may offer additional support that this is the primary function of the cingula. Other highly specialized insectivorous mammals have developed molar cingula and/or hypocones in a similar fashion and presumably for similar reasons (shrews, moles, etc.).

A tendency to first lose the metacrista from M3, and eventually the metacone and pre-metacrista, developed independently in many microchiropterans. This is not unique to bats, however. The same trend started very early in most tribosphenic dentitions, whether marsupial or placental.

EVOLUTIONARY TRENDS OF CHIROPTERAN DENTITIONS

Different characters evolve at different rates. One group places priority on one character while emphasis is placed on a different character by another group. For example, the dentition of megachiropterans has diverged from the primitive condition somewhat further than that of microchiropterans. On the other hand, this specialization for a frugivorous habit requires less sustained and maneuverable flight. The insectivorous habits of most microchiropterans have selected for retention of the essentially basic and primitive insectivorous dental pattern; but the flight mechanism has developed to a much greater degree as a requirement for catching insects in flight. This is an extreme example, but there are others somewhat more subtle. Therefore, the fact that the post-cranial anatomy of *Rousettus* is said to be more primitive than

that of *Pteropus* does not invalidate the fact that at some time in the evolutionary history of *Rousettus* its dentition was very like that of *Pteropus*. The dental pattern of *Pteropus* has diverged less from the prototypic megachiropteran type. With this in mind, the following section is an attempt to plot the evolutionary routes taken to arrive at the known dental patterns. Numbers represent types of dentitions (sometimes hypothetical) that could be prototypic to all dental types further up the trees. Letters represent trends in dental evolution radiating from the prototypes.

There can be no doubt that bats took origin from within the Insectivora. However, in the absence of a fossil intermediate between an arboreal form and the free-flight form, speculation as to which specific group is ancestral is pure conjecture, complicated by the knowledge that the ancestors of bats may have left no non-bat descendants. In an exercise of this type it seems worth pointing out that the immediate predecessor would be rather like modern tree shrews (*Tupaia*, Fig. 2, B), even though modern forms have no conules. Until rather recently some taxonomists have considered tupaiids primitive primates. Van Valen (1965), Szalay (1968) and others have strengthened the case against close affinity and referred them back to the Insectivora. *Tupaia* does share the presence of a complete post-orbital bar with primates and some bats (e.g., *Pterolopex*), and is arboreal, as bat ancestors must have been. Its dentitions present all characters, other than conules, that I consider prerequisite to bat ancestry: W-shaped ectoloph, three-rooted P3 and P4 with protocones, metaconid on p4, and well developed hypoconulids twinned with the entoconids. This is not to suggest that bats are merely flying tupaiids, but that the prototypic chiropteran must have had habits and dentitions very similar to those of *Tupaia*.

An early trend toward brachycephaly in bats initiated simplification and number reduction of the premolars. The root-supported protocone of P3 is the rarest surviving trait. The oldest known bat, *Icaronycteris*, has a dentition more like the ancestral condition than any other known chiropteran. It retains both three-rooted P3 and well developed metaconid on p4 (Jepsen, 1966). *Cecilionycteris* Heller (1935) is from Eocene deposits slightly younger than those producing *Icaronycteris* and its familial affinity is uncertain. The premolar series had begun to demolarize, in that P3 has but two roots. There is a slight suggestion of a protocone visible, however. The metaconid remains on p4 which is primitive. Another Eocene form from Europe is *Palaeochiropteryx*. The upper dentition is unknown but it too has a well developed metaconid on p4. *Archaeonycteris*, a contemporary of *Palaeochiropteryx*, had already

begun simplification and reduction of the premolars. It has but two lower premolars and apparently neither had metaconids.

1

- 1a The trend leading to the basic microchiropteran dentition that was to give rise to most superfamilies, involved few changes from the dentition prototypic to all Chiroptera. There would be development of lingual cingula on the upper teeth and labial cingula on the lowers. The protocone of P3 might be slightly reduced but would be retained. *See prototype 2.*
- 1b Very early in the megachiropteran divergence the paracone and metacone migrated to the labial border of the upper molars, and the molariform teeth tended to square up by an increase in the size of the proto-hypoconal and talonid basins. (Fig. 1, H). *See prototype 16.*

FIG. 2

- A. Nomenclature of crests; CON-W, conule wings; CR OB, crista obliqua; ENCRD, entrocristid; MTCR, metacrista; PACR, paracrista; PALD, paralophid; POCD, posteristid; POPA, post-paracrista; POPRCR, post-protocrista; PREMETCR, pre-metacrista; PREPRCR, pre-protocrista; PRLD, protolophid.
- B. Upper and lower post-canine dentition of *Tupaia*;
- C. M3 with metacrista and pre-metacrista;
- D. M3 with full metacrista;
- E. Anterior upper premolar displaced lingually;
- F. Lower milk dentition of *Pipistrellus*;
- G. Lower milk dentition of *Eidolon*;
- H. M3 with reduced pre-metacrista;
- I. M3 with no metacrista or pre-metacrista;
- J. Anterior upper premolar displaced labially;
- K. Lingual view of m1 and m2 of typical insectivorous rhinolophid; (KK occlusal view of same);
- L. Lingual view of m1 and m2 of carnivorous megadermatid (LL occlusal view of same);
- M. Lingual view of p4 and m1 of primitive miacid (MM occlusal view of same);
- N. Upper molar of *Docodon* (occlusal view above; lingual view below);
- O. Upper molar of *Dobsonia* (occlusal view above; lingual view below);
- P. P4 of *Nasalis* (occlusal view above; lingual view below);
- Q. Lower molar of *Docodon* (occlusal view above; lingual view below);
- R. Lower molar of *Dobsonia* (occlusal view above; lingual view below);
- S. P4 of *Nasalis* (occlusal view above; lingual view below).

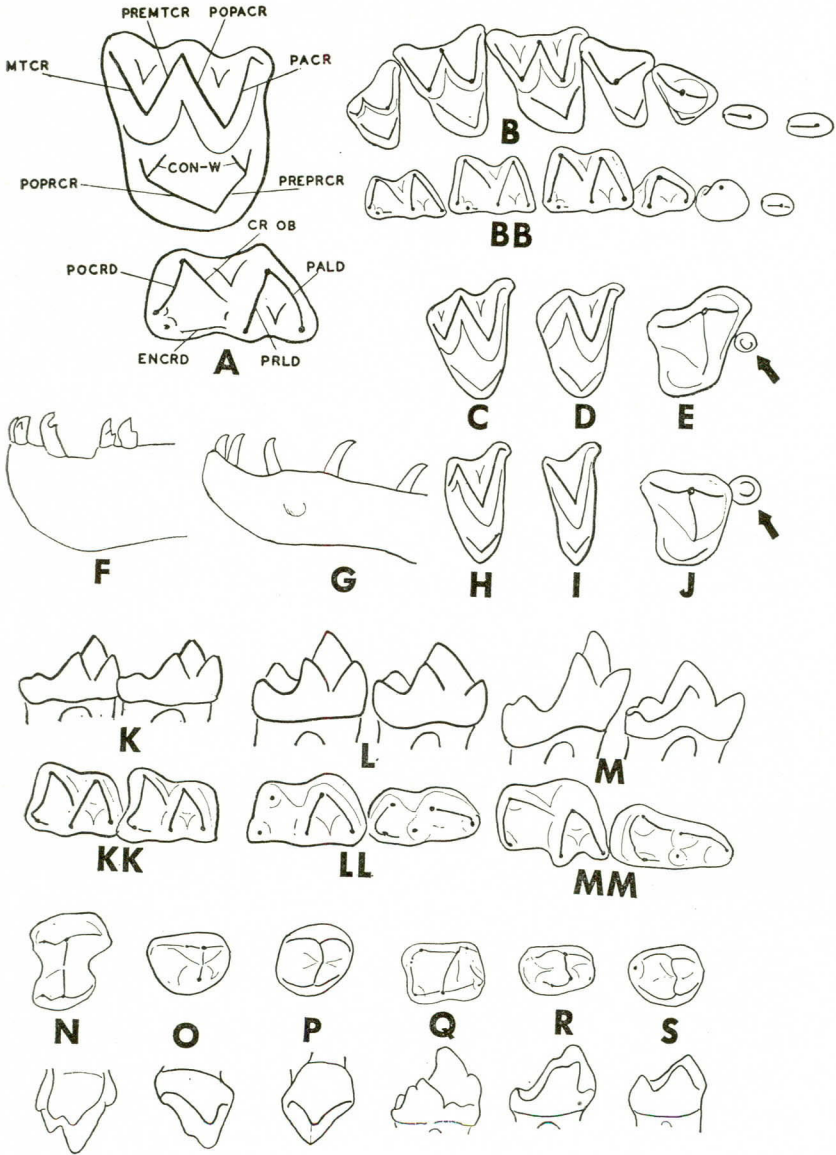


FIG. 2

2

The Rhinolophoidea (Fig. 5) include among its members some of the oldest known specimens referable to living families. There was considerable divergence within the group before its first appearance in the geologic record, and no known form retains a dentition that could be considered ancestral to the whole superfamily. Such an ancestor would have a dental formula of 2/3; 1/1; 3/3; 3/3. Both upper and lower incisors would be trifold. P2, P3, and p2 could be single-rooted, but P4 would have three roots and p3-p4 two each. Development of the hypocone would probably be weak and there would be a well developed pre-metacrista and short metacrista on M3 (Fig. 2, C). The hypoconulid of the lower molars would be crowded against entoconid but equally well developed.

2a Loss of I2 and P3; 1/3; 1/1; 2/3; 3/3.

3

Eocene species of *Rhinolophus* (e.g., *R. cluzeyi*, Hougoney) had not reduced p3 to the extent that modern species have, but it was single-rooted and crowded. The dentition of these archaic rhinolophids makes a satisfactory prototype to the dentitions of all members of the superfamily other than *Nycteris* and *Palaeonycteris*.

- 3a Slight enlargement of the hypocone of the upper molars; further reduction of p3, and alignment of the small anterior upper premolar with the tooth row (e.g., *Rhinolophus affinis*).
- 3b Crowding of the anterior upper premolar lingual to the tooth row (Fig. 2, E) and loss of remaining upper incisor (e.g., *Megaderma*). Modern megadermatids have lost the pre-metacrista from M3 (Fig. 2, D) and the hypoconulids from the lower molars, but both of these are retained in some forms well into the Miocene; pre-metacrista on M3 of *M. luguensis* Mein (1964); hypoconulids on *M. railloni* Sige (1968). Two other tendencies of megadermatid dentitions are (a) failure of the post-paracrista and pre-metacrista to reach the labial border of the tooth; (b) labio-lingual compression of the trigonid of m1 bringing the paralophid more into an antero-posterior line. Both of these tendencies probably relate to the carnivorous habits of megadermatids. Shears aligned antero-posteriorly are clearly advantageous to meat-eaters (e.g., shears of triconodonts, zeuglodonts, dogs, and cats). As a matter of fact, the form of the megadermatid m1 is very similar, both in form and function, to p4 of early carnivores (e.g., miacids; Fig. 2, K-M). The megadermatid m1 seems to have about the same relationship to P4 and M1 that the miacid p4 has to P3 and P4. Megadermatid

M1s even reduce the protocones in a similar fashion as the miacid carnassial. The post-protocrista of *M. vierti* Mein (1964) is so reduced as to abut against the anterolingual face of the metacone, rather than at the metacone's lingual-most point.

Necromantis Weithofer (1887) of the European Eocene is clearly a megadermatid, but it retains a small p3 and the anterior upper premolar is in line with the tooth row. These are characters of rhinolophids and suggest that *Necromantis* was an early branch.

3c Crowding of anterior upper premolar out of the tooth row labially (e.g., *Rhinolophus ferrumequinum*; Fig. 2, J).

4

4a The Palaeophyllophorinae of the Eocene and Oligocene of Europe has P2 in the labial position typical of the Hipposiderinae and still retain the small p3. The pre-metacrista is present on M3 but much shorter (Fig. 2, H). The juncture of the post-paracrista and pre-metacrista fails to reach the labial border of the molars. This results in a wide styler shelf (Fig. 3, D) not unlike that of didelphid marsupials, *Megaderma vierti*, and *Necromantis*. This short-lived group apparently left no descendants.

4b Sige (1968) recently proposed *Brachihipposideros* as a Tertiary subgenus of *Hipposideros*. The group is distinguished by the presence of four roots on M1 and M2 and an accessory cusp on the upper canines. A primitive character is the retention of a fairly well developed pre-metacrista on M3. Sige also reduced *Pseudorhinolophus* to subgeneric status. This Eocene form is more typical of the Hipposideridae. P2 is still present and labially displaced. The tiny p3 has been lost and the pre-metacrista of M3 shortened to about one-half that of *Rhinolophus*.

One step farther along this trend is exemplified by modern *Hipposideros*, where the pre-metacrista is completely lost from M3 (Fig. 2, I) while all other characters are maintained.

4c Another trend involves the loss of P2 but retention of the pre-metacrista of M3 (e.g., *Asellia*).

2b The monogeneric family, Nycteridae, differs from the other members of the superfamily in its retention of two upper and three lower trifold incisors. The hypoconulids of m1 and m2 remain well developed. P2 and p3 are lost, the metacrista is lost from M3 and the pre-metacrista is much reduced.

2c Although Friant (1963) refers the Oligocene genus *Palaeochiropteryx* to the Rhinolophinae, its retention of three upper premolars makes it unique among known rhinolophids and can only be related through the hypothetical prototypic dentition 2.

Vespertiliavus (Emballonurinae) of the European Eocene is the oldest known member of the Emballonuridae. The number of incisors is unknown but the form is relatively primitive; the P3 is double-rooted, and the upper molars retain rudimentary conules. I consider a separate hypocone like that of *Noctilio* (Fig. 3, A) more primitive than one in which the protoconal and hypoconal basins are broadly confluent (Fig. 3, C) and one in which the two basins have a small confluency, intermediate (Fig. 3, B).

5

The prototypic dentition for the entire superfamily would therefore be similar to that of *Vespertiliavus* but the hypocone would be separate and there would be two upper incisors. Also, conules would be present on the upper molars and hypoconulids on the lower molars (Fig. 1, C).
5a Loss of upper incisor.

6

A dentition prototypic to the Emballonuridae would be *Vespertiliavus*-like with three lower premolars and incipient confluency of the hypoconal and protoconal basins.

FIG. 3

- A. Molar with isolated hypocone;
- B. Molar with small commissure between hypoconal and protoconal basins;
- C. Molar with hypoconal and protoconal basins broadly confluent;
- D. *Palaeophyllophora*
- E. *Vampyrum*
- F. *Macrotus*
- G. *Trachops*
- H. Upper post-canine dentition of *Pterolopex* (occlusal view); (HH lower of same);
- I. Upper post-canine dentition of *Harpyionycteris* (occlusal view) (II. lower post-canine dentition of same);
- J. Lower canines and incisors of *Tadarida* (*Tadarida*);
- K. Lower canines and incisors of *Tadarida* (*Chaerophon*);
- L. Lower canines and incisors of *Molossus*;
- M. P3-M1 of *Miniopterus*;
- N. P2-M1 of *Myotis*;
- O. P2-M1 of *Natalus*;
- P. P2-M1 of *Murina*;
- Q. Upper dentition of hypothetical prototype of Desmodontidae; (QQ lower dentition of same);
- R. M2 of *Sturnira*; (RR M2 of same);
- S. M2-M3 of *Glossophaga* (SS m2-m3 of same);
- T. M1-M3 of *Carollia* (TT m1-m3 of same);
- U. M1-M3 of *Rhinophylla* (UU m1-m3 of same).

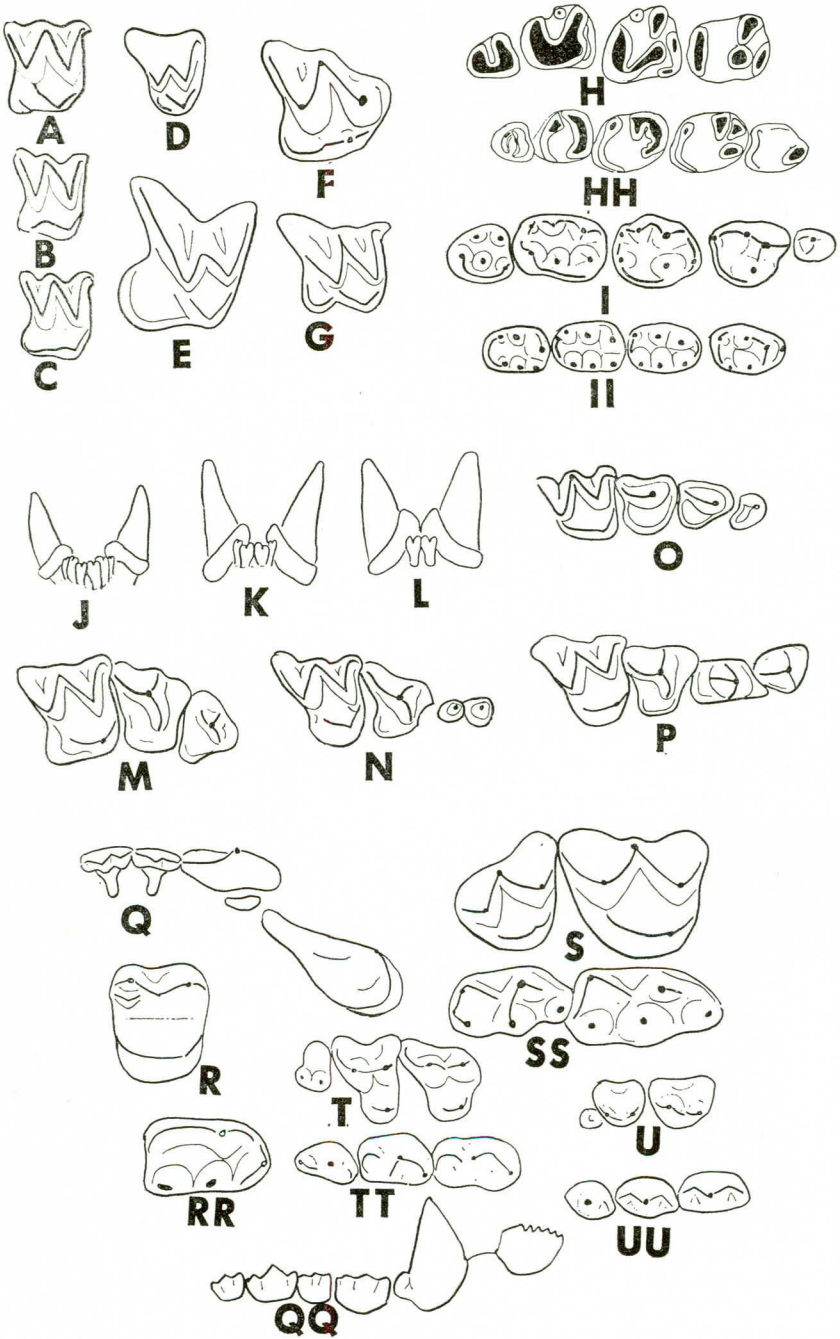


FIG. 3

- 6a Trend 6a develops the *Saccopteryx*-like dentition, in which there is great reduction of P3 and loss of p3. The confluency of the hypoconal and protoconal basins is broad, and all trace of conules has been lost (Fig. 1, E). There remains, however, a well developed pre-metacrista on M3.
- 6b Dentitions of 6b (e.g., *Taphozous*) share the characters of the hypo-protoconal basin with 6a; but there is great reduction, or loss, of the remaining upper incisor, loss of i1, and the pre-metacrista from M3 (Fig. 2, I). These modifications could suggest an ancestor-descendant relationship were it not for the fact that P3 of Trend 6b is less reduced than that of 6a. It would appear therefore that both *Saccopteryx*-like and *Taphozous*-like dentitions must trace their ancestry directly to the prototype of the family.
- 6c The family Rhinolophidae exhibits a dentition with several advanced characters, such as reduced dental formula 1/2; 1/1; 1/2; 3/3 and lack of the pre-metacrista on M3, and could conceivably have taken origin from within the Emballonuridae. However, the hypocone of the upper molars of *Rhinopoma* are completely separate from the protoconal basin, a character I consider primitive. This type of dentition could derive directly from the superfamily prototype (5) and therefore be no more closely related to the Emballonuridae than to the *Noctilionidae*, a possibility suggested by Miller (1907). On the other hand, rhinopomids could derive from incipient emballonurid stock prior to the development of the confluent hypo-protoconal basin. The latter possibility seems more probable.
- 5b The *Noctilionidae*, as represented by *Noctilio*, retains several primitive characters of the superfamily prototype; retention of two upper incisors, hypocones separate from protoconal basins, and well developed pre-metacrista on M3. A unique dentition is almost created by this combination of primitive characters with such advances as retention of but a single upper premolar (P4), a single lower incisor and two lower premolars, and exclusion of the hypoconulid from the posteristid. This dentition could neither be derived from, nor be ancestral to, that of any other known member of the superfamily.

The dentition of the Chilonycterinae has more primitive characters than any other member of the Phyllostomatoidea, although other aspects of the anatomy may be rather curiously adapted. The maximum dental formula is 2/3; 1/1; 2/3; 3/3. The molars contain confluent hypercones not unlike those of typical emballonurids. P3 and p3 are double-rooted, while those of modern emballonurids have but a single root

each. However, the Eocene emballonurid, *Vespertiliavus* has P3 and p3 double-rooted. The number of incisors is unknown in this fossil form, but even if it were but one, its dentition is similar enough to *Mormoops* to offer evidence that the whole of Phyllostomatoidea may have taken origin from within the Emballonuridae.

7

The prototypic dentition of the Phyllostomatoidea was probably very nearly like that of *Mormoops*. The suggested differences are: double-rooted P3 and p3, winged conules, metaconid on p4, better developed hypoconulids on lower molars, and presence of short metacrista on M3.

- 7a Trend 7a loses one root from P3 and p3 and the metacrista from M3. It does retain a fairly well developed pre-metacrista on M3 and three lower incisors (e.g., *Mormoops*).
- 7aa Trend 7aa, as represented by *Chilonycteris*, loses one lower incisor and one root from p3. It still retains the metaconid on p4.
- 7b Trend 7b differs from prototypic dentition 7 only in that the number of lower incisors is reduced to two.

8

The prototypic dentition of the Phyllostomatinae would have a dental formula of 2/2; 1/1; 2/3; 3/3. I1 would be somewhat larger than I2. The upper molars would have the typical W-shaped ectoloph, low hypocones, and winged conules. Both pre-metacrista and a short metacrista are retained on M3 (Fig. 2, C). The lower incisors were probably trifold and the three lower premolars nearly equal in size. The first two lower molars should have distinguishable hypoconulids, and the metaconid of p4 was probably still present.

- 8a The type of dentition represented among living forms by *Macrotus* maintains the primitive characters of double-rooted P3 and p3 subequal to the other lower premolars. At the same time there is reduction and loss of the paracrista from M1 (Fig. 3, F).
- 8b Dentitions of trend 8b have a tendency toward the reduction and loss of p3, and loss of one root from P3.

9

An unknown intermediate form differing from prototype 7 only through changes outlined under 8b, must have been passed through by all remaining phyllostomatids. Although the intra-relationship of these forms is quite close, there does appear to be two minor trends.

- 9a The normal condition of the ectoloph is maintained but p3 is greatly reduced (e.g., *Lonchorhina*) or lost (e.g., *Phyllostomus*, *Mimon*).

- 9b This trend is toward the elongation of the metastylar area of M1 and M2 (Fig. 3, E, G).

10

The unknown intermediate between participants of trend 9b would have an upper dentition not unlike that of *Trachops* but p3 would be slightly better developed than in 7a forms. Nevertheless, it would still be smaller than p2 or p4.

10a There is great reduction of p3 and it is crowded lingual to the tooth row (e.g., *Trachops*).

10b Although smaller than p2 or p4, p3 is still fairly well developed. The post-paracrista and pre-metacrista of the upper molars meet some distance from the tooth's labial border (e.g., *Vampyrum*; Fig. 3, E). This creates a wide stylar shelf reminiscent of the condition seen in the Eocene rhinolophid, *Palaeophyllophora*. The latter does not have the attenuated metastylar area, however.

11

It is possible that the glossophagines took origin from within the Phyllostomatinae, but their dentitions could not have arisen from those of any known member of that subfamily. *Lonchorhina* and *Phyllostomus* have lost the metacone from M3 while glossophagines have a well developed pre-metacrista and a short metacrista (Fig. 3, S). The dental formula of the glossophagines is also greater and all premolars are double-rooted. P3 and p3 are single-rooted in *Lonchorhina* and *Phyllostomus*. *Macrotus* has the same dental formula as *Glossophaga*, but p2 is single-rooted, and has lost the paracrista from M1 and the pre-metacrista from M3. In addition, some glossophagines have molars retaining weakly developed conules, a character unknown among the other forms under discussion. Therefore, the relationships between these groups can only be through an unknown form (prototype 8).

To me, the dentition of *Phyllonycteris* is clearly derivable from that of the glossophagines. Miller (1907) apparently felt that the antero- and posterolabial "cusps" were the paracone and metacone which had migrated there in the fashion of the stenodermines. Close comparison with glossophagines has convinced me that the labial ridge (and its protuberances) is exactly homologous with the stylar ridge, and the paracone and metacone must have been reduced in place. As a matter of fact, in some unworn specimens there are faint elevations in the position of the paracone and metacone of glossophagines. All that would be necessary to derive the dentition of *Phyllonycteris* from one like that of *Glossophaga* would be the suppression of the paracone and metacone of the upper molars and the loss of one lower premolar.

11b Glossphagine-like dentitions seem the best known candidate for the ancestry of the Carollinae. Neither have hypocones, the lingual concave facets of the upper canines lack basal cingula, and both have metacones on M3. The transition would involve the loss of the protocone from M3, loss of the mesostyles, and failure of the post-paracrista and pre-metacrista to reach the labial border (Fig. 3, T).

There can be no doubt that *Rhinophylla*-like dentitions passed through a condition like that of *Carollia*. There is little change in the styler shelf of the upper molars but the protocones are lost, thus placing the paracone and metacone at the lingual border of the tooth (Fig. 3, U). Reduction in the size of the lingual cusps of the lower molars (metaconid and entoconid) had already begun in *Carollia* but these cusps are completely lost in *Rhinophylla* and the protoconid is positioned more centrally, enhancing the shearing effect.

12

The method of developing a cusp-in-line shearing mechanism in desmodontids must have been similar to that of *Rhinophylla*. This is not to say that the latter could have given rise to the desmodontids, however, for *Rhinophylla* has lost all trace of protocones while they are preserved in *Desmodus*. If the desmodonts did originate from within the Carollinae, as seems possible, it would have to have been between the grades which are represented by the dentitions of *Carollia* and *Rhinophylla*.

None of the known desmodontid dentitions could have been ancestral to the others, although they are very similar. An intermediate common ancestor (Fig. 3, Q) would have at least the dental formula of *Diphylla*; 2/2; 1/1; 1/2; 2/2, but would retain protocones on P4 and M1, as in *Desmodus*.

12a I2, M2 and m2 are retained but all protocones are lost (e.g., *Diphylla*).

12b The dental formula is reduced to 1/2; 1/1; 1/2; 1/1, but P4 and M1 have small but root-supported protocones which serve as shear-stops much as the protocone of the carnassial of cats.

13

A prototypic dentition that could give rise to the Stenoderminae *Sturnira* and *Brachyphylla* would have a formula of 2/2; 1/1; 2/2; 3/3, hypocones and winged conules on upper molars, a paraconid, metaconid, and basin talonid on p4. Although the teeth of stenodermines and their allies are rather curiously adapted, no other phyllostomatid

shares *all* of their primitive characters. Certain glossophagines retain winged conules on their upper molars, paraconids, basined p4 talonids, and even vague rudimentary metaconids on p4. They do not, however, have hypocones. *Macrotus*, *Phyllostomus* and related forms have well developed hypocones, but the talonid of p4 is not basined and certainly there is no suggestion of a metaconid. Under these circumstances the dentition with all of the characters prerequisite to the ancestry of the stenodermines *Sturnia* and *Brachyphylla* would be that of prototype 8. New-World fruit-bats, therefore, may be as closely related to the Glossophaginae as to the Phyllostomatinae. As a matter of fact, the dentition of *Sturnia* shares characters with that of *Glossophaga* which are not present in the typical stenodermines; lack of hypocone and retention of some of the styler shelf. It is difficult to say whether stenodermines arose from glossophagines; glossophagines took origin from within the Stenoderminae; or if stenodermines, glossophagines, *Sturnia* and *Brachyphylla* originated from a common but unknown group. The latter seems most probable. In the absence of fossil intermediates, however, the dentition offers no hint as to which they may be most closely related.

13a Within the modern Stenoderminae there appear to be two trends discernible. These are best represented by *Uroderma* (a) and *Vampyrops* (aa). Neither of these genera could have given rise to the other, but both are very nearly at the same grade of divergence from the normal microchiropteran dental type. *Uroderma* p4 retains a paraconid, and when viewed from the posterior, this tooth often has a swelling in the position of the metaconid. In this character the dentition of *Uroderma* is more primitive than that of *Vampyrops*. On the other hand, the hypocone is much better developed in *Uroderma*, even forming a cusp lingual to the protocone (Fig. 4, D). Both paraconule and metaconule are winged, thus forming a continuous secondary "ectoloph."

Uroderma also retains the maximum dental formula for the subfamily and serves as a basic type of dentition from which several other forms of the trend could originate. A tendency toward brachycephaly crowds the dentition and results in reduction of M3 and reduction of the metastylar area of M2 (e.g., *Stenoderma*). One step further is represented in *Artibeus* in which M3 is lost but m3 retained, and further crowding of the tooth row results in the loss of m3 as well (e.g., *Centurio*).

13a *Vampyrops* seems to stand at the base of another trend. It shares the primitive characters of maximum dental formula for the subfamily, and paraconid on p4 with *Uroderma*. It is even more primitive in the lesser development of the hypocone (Fig. 4, E).

It does not however, have any suggestion of a metaconid on p4. The most significant character is the minor role the hypocone plays.

The *Chiroderma*-like dentition could easily take origin from something like that of *Vampyrops*. The metaconule remains cuspid but M3 and m3 are lost. The paracone of M1 becomes taller and more trenchant than the metacone, giving a more premolariform appearance. Although the hypocone of M2 may still affect the overall shape of the tooth, it does not participate in the tooth's basin.

The type of dentition presented by *Ectophylla* could easily derive from one similar to that of *Chiroderma*. It is little more than a subdued replica of that pattern.

13b Although *Sturnira* is usually placed in a separate subfamily, it seems clear that its origin is closely interwoven with that of known stenodermines. Even so, the fact that all three cusps of the trigonid of lower molars are well developed, and that if there had been any development of a hypocone it has been obscured through confluency with the protoconal basin (Fig. 3, R) suggests it could only be related through a common ancestor. The paraconule is not in evidence but the metaconule is at about the same stage as in stenodermines. The old stylar shelf is in evidence as a rounded, labial cingulum.

13c Allen (1939) removed *Brachyphylla* from the Stenoderminae, but Miller (1907) maintained the genus in that subfamily. Most subsequent workers have followed Miller. Whatever is correct, the dental pattern is certainly unique within that group. There are five cusps on the crowns of the upper molars; two blade-like cusps at the labial border; one lingual cusp, and two broad, low cusps in the intervening basin. The labial cusps presumably are the paracone and metacone. Miller (1907) considered the basin cusps conules, which in this single case among the stenodermines did not follow the paracone and metacone on their labial migration. The lingual cusp Miller considered the protocone and there was no hypocone. The lack of a hypocone would have indeed been unique for the group.

We are indebted to Butler (1937) for his development of the Field Concept of dental evolution. He and Marshall & Butler (1966) have demonstrated that upper and lower dentitions develop and presumably evolve as a unit rather than separately, and show that gross change in pattern of the cusps in one series does not greatly affect the individual cusp's occlusal relationship

with its partner in the opposing dentition. When we examine the occlusal relationship of the anterior basin cusp of *Brachyphylla*, we find that it occludes with the talonid of the adjacent lower molar in the same fashion as the protocone of typical stenodermines (Fig. 4, F, G). Other evidence comes from the fact that when one draws a line through the apex of the protocone of P4 and across the protocones of the molars of any primitive dentition, the line roughly parallels a line drawn through the paracones of the same teeth. In this regard, the anterior basin cusp of *Brachyphylla* qualified best as the protocone. The hypocone (Miller's protocone) occludes at the lingual border between the opposing lower molar and the one behind. This is the same occlusal relationship of the hypocone of typical stenodermines (e.g., *Artibeus*; Fig. 4, F). If the anterior basin cusp is the protocone and the lingual cusp is the hypocone, what could be the origin of the posterior basin cusp? To me it seems probable that it is the metaconule that remained behind when the paraconule moved labially. Reason: Although weakly distinguishable, there is an enamel ridge near the apex of the paracone which must represent the paraconule. On the other hand, there is no suggestion of participation of the metaconule in the metacone blade. This appears important when we remember that in all other stenodermines, the metaconule maintains its integrity longer and stronger than the paraconule. A similar condition has developed in M1 of canids (Fig. 4, A) in which the paracone and metacone lie at the labial border, and the hypocone lingual to the protocone; while the paraconule is small or absent, and the metaconule is positioned like that of the posterior basin cusp of *Brachyphylla*.

This dentition could not take origin from any known stenodermine. Any common ancestor of *Brachyphylla* and typical stenodermines would still have conules in normal position. Even though the development of the hypocone is stenodermine-like, the metaconule position of *Sturnira* more closely resembles that of stenodermines than *Brachyphylla*. The dentition therefore offers no evidence that *Brachyphylla* is any more closely related to stenodermines than *Sturnira*.

14

Icaronycteris is the only known bat that retains in its dentition all prerequisites prototypic of dentitions of all Vespertilionidae. Although each character that is considered primitive may be found in some vespertilionid, no single form retains all such characters.

14a The dentition of *Natalus* (Fig. 3, O) presents few changes from the primitive condition. It retains a root-supported protocone on P3 which is lost in most microchiropterans. Even so, it has lost all trace of conules from the upper molars and the metaconid from p4. There is no real hypoconulid but the postcristid is not directed to the entoconid (Fig. 2, KK).

An early *Natalus*-like form could possibly have given rise to the type of dentition presented by modern Thyropteridae by the loss of the root-supported protocone from P3 and the direction of the posteristid of the lower molars to the entoconid (Fig. 1, E).

14b Another branch from the more-or-less basal stock of the Vespertilionoidea gave rise to *Mystacina* and possibly molossid. The former has but two upper premolars, but both have functioning protocones (Fig. 3, M) Miller considers the most anterior to be P2 and the posterior, P4. In *Myotis*, P3 is the smallest upper premolar. It is highly probable therefore that in this lineage it is P3 that is often lost (e.g., *Plecotus*). However, I believe the missing premolar in *Mystacina* to be P2. A functional protocone is almost

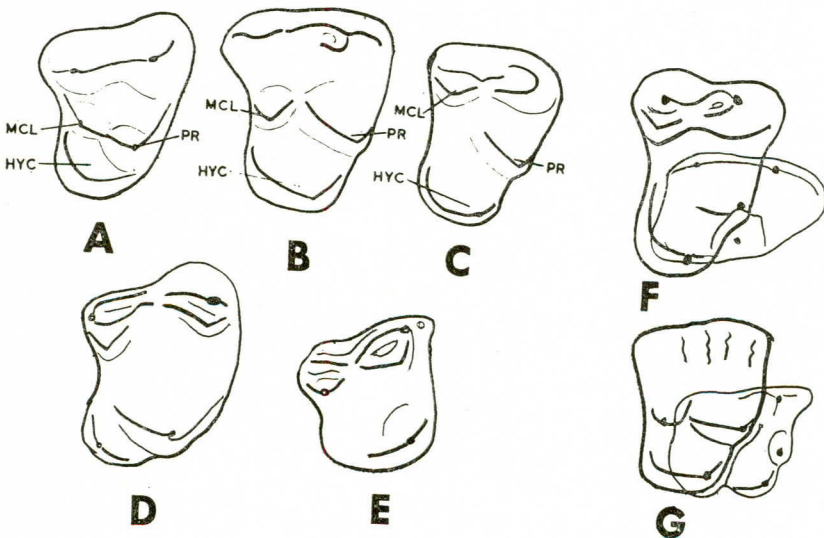


FIG. 4

- A. M2 of *Canis*;
- B. M2 of *Branchyphylla*;
- C. M2 of *Artibeus*;
- D. M2 of *Uroderma*;
- E. M2 of *Vampyrops*;
- F. M2 of *Artibeus* with m2 superimposed;
- G. M2 of *Brachyphlla* with m2 superimposed.

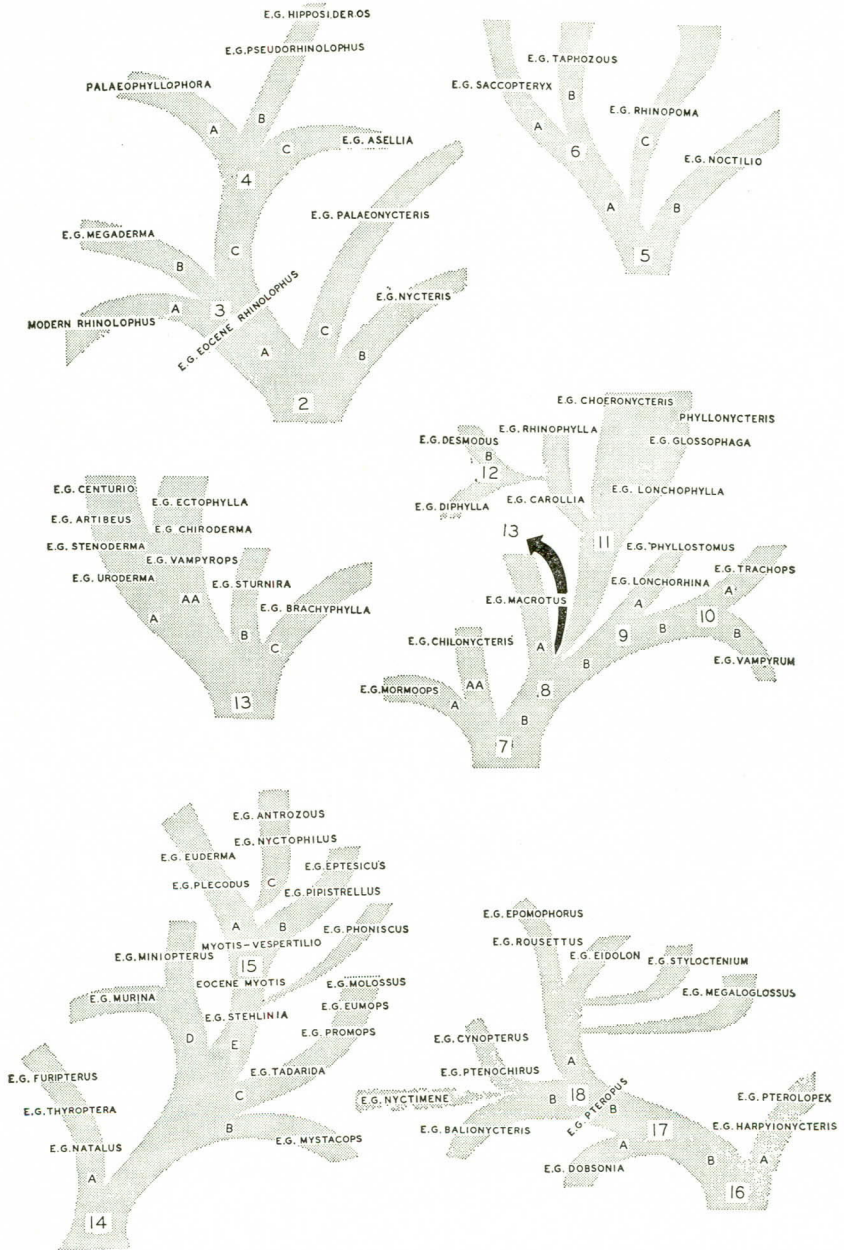


Fig. 5. Dental morphology tree suggesting types of dentition possessed by ancestral forms of chiropteran groups. Generic names are used merely to denote certain types and/or grades of dental forms.

never present on P2 of Chiroptera. Furthermore, in *Natalus*-like dentitions, emphasis seems to be placed more on P3 than P2. In any case, *Mystacina* retains two upper premolars with functional protocones, while it loses one upper and lower premolar. *Mystacina* has also lost one upper and one lower incisor, eliminating the genus from direct ancestry of the Molossidae. Even so, a *Tadarida*-like dentition could have originated from this branch prior to the reduction of the lower incisors. All that would be required would be the loss of the protocone from the anterior premolar. There are at least three character-trends demonstrated in modern molossids, indeed even within the genus *Tadarida*. In subgenus *T.* (*Tadarida*) the pre-metacrista of M3 is equal in length to the post-paracrista. Some species of *T.* (*Chaerophon*) have the pre-metacrista of M3 about half the length of the post-paracrista (Rosevear, 1965); and *T.* (*Mops*) has only a very short pre-metacrista on this tooth. The pre-metacrista is virtually lost in *Eumops* and *Promops*. The most anterior upper premolar of *T.* (*Tadarida*) is single-rooted but contains a strong cingulum completely around the crown, as also does *T.* (*Chaerophon*). The anterior upper premolar is smaller and crowded labial to the tooth row in *Eumops* and is reduced to a featureless point in *Promops*. *T.* (*Tadarida*) retains three bifid lower incisors (Fig. 3, J). *T.* (*Chaerophon*) has but two bifid lower incisors (Fig. 3, K). *Molossus* has extended all three of these trends one step further. There is no remnant of the pre-metacrista on M3, the anterior upper premolar is lost, and there remains but a single lower incisor in each ramus (Fig. 3, L).

- 14d *Miniopterus* and *Murina* are usually placed in separate subfamilies of the Vespertilionidae. Their dentitions appear to be at about the same grade of divergence from the basal type. Both have lost one upper premolar but the remaining two have retained functional protocones. Neither of the known forms could have given rise to the other, however. *Murina* has lost one lower premolar and the pre-metacrista from M3, while retaining a lingually placed paraconid and rudimentary metaconid on p4. *Miniopterus* retains all lower premolars and the pre-metacrista on M3, but p4 is relatively simple.
- 14e Another trend from the basic stock retains all upper premolars but only P4 has a functional protocone (Fig. 3, N). The Eocene form, *Stehlina Revilliod* (= *Nycterabius*=Revillioidea; Handley, 1955) would seem to be intermediate between the basic vespertilionid stock and the main-line members of the family, since it retains the maximum formula, like *Myotis*, has conules and hypo-

conulids, and P3 is double-rooted. P3 does not present a protocone on *Miniopterus*, however.

The genus *Myotis* is present in Europe by early Oligocene. All upper premolars were present but already single-rooted as in modern species. Most of the early species retained hypoconulids on the lower molars and conules on the upper molars. These are lost in all modern species of the genus. Quinet (1965) observed that the paraconid of p4 is better developed in Early Oligocene species (e.g., *M. misionnei*) than any modern myotid. I have observed in an occasional modern specimen of *Myotis* and *Vespertilio* rudimentary metaconids on p4. This is presumably atavistic, and was more common in the past.

15

- 15a The dentition of *Pipistrellus* is easily derivable from the *Myotis-Vespertilio* type. The minor change required is the loss of P3, great reduction of P2, and loss of p2. P2 is crowded lingual to the tooth row (Fig. 2, E).

The *Eptesicus*-like dentition may merely represent one further step along this trend for P2 is lost.

- 15b *Plecotus*-like dentitions also probably took origin from the *Myotis-Vespertilio* type. P3 is lost and P2 is reduced, although not extremely so and remains in line with the tooth row. It not only retains the maximum inferior dental formula but there is usually a faint trace of a metaconid on p4.

The dentition of *Euroderma* could originate from one like that of *Plecotus* by the loss of one root from p4. P2 is more reduced than in *Plecotus* but remains in line with the tooth row, unlike *Pipistrellus*.

- 15c The subfamily Nyctophilinae almost certainly took origin from within the Vespertilioninae. The group's basic form, *Nyctophilus* has a dental formula of 1/3; 1/1; 1/2; 3/3. Although both *Plecotus* and *Pipistrellus* trends have a tendency toward the loss and reduction of premolars, the known forms of the former present greater reduction of lower premolars before P2 is lost. Trend 15b, on the other hand, shows that p4 remains well developed and double rooted until after P2 is lost (e.g., *Eptesicus*). To be sure this subfamily arose from some derivative of the *Myotis-Vespertilio*-like forms and of the known forms some member of trend 15a seems most probable.

The only significant difference between the dentitions of *Antrozous* and *Nyctophyllus* is the loss of one incisor of the former.

MEGACHIROPTERA

The form of the skull, outer ear, eyes, and post-cranial skeleton of members of the Megachiroptera have departed less from that of normal terrestrial forms and in these regards must be considered rather primitive. On the other hand, the teeth of the suborder differ vastly from the primitive pattern, while that of insectivorous microchiropterans is virtually indistinguishable from that of tupaiids.

The dental patterns of all living megachiropterans are significantly different from those of microchiropterans, but within the suborder there is a basic theme, and all could easily have derived from a single divergence. The earliest known member of the Megachiroptera is *Archaeopteropus* (Meschinelli, 1902) from the Oligocene of Italy. It is a large form with a wingspread of some 18 inches and the characters of the post-cranial skeleton are typically megachiropteran except one; the second digit is somewhat reduced. The dentition is rather badly fragmented and little could be ascertained as to the actual pattern. It is said, however, to be somewhat different from modern members of the suborder; the cusps are relatively tall and conical, not unlike those of insectivorous microchiropterans. Meschinelli also says that one upper molar appears to be rather "quadrangular." This may suggest that the paracone and metacone had already migrated to the tooth's labial border, and that the great development of the hypocone had taken place.

One living megachiropteran, *Harpyionycteris*, has a dentition which could possibly fit these two vague observations. The cusps are indeed conical and relatively tall (Fig. 1, H). The paracone and metacone are at the labial border and upper molariform teeth are roughly quadrangular.

In the vast majority of the megachiropterans an antero-posterior ridge along the labial edge of the upper molars has absorbed the metacone (Fig. 1, I). The paracone is the tallest portion of the ridge. The protocone and hypocone are absorbed in the opposite, or lingual, ridge. Similar ridges on the lower molariform teeth include the protoconid and hypoconid labially and the metaconid and entoconid lingually. That the cuspid condition seen in *Harpyionycteris* is closer to the primitive condition is indicated by the fact that *Dobsonia*, *Nyctimene*, and sometimes *Cynopterus* have rudimentary metacones present in the form of small, weakly-developed accessory cusps on the posterior slope of the paracone. Likewise, *Dobsonia* and *Nyctimene* have rudimentary protostylids in a similar position on the posterior slope of the protoconids of p3. I have never seen protostylids or metastylids on the teeth of any microchiropteran.

16

It would seem, therefore, that any prototypic dentition to all of Megachiroptera would be rather like that of *Harpyionycteris* in that the cusps were tall and conical, that protostylids and metastylids may have developed on the lower molariform teeth, that the paracone and metacone had moved to the labial border of the teeth, and that there was great development of the hypoconal basin. The dental formula would be at least 2/2; 1/1; 3/3; 2/3. There are certain characters, however, that remove the exact dentition of *Harpyionycteris* from direct ancestry.

16a The paraconid is lost from the lower molars although it remains as a small, low anterior cusp on p4. Immediately behind this cusp is a tall protoconid, flanked postero-lingually by a well developed metastyle, and postero-labially by a well developed protostylid. There is no metaconid. The stylids are also important on lower molars, being as well developed as the other cusps.

Pterolopex presents a dentition unique to the Chiroptera (Fig. 3, H). Emphasis apparently shifted very early from the cuspid condition to one of broad U-shaped lophs. Minimal wear exposes considerable dentine, lending a rodent-like appearance to the molariform teeth. Peculiar as these patterns are, their origin is easily understood by comparison with *Harpyionycteris*. A partially worn upper molar presents a U-shaped, enamel-rimmed fossette opening labially. The ridge involves the paracone-protocone-hypocone and a cusp in the metastylar area (metastyle). In addition there is a low precingular ridge. Excluded from the fossette and low on the posterior slope of the paracone is a rudimentary metacone (compare with *Harpyionycteris*; Fig. 3, I). The lower dentition is also derivable from the *Harpyionycteris*-like form. There are two U-shaped lophs, the anterior opening to the rear, and the posterior opening forward. The anterior ridge is the larger, and involves the protostylid-protoconid-metaconid-metastylid. The posterior loph incorporates the hypoconid and entoconid, the former being more prominent. One real similarity between *Pterolopex* and *Harpyionycteris* is that a "secondary" trigonid has developed on p4 made up of the protoconid-protostylid-metastylid. There does not appear to be a metaconid present.

16b The trend leading to most megachiropteran dental types placed more emphasis on the precingular basin of the upper molariform teeth and the paraconid basin of lower molariform teeth (Fig. 1, I). The metacone, metastyle, and protostylid are much reduced.

17

There are no known forms with all of the prerequisite characters to

be prototypic to all remaining megachiropterans, but such a form must have been similar to *Dobsonia* and *Pteropus*. The dental formula would be that of *Pteropus*: 2/2; 1/1; 3/3; 2/3, and the lower incisors would still be trifold or bifid. The form of the molariform teeth were probably more like those of *Dobsonia*: precingular basins well developed and completely separated from the hypoconal basins. The metacone and protostylids are weak, but distinguishable as accessory cusps. 17a Form essentially like 17, but with dental formula reduced to 1/1; 1/1; 2/3; 2/3 (e.g., *Dobsonia*).

17b The precingular basin is less prominent than in 17a, but is still distinctly separated from the hypoconal basin by an elevated and notched paraloph, even on P3. The protolophid of p3 and p4 is interrupted. Although the paraconid basin is less pronounced, it is still very much in evidence.

18

A *Pteropus*-like dentition could well serve as prototypic dentition 18 with minor alterations: less reduction of P2, trifold or bifid lower incisors, and rudimentary metacones and protostylids, at least on P3 and p3.

18a This trend involves the complete merger of the protocone of P3 with the paracone. In *Eiodolon* p4 retains a shallow groove separating the metaconid from the protoconid, and this must be considered more primitive than p4 of *Rousettus* in which the protoconid and metaconid have completely consolidated, forming a single cusp. This dentition has, therefore, taken a slightly different route from the *Rousettus*-like forms. In *Rousettus* the gross shape of p4 is affected by the former presence of the metaconid, but there is no groove-separation from the protoconid. In this character, *Rousettus* is further from the primitive condition. The protocone and hypocone of M1 are still very much in evidence, however.

Epomophorus has lost M2 and m3, but has bifid lower incisors and is probably closer to *Rousettus* than *Eiodolon*, although all are closely related.

18b This trend is easily distinguished from 18a by its maintenance of distinct precingular basins on P3 and P4. The metaconid is in evidence on p3, either separated from the protoconid by a notch (e.g., *Ptenochirus*) or a flaring of the protolophid (e.g., *Balionycteris*).

That *Balionycteris* represents an early branch of the trend is evidenced by the presence of both upper molars; 2/1; 1/1; 3/3; 2/3. It is excluded from ancestry of similar forms, however, by the excessive reduction in size of M1 and loss of one lower incisor.

The dentition of *Ptenochirus* and *Cynopterus* are almost similar enough to demonstrate an ancestor-descendant relationship. Both have lost M2, but M1 is better developed than that of *Balionycteris*. The only significant difference between these two dentitions is the loss of one lower incisor in *Cynopterus*.

18bb Still another type of dentition belonging to this general group is represented by *Nyctimene*. It shares some characters with 4a: no precingular basin on P3, metaconid of p3 merely represented by a flare in the protolophid and not separated from the protoconid by a notch. It also shares characters with 18b: protocone of P3 separated from the paracone, and metaconid separated from the protoconid by notches. One character presented is unique to the group; there are no precingular basins or paraconid basins on any of the molariform teeth. This brings the paracone, protocone, protoconid, and metaconid to the anterior edge of the teeth. The dental formula is 1/0; 1/1; 3/3; 1/2. In spite of this curious combination of characters, *Nyctimene* is one of the very few modern forms that retains a rudimentary metacone on P3 and protolophid on p3. This suggests to me that *Nyctimene* may have taken origin from basal 18b stock.

The Macroglossinae, as represented by *Megaloglossus* maintain the maximum megachiropteran dental formula and bifid lower incisors. The teeth have been greatly reduced in size and simplified. Even so, the form of the teeth suggests a greater affinity with 18a: *i.e.*, no protocone or precingular basin on P3, but both well developed on P4, bifid lower incisors, metaconid of p4 separated from the protoconid. I suggest that the dentition of this subfamily could have taken origin from basal 18a stock.

Styloctenium with its globular enamel-less cheek teeth has cusps and loph rounded and subdued. There is enough form, however, to demonstrate that there is no precingulum or notch-separated protocone on P3. In this, it is similar to both *Nyctimene* and 18a forms. However, the protocone of P4 is notch-separated like 18a. It therefore appears probable that *Styloctenium*-like forms have arisen either from basal 18a stock or directly from a *Pteropus*-like form (4).

SUMMARY

It is now apparent that the basic eutherian pattern arose from something like that of *Kuehneotherium* of the late Triassic. The upper and lower molars form scalene triangles with the apex of the uppers lingual, and that of the lowers labial. The paracone, metacone, and stylar cusps of the upper teeth and the protoconid, paraconid, and metaconid of the

lowers are the same as those of chiropterans and other placental mammals. By mid-Cretaceous the protocone had been added to the upper molars and a three-cusped talonid to the lowers (*e.g.*, *Pappotherium*). It was from this type of tooth that all placental dental patterns arose.

It is still debated as to whether megachiropterans and microchiropterans have a common flying ancestor. Certainly, little evidence is offered by a study of the dentitions. The patterns of both can be traced within the suborders, but there are no chiropteran dentitions known which are intermediate between the two widely different types.

Several different species of the same genus of chiropterans often live in sympatry, utilizing micro-niches while maintaining essentially the same diet. This similarity of habits of sympatric animals with nearly identical gene-pools has led to extreme cases of parallelism and convergence, and severely limits the usefulness of dental characters for demonstrating taxonomic relationships. Even so, several trends developed, some of which are shared by relatively unrelated forms, and some of which are unique in certain groups. By taking each character separately and deciding which is primitive and which is derivative, a combination of characters can predict what dentitions were like in ancestral forms.

Megachiroptera:—The oldest known megachiropteran, *Archaeopterus*, from the Oligocene, apparently had already migrated the paracone and metacone to the labial border of the upper molars, but the cusps remained tall and conical. The lower molars probably had added a protostylid and metastylid, cusps unknown among the Microchiroptera. Another unique feature of megachiropterans is the molarization of p3. This has happened only in some ungulates among other eutherians. Very early in the evolution of this suborder the dentition evolved, in which the molars are divided into anterior and posterior portions by a notched paraloph above and a protolophid below. The shear, therefore, is transverse across the teeth while grinding action is restricted to the anterior and posterior basins. The only similar occlusal relationship developed by mammals are the premolars of certain leaf and fruit eating primates (*e.g.*, *Nasalis*) and the molars of docodonts, a Jurassic group currently believed to be related to monotremes.

Microchiroptera:—Insectivorous microchiropterans have dentitions very similar to certain insectivores (*e.g.*, *Tupaia*), although there are no known bats with the primitive placental dental formula. One upper incisor, and one upper and lower premolar had been lost in the earliest bat, or incipient bat. The earliest microchiropterans share certain inherited characters of the Insectivora, with the most primitive members of all placental orders: submolariform P3, P4, and p4 (premolar

molarization Stage II), conules on upper molars and hypoconulids on lower molars. These characters are therefore considered primitive. Some lineages maintain certain of the primitive characters while specializing and/or losing others. The different combinations of the retained or lost characters allow some tracing of trends of certain groups.

Icaronycteris is the only known bat that is still at Stage II in premolarization: I therefore consider its dentition the most primitive among the Chiroptera. As there seems to be an almost universal trend toward loss of incisors and premolars within individual groups, the mere dental formula offers some evidence of pathways of evolution only within a given lineage. The same result of face-shortening through simplification and loss of premolars sometimes takes different paths, however, and it is these that may be more useful in determining degrees of relationship. For example, among the Vespertilioninae *Murina* and *Miniopterus* one upper premolar is lost but the two remaining have protocones. The other members of the family maintain all three, but all are quite simple.

The trend toward reducing the angle of the shear of the molars by failure of the post-paracrista and pre-metacrista to reach the tooth's labial border has taken place in several groups independently: Emballonurinae (*Vespertiliavus*), Megadermidae (*Megaderma*), Phyllostomatidae (*Vampyrum*), and probably is related to a more omnivorous diet.

FUTURE WORK

The most desperate need for a better understanding of chiropteran evolution is the need for more and better fossil specimens from the early Tertiary. Even middle and late Tertiary material is much needed from the lower latitudes where most chiropteran evolution has taken place. Until these are forthcoming, however, there are many interesting and important studies involving dentitions. Comparatively, functional morphology as it relates to dietary habits has been neglected in most studies of bat dentitions. There is a limit to the number of dental patterns available to evolving animals and therefore convergence of types with similar dietary habits is often striking. This is a handy tool of the paleontologist attempting to ascertain everything possible about extinct groups. There are certainly applications of this type of exercise among the chiropterans. Examples: The oblique shear is clearly advantageous to insect mastication. It occurs in most microchiropterans, shrews, moles, tupaiids, and early therians. The anteroposterior shear, on the other hand, lends itself better to the slicing of meat (e.g., triconodonts, zeuglodonts, creodonts, and Carnivora). It is not too surprising, therefore, that the most anterior molariform tooth (m1) of the carnivorous

megadermatids is trending in this direction. Indeed, this tooth is very similar to p4 of primitive carnivores such as the miacids. In both, the paraconid becomes oriented anteroposteriorly (Fig. 2, L). In addition, the protocone of the opposing tooth is reduced to the point that its function is little more than as a shear-stop. In miacids p4 continues to "simplify" until the metaconid is lost, the tooth is essentially premolari-form again, and the same trend begins to develop in m1.

Unlike the insectivorous oblique shear and the carnivorous anteroposterior shear, the basic megachiropteran dental pattern presents a single, notched transverse loph on each molariform tooth. This is a unique mastication system among living mammals, but very similar to that of the Jurassic order Docodonta. Not only do the upper molariform teeth of docodonts have a single transverse shear per tooth, but also have both anterior and posterior basins (Fig. 2, N and Fig. 2, Q). This type of dentition differs much from that of the New World fruit bats (stenodermines). In these, most of the shearing is accomplished by the posterior premolars, each of which has a slightly oblique shearing ridge connecting the apex of the primary cusp to the anterolingual corner of the tooth. The elevated labial ridge of the upper molars may assist in cutting the skin of soft fruit, but has little rear shear against the lower dentition. The primary function of the molars seems to be a mashing action. Greenhall (1965) while discussing *Centurio* surmised that fleshy papillae of the lips and gums were used to strain mashed soft pulpy fruits and their juices. He observed that this bat sucks and strains food when fed bananas and the juices of other fruits. Megachiropterans, on the other hand, actually masticate and eat the fruit, the skin and meat of which is often rather tough (e.g., guava). This may account for the development of the transverse loph with fore and aft basins. In any case, the cheek teeth of Old World fruit bats and the premolars of certain frugivorous primates are similar enough to the cheek teeth of docodonts to suggest that the latter may also have fed on early fruits such as mango.

Other interesting questions might include: Was the blood-feeding habit of vampires an outgrowth of a carnivorous habit, or simply a shift from "bleeding" large fruit?

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