THE EVOLUTION OF BATS[1]

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Abstract: I develop the first explicitly justified phylogeny of the
known families of bats, using all available characters. This phylogeny
permits the adaptive evolution of the order to be outlined. Two main clades
emerge within the Microchiroptera and are called new infraorders, Vespertilionia
and Phyllostomatia. In each infraorder there is a series of grades of progressively
stronger flight, and there is a radiation of diet within the Phyllostomatia.
Parallel evolution is extensive. Most grades still exist, presumably by a
poorly understood partitioning of the resource space. The Megachiroptera may
have originated in the late Oligocene or early Miocene from surviving members
of the Eochiroptera (new suborder). The Kerivoulidae, Myzopodidae, Thyropteridae,
and Furipteridae are placed in the Natalidae, and the Icaronycterididae in
the Palaeochiropterygidae. The features of an ancestral bat are predicted.
Bat origins are poorly known but may be found in Paleocene members of the
Adapisoricidae.
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Bats constitute the second largest order of mammals and have a readily
decipherable adaptive history, at least compared with the Rodentia and Insectivora.
Nevertheless, there is no treatment of this adaptive history nor even a
general phylogeny, which must form its foundation. I noticed this lack when
revising a course on the paleobiology of mammals and undertook to remedy it.
Although I still lack much familiarity with bats, the result may be of more
general interest.

ORIGIN OF BATS

One may hypothesize that bats did originate, but it is harder to go
beyond this. Bats have no Archaeopteryx as yet. However, the suggestion of
Smith (1976, 1977) that bats are diphyletic is hard to take seriously. He
says that flight has originated independently in other animals, so why not
independently in the Megachiroptera and Microchiroptera? One needs do little
more than glance at members of these two groups to note the fallacy. All the
major external adaptations for flight are the same in these two groups, and
almost all differ from those of other flying animals. That the two groups
of bats differ from normal mammals in the same ways would itself be evidence
of monophyly even if there were much structural convergence of bats with
nonmammalian fliers. There is, perhaps, some conceivable shadow of doubt
(based on early fossils) that all the recent members of the Artiodactyla,
Perissodactyla, Primates, or Carnivora had a common ancestor which could
well be placed within the respective order. I see no basis for even such
flimsy doubt with respect to the Chiroptera. The earliest fossils of bats
lack the derived characters of both living suborders. Appendix 2 reconstructs
an ancestral bat by predicting its characters.
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     Leche (1886) and Weber (1928) proposed a special relationship between
bats and the Dermoptera, especially because their patagial musculature appeared
to be homologous and, moreover, different from that of other mammalian gliders.
Winge (1893, 1923) disputed this evidence. The evidence is important and needs
re-examination. Gregory (1910) repeated Leche's view and gave several other
resemblances between Dermoptera and primitive Chiroptera, but most of those
other resemblances are primitive rather than derived (as were some of Leche's).
Any relationship must be remote. The Plagiomenidae are good Dermopters in the
late Paleocene with very derived and unbatlike teeth. The Dermoptera seem to
have originated near the genus Elpidophorus, which occurs in the middle and
late Paleocene, and Rose (1975) has in fact transferred Elpidophorus to the
Plagiomenidae. Such an affinity does not remove the special resemblances of
Elpidophorus to the Mixodectidae, where it has customarily been placed (Szalay,
1969). Even the Mixodectidae are morphologically far from possible ancestors
of bats, and I (Van Valen, 1967) referred the whole family to the suborder
Dermoptera because of the mutual relationships of Elpidophorus.
     The Picrodontidae are a Paleocene family which has occasionally been
considered related to bats (Matthew, 1917) and even dermopterans (Romer, 1966),
the latter for no reason I can discover. Their molars do indeed rather vaguely
resemble those of some stenodermatine phyllostomatids, which are dentally among the
most derived bats. However, it is clear that this resemblance is convergent
(McGrew and Patterson, 1962) and that picrodontids are primates (Szalay, 1968).
A recent association of picrodontids with another primate genus, Phenacolemur
(Schwartz and Krishtalka, 1977), is also clearly based on convergence; in fact
the regions of the molar teeth which are similar are in part nonhomologous.
     Most dentally primitive bats have cheek teeth which resemble those of
the Tupaiidae. This resemblance is in part a derived one and is what Menu and
Sigé (1971) have called nyctalodonty (see also Van Valen, 1965). However,
although Icaronycteris is nyctalodont in the early Eocene, Ageina and
Archaeonycteris are not (Russell, Louis, and Savage, 1973). Therefore the
ancestral bat is unlikely to have been nyctalodont. A W-shaped ectoloph is
absent in Ptilocercus and therefore is presumably of independent origin in
tupaiines. The hypoconulid of Archaeonycteris is even less tupaiid-like than
is that of the adapisoricid Leptacodon.
     Except for the surviving tupaiids and dermopterans, no group of
Insectivora which could have been ancestral to bats is known from more than
teeth and associated jaw fragments. Because early Eocene bat teeth are not
particularly characteristic, being recognizable only by similarities in
details to teeth of more adequately preserved specimens, it is not yet
possible to specify any particular family as ancestral. Members of the
Adapisoricidae come closest, but this may be coincidental. (As I mentioned
when I established this family in its modern sense (Van Valen, 1967),
Adapisorex may well not belong to it but is the base of the oldest name.
I have not seen adequate adaptive justification for splitting the
Adapisoricidae into several families, although of course there are definable
subgroups as for any large family.)
     Moreover, there may well be Paleocene bats already named. Perhaps
Adapisoriculus is one, rather than a tupaiid. Perhaps other tupaiid-like
genera, or even something as primitive as Leptacodon, are bats or semi-bats.
Unfortunately we can't look to Batodon, of the last years of the Cretaceous,
because it is already too derived in other ways. And there is no reason yet
to place bat origins in the Cretaceous. As with whales, where the temporal
control is stronger (Van Valen, 1966, 1968; see Sahni and Mishra [1975] for a
morphologically intermediate form surviving to the middle Eocene), evolution
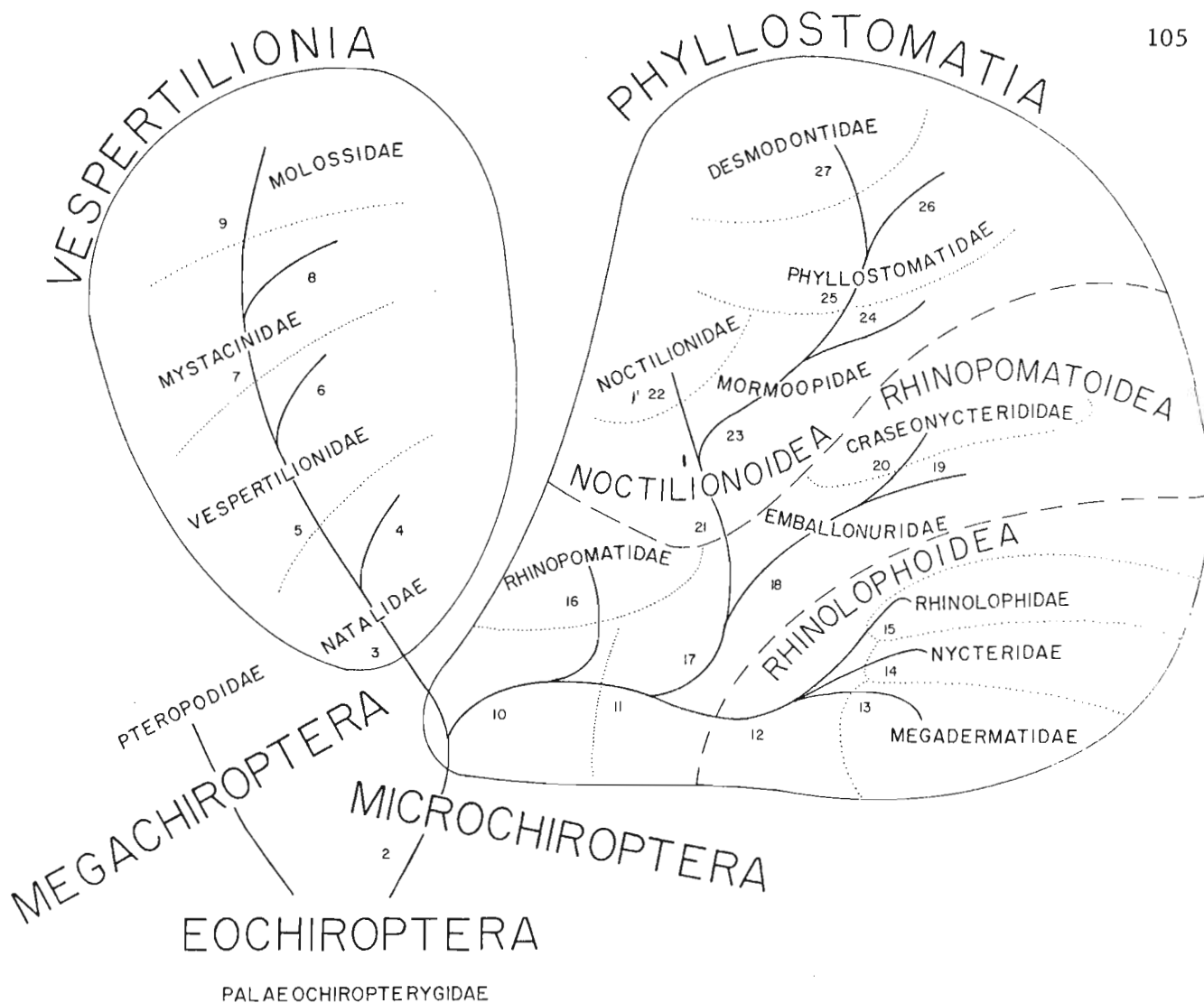can proceed rapidly when there is a major change in adaptive zone.

Figure 1. Phylogeny of the known families of bats. The numbers refer to lists of characters in Appendix 1. Infraorders, superfamilies, and families of the Microchiroptera are separated by solid, dashed, and dotted lines respectively.

*   *   *

PHYLOGENY OF BATS

The phylogeny (Figure 1) is based on all characters I found for which a primitive-derived polarity could be established (for criteria see Van Valen, 1978), for which enough information was available for two or more related families, and which were consistent within families unless additional changes occurred within families. For many characters, notably most characters of muscles, I was unable to establish polarity. Tooth number, often given a prime place in bat classifications, I found too variable within families to be of much help, especially when extinct genera are considered. Nevertheless I used such characters whenever possible.

The numbers in the figure refer to the character changes listed in Appendix 1. Unless modified farther along a branch, all character changes apply to all families listed beyond the position of the number. The changes apply to the inferred condition of the initiator (latest common ancestor) of a clade unless otherwise noted, and they may not apply to all members of a single family if there is further evolution in that family.

The justification for the phylogeny is found in the lists of character changes. Some aspects of the phylogeny are insecurely based. The position of the Craseonycteridae (Hill, 1974) as a descendant of primitive emballonurids is open to doubt; <u>Craseonycteris</u> may instead be specially related to the Rhinopomatidae, as Hill thought. In either case there is appreciable parallel

TABLE 1. Derived characters shared by each pair of families of the Rhinolophoidea

Rhinolophidae and Megadermatidae
       bony circle of thorax complete
       nose leaf
       head of humerus oval or elliptical
       infraspinous fossa of scapula divided by sharp ridge
       $I_{\underline{3}}^{3}$ lost
Rhinolophidae and Nycteridae
       phalanx 1 of finger 2 cartilaginous or lost
       sacrum dorsoventrally flattened
       ischium and pubis reduced
       pelage hairs lack medullae (Benedict, 1957)
Nycteridae and Megadermatidae
       fibula-calcaneum articulation lost
       proximal half of fibula lost, distal half threadlike or lost
       acromion process of scapula with thin spine projecting ventrolaterally
       P^3 lost (retained in Oligocene rhinolophid _Palaeonycteris_; P_3 retained
          in Oligocene megadermatid _Necromantis_)

   *   *   *

evolution. Similarly, the Rhinolophoidea and Emballonuridae may not be
phyletically closer to the phyllostomatid stem than to the Rhinopomatidae.

The mutual relationships within the Rhinolophoidea are too confused to
justify any preference. Here too there has been much parallelism. The
respective numbers (13, 14, and 15) in Appendix 1 refer only to character
states unique to each family. Table 1 gives, for each of the three possible
combinations of two families, a list of shared derived characters. A suitable
choice of characters would give a good justification for each of the three
possibilities. I see no basis for rejecting any of the three combinations,
much less for preferring one above the others.

I have examined few specimens of bats critically, so my reliance on the
literature may be greater than desirable. Unless there is some reason to
question a character, or it is probably not well known, I do not give specific
references for each character. I used the following sources in obtaining
characters: Barghoorn (1977); Benedict (1957); Dal Piaz (1937); Dechaseaux
(1958); de Fenis (1919); Goodwin and Greenhall (1961); Grassé, Bourlière,
Heim de Balsac, and Viret (1955); Heller (1935); Hill (1974); Kingdon (1974);
Koopman and Cockrum (1967); Lanza (1959) Lawlor (1967); Menu and Sigé (1971);
Miller (1907); Murray and Strickler (1975); Revilliod (1917, 1917-1922);
Russell, Louis, and Savage (1973); Russell and Sigé (1970); Sigé (1971, 1974);
Slaughter and Walton (1970, all volume); Smith (1972); Starck (1959); Storch
(1968); Strickler (1978); Thomas (1904); Vaughan (1966); Vaughan and Bateman
(1970); Walton and Walton (1968); Wimsatt (1970, 2 volumes); Winge (1941,
translation of 1914, based on 1893).

POSITION OF THE KERIVOULINAE

Apart from the very existence of a justified phylogeny, the only major
innovation in Figure 1 is the allocation of the Kerivoulinae. These small
insectivorous bats are variably common, usually in forests, from West and
South Africa to Australia. One genus (sometimes two) and about two dozen species
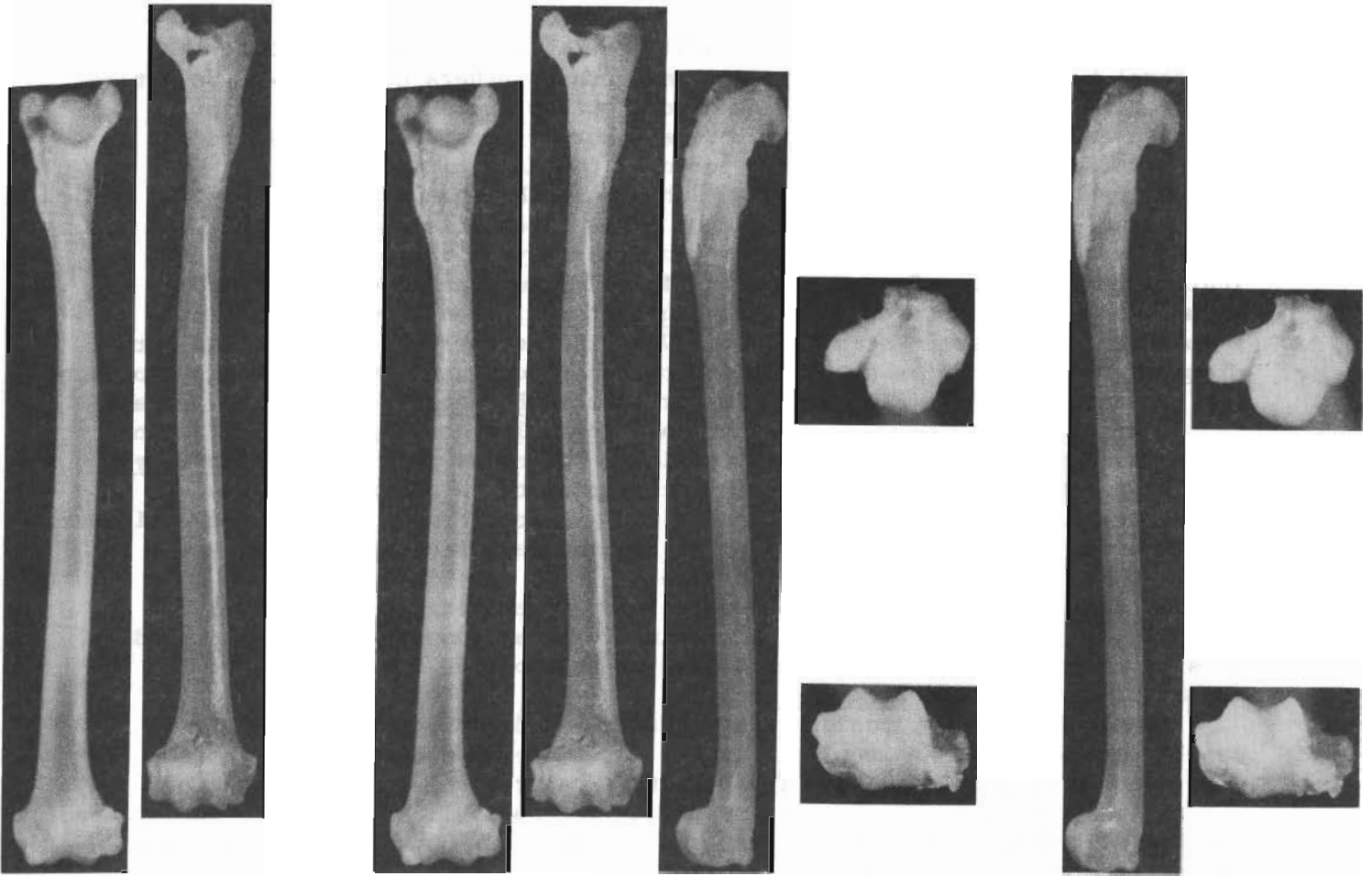
Figure 2.   Right humerus of <u>Kerivoula</u>,   stereophotographs.

*   *   *

are recognized. Since Miller's (1907) establishment of the modern classification
of bats they have been placed in the Vespertilionidae.

However, Sigé (1974) recently separted the Kerivoulidae as a distinct
family, placing in it <u>Stehlinia</u>, which is known from the middle Eocene to early
Oligocene of Europe. He noted some degree of resemblance to the Natalidae but
failed to support the new family adequately. I have dissected a specimen of
<u>Kerivoula</u>, <u>K</u>. <u>papillosa</u> by the key of Dobson (1878), and show its humerus in
Figure 2. The specimen is number 46607 in the Field Museum collection, from
Ban Me Thuot, Vietnam. Van Peenan (1969) also cited the species from this
locality from Field Museum specimens.

The trochiter is intermediate in size between those of <u>Natalus</u> and
vespertilionids, as in the trochiter of <u>Thyroptera</u> figured by Smith (1972).
However, as in natalids, <u>Kerivoula</u>'s trochiter extends proximally beyond
the head of the humerus for a distance less than half its anteroposterior
width. The epitrochlea is also intermediate in size (larger in the otherwise
similar humerus of <u>Stehlinia</u>), while the capitellum remains relatively wide.
The head of the humerus is nearly round. <u>Kerivoula</u> also lacks other derived
features of vespertilionids as indicated in the Appendix, and shares most of
the derived features common to recent natalids.

CLASSIFICATION OF BATS

Several modifications in bat classification seem to be desirable. The
ancestral bats (Palaeochiropterygidae and perhaps others now unknown) do not
fit readily into either existing suborder, both of which have made major
adaptive changes. I therefore propose a suborder Eochiroptera, defined as
bats insufficiently derived to be placed in the Megachiroptera or
Microchiroptera, the characters of which are in the Appendix.

Russell and Sigé (1970) lumped the Archaeonycter(id)idae into the
Palaeochiropterygidae as a subfamily, and I hereby do the same for the
Icaronycter(id)idae. Icaronycteris is in different characters both more
primitive and more derived than Palaeochiropteryx, even reportedly having
a small scapulohumerus catch (Jepsen, 1966) in the early Eocene. I have not
examined the specimen as to this point but am unconvinced by published photographs.
The presence of only a single sacral vertebra in Palaeochiropteryx and perhaps
Cecilionycteris is equally startling, only Perameles sharing this trait among
known mammals or therapsids. However, it is not clear that Palaeochiropteryx
and Icaronycteris are adaptively distinct enough to be separated at the
family level. The familial position of the Archaeopteropodinae remains ambiguous,
but I retain "them" (one specimen known) in the Palaeochiropterygidae until
they are better known. Propotto Simpson
(1967), from the early or middle Miocene, is a pteropodid (Walker, 1969)
known from lower teeth a little more primitive than those of recent pteropodids.
It supports a relatively late derivation of pteropodids from persistent
eochiropterans such as Archaeopteropus.

Similarly, the Myzopodidae, Furipteridae, and Thyropteridae can all
easily rest with the Kerivoulinae in the Natalidae as subfamilies. In fact
most used to be placed there. The resulting pantropical family is not more
diverse adaptively than is the Pteropodidae or the Phyllostomatidae. The Myzopodinae
are the most divergent of the recent subfamilies, but of these none of these
subfamilies approach the vespertilionid grade closely.

Mein and Tupinier (1978) have recently proposed that the vespertilionid
subfamily Miniopterinae be raised to the rank of a family. The characters they
discuss do not justify such a change; they are adaptively minor and phyletically
uninformative. The group (on which see mainly Lanza, 1959, and Barbu, 1960)
contains strong fliers with humeri and coracoid process approaching the grade
of the Mystacinidae. In Miniopterus, like molossids and most other mammals but
unlike other vespertilionids, fertilization follows copulation immediately rather
than the sequence being interrupted by hibernation. The Mystacinidae may well
have come from miniopterine-like vespertilionids.

I do not accept placement of the Desmodontidae in the Phyllostomatidae,
mainly because of the large adaptive shift of each family. They diverged from
an insectivorous diet in different directions. Additionally, the characters in
26 (Appendix), notably the uterus, indicate that the recent members of these
families had separate ancestries rather than the Desmodontidae being an exgroup
from the known diversity of the Phyllostomatidae. The opposite conclusion of
Forman, Baker, and Gerber (1968) is based on similarities rather than directions
of evolution; they did not distinguish primitive states. Their immunologic
evidence is from whole-serum comparisons and therefore confounds differences
in proteins with amounts of proteins; this method also assumes constant evolutionary
rates. The genera they found most similar to desmodontids are far from those
with the most similar teeth. Slaughter (1970) and Smith(1976) based their
phylogenies on the teeth, which give the only available, but weak, evidence
against a separate ancestry of the known members of the two families.

TABLE 2. Classification of bat families.

Order Chiroptera
    Suborder Eochiroptera
        Family Palaeochiropterygidae (including Archaeonycter(id)idae
            and probably Icaronycter(id)idae and Archaeopteropodinae as
            subfamilies)
    Suborder Megachiroptera
        Family Pteropodidae
    Suborder Microchiroptera
      Infraorder Vespertilionia
        Superfamily Vespertilionoidea
        Family Natalidae (including Kerivoulidae, Myzopodidae,
            Thyropteridae, and Furipteridae as subfamilies)
        Family Vespertilionidae
        Family Mystacinidae
        Family Molossidae
      Infraorder Phyllostomatia
        Superfamily Rhinopomatoidea
        Family Rhinopomatidae
        Family Emballonuridae
        Family Craseonycter(id)idae
        Superfamily Rhinolophoidea
        Family Rhinolophidae (including Hipposideridae as subfamily)
        Family Nycter(id)idae
        Family Megadermatidae
        Superfamily Noctilionoidea
        Family Noctilionidae
        Family Mormoopidae
        Family Phyllostomatidae
        Family Desmodontidae

   *   *   *

The two main clades of the Microchiroptera differ on the whole adaptively
as well as phyletically, although there is some parallelism. I therefore
propose the infraorders Vespertilionia and Phyllostomatia for these clades. They are
defined by inclusion (in Figure 1) and by the characters under 3 and 10
respectively in Appendix 1. It has become good practice to call members of
the orders Carnivora and Insectivora carnivorans and insectivorans respectively,
to distinguish them from other carnivores and insectivores. I suggest that
members of these bat radiations be referred to as vespertilionians and
phyllostomatians.

    Unfortunately the names of two superfamilies must be changed by Article
36 of the rules. According to Palmer (1904) and Simpson (1945), Noctilionidae
Gray (1821) antedates Phyllostomatina Gray (1825) and Rhinopomatina Bonaparte
(1838) antedates Emballonurina Gervais (1855). Their superfamilies must therefore
be called Noctilionoidea instead of Phyllostomatoidea, and Rhinopomatoidea
instead of Emballonuroidea, if their contents are as in Figure 1 and in other
recent papers. If the Noctilionidae were returned to the "Emballonuroidea,"
the latter would become Noctilionoidea. However, such potential ambiguity
seems to be required.

    Many taxa are paraphyletic, which reflects the progressive evolution of
grades of adaptation in both microchiropteran infraorders. I have discussed the
general topic of paraphyly elsewhere (Van Valen, 1978).

    A summary of the classification appears as Table 2.

ADAPTIVE EVOLUTION OF BATS

By their evolution of flight, bats escaped almost all predation as well as gaining a more diverse supply of insects. Bats are occasionally eaten, but it is surprising that there are so few species which normally prey on bats (a megadermatid or two, <u>Vampyrum</u> <u>spectrum</u> [Peterson and Kirmse, 1969], and the hawk <u>Macheiramphus</u> <u>alcinus</u> [Lang and Chapin, 1917]). Bats thereby can live several times as long as other mammals their size (Gillette and Kimbrough, 1970).

Although the time bats became bats can't yet be specified, their early evolution was undoubtedly rapid. Their later near stagnation, in terms of most major evolution, is too well known to elaborate. There is even a fully developed molossid in the middle Oligocene, of a still surviving genus (Sigé, 1971). However, the ostensibly late origin of the Megachiroptera (<u>contra</u> Sussman and Raven, 1978) is perhaps relevant to their ecologically vicariant replacement by phyllostomatids in the neotropics. The only known pre-Pliocene phyllostomatid is well within the phyllostomatid radiation (Savage, 1951; Slaughter, 1970; Smith, 1976) and so gives only an upper bound (late Miocene) on the time of origin of this family.

Most of the characters in Appendix 1 can be used directly in determining major adaptive changes in bat evolution. I will merely summarize some of the more obvious of these, but it is necessary to emphasize that a good phylogeny is a prerequisite to any such study.

The lower branches of each part of the phylogeny are composed of relatively slow and maneuverable fliers, while most of the higher branches are composed of faster and more enduring fliers. Hoverers occur sporadically in the latter group (cf. also Peterson and Kirmse, 1969), a conclusion agreeing with Clark (1977) rather than with Pirlot (1977).

However, each kind of flight (and the apparently more direct flight of megachiropterans) is advantageous for different purposes and all can coexist. Therefore, although there is a series of evolutionary grades within each microchiropteran infraorder, for the most part the grades are not progressively better ways of filling the same adaptive zone. Thus members of most grades are still with us. The Microchiroptera seem an even better example of this phenomenon than the Primates, although in the latter case the ancestral suborder can reasonably be said to survive.

In many bats the trochiter (greater tuberosity) of the humerus extends past the head of the humerus into the shoulder-joint capsule. The scapula catches it on the upstroke and automatically prevents overswing. This important mechanism seems to have evolved at least six times in the Microchiroptera (clades 3, 12, 16, 20, 22, and 25 of Figure 1). It is not equally developed in all six clades, but the same structures participate in the same way in each.

Parallel evolution occurs extensively in other aspects of bat evolution also, but there are usually enough characters available to identify it. This has not been possible for the Rhinolophoidea and perhaps the Craseonyter(id)idae, for both of which groups several characters must have evolved in parallel.

Gillette (1975) gave an interesting analysis of the probable nature of the adaptive transitions in bat diets. In most cases he found some evidence for surviving intermediate stages. My phylogeny supports his ideas, which could be extended to those megadermatids and phyllostomatines which are carnivores.

The Noctilionidae, Megadermatidae, Phyllostomatidae, Desmodontidae, and Pteropodidae are separated adaptively by diet and (Pteropodidae-Phyllostomatidae) by ecologically vicariant replacement. The Rhinopomatidae may survive by their

desert adaptations, while most of the remaining eight families seem to partition a generally similar array of food in ways that need to be discovered in detail. The ground-foraging of rhinolophoids is a partial exception, and the narrow distribution of the bumblebee-sized Craseonycterididae (the smallest recent mammals: Lekagul and McNeely, 1977) suggests another partial exception. We may infer that the Molossidae do about what the Mystacinidae do, only better, and have outcompeted them except for a refuge in New Zealand, which lacks molossids as yet. Mystacina itself is a very derived mystacinid, eating much fruit when seasonally available (as well as arthropods all year) and spending much time on the ground and climbing. Such habits are probably related to the absence of native terrestrial mammals. Mystacina itself might survive a molossid invasion, but its more normal relatives elsewhere probably succumbed.

The concentration of bats in the tropics is presumably related to the greater diversity of food there and its availability at all seasons (Wilson, 1974; Findley, 1976). Wilson (1974) showed that the number of approximately coexisting bat species rises rapidly and exponentially from southern Canada to northern South America, although it then levels off. The remainder of the Mammalia show no latitudinal trend in diversity at all in this region, a fact which deserves to be better known. The extraordinary exponential increase in bat diversity should be tested for other continents when data become available.

APPENDIX 1: Derived characters of the initiators of clades numbered in Figure 1.

1: MEGACHIROPTERA, Pteropididae
     Old World
     angle of mandible reduced or less discrete
     molar dilambdodonty lost, with loss of mesostyle, stylar shelf, and crests
     large molar hypocone
     large basin between molar hypocone and protocone
     large molar metastylid and protostylid
     large central basin lower molars
     I_{1-2} lobed
     I_3 lost
     temporalis musculature reduced
     diet of fruit
     dorsal part of premaxilla lost
     neocortex, neothalamus, and neocerebellum enlarged (Henson, 1970)
     vomeronasal organ lost (Suthers, 1970)
     humerus somewhat S-shaped (perhaps primitive)
     5 sacral vertebrae, urostyle-like
     ischia fused together
     sternebrae fused into single bone (unfused in Icaronycteris)
     mesosternum with keel
     deciduous teeth reduced, modified for clinging

2: MICROCHIROPTERA, undiscovered family
      echolocation by ultrasonics from larynx
      middle-ear muscles enlarged
      cochlea enlarged and acoustically isolated from skull (Henson, 1970)
      inferior colliculi and auditory medulla enlarged
      pinna interrupted anteriorly; tragus present
      dorsal roots of spinal nerves enter spinal cord at dorsal ("posterior")
         sulcus (Henson, 1970)
      spinal cord shortened (Henson, 1970)
      falx cerebri lost (Henson, 1970)
      finger 2 rather closely appressed against finger 3 and totally included
         in wing membrane, its phalanx 3 lost
      trochiter (greater tuberosity) and trochin (lesser tuberosity) of
         humerus somewhat enlarged
      pectoral and deltoid ridges of humerus united into single large flange
         (also true of known eochiropterans except perhaps Archaeopteropus,
         but not of Megachiroptera or other mammals)
      fibula reduced
      molar hypoconulid far lingual, with sharp, straight postcristid to
         hypoconulid (nyctalodonty)
      sternebrae fused into single bone
      mesosternum with keel
      deciduous teeth reduced, modified for clinging
      nocturnal habits
      vision reduced; optic system of brain reduced (Schneider, 1957)

3: VESPERTILIONIA, Vespertilionoidea, Natalidae
      trochiter extends past head of humerus into shoulder-joint capsule,
         forming catch with scapula
      supraglenoid fossa in proximal end of humerus
      trochlea at distal end of humerus well developed
      epitrochlear process of humerus present
      distal trochlea of humerus displaced outwards
      phalanx 3 of finger 2 lost
      fibula-calcaneum articulation lost
      postorbital process lost (present in at least Cecilionycteris of the
         Eochiroptera)
      premaxillae fused to maxillae
      postprotocrista of M^{1-2} obsolete before reaching metacone
      musculus omohyoideus lost (Strickler, 1978)
      musculus pectoralis abdominalis inserts distal to apex of deltopectoral
         crest of humerus
      musculus brachialus inserts on radius, ulna being too reduced
      pelage hairs lack medullae (Benedict, 1957)

4: RECENT NATALIDAE
      skull strongly saddle-shaped, with marked supraorbital concavity in
         lateral view (even in Eocene Stehlinia, but less so in Myzopodinae)
      gap between I^2s
      pinnae funnel-shaped (except Myzopodinae)
      hind foot small
      phalanx 1 of finger 2 lost or cartilaginous (except probably Kerivoulinae)
      thumb reduced (except Myzopodinae)
      paracone and ectoloph dominate upper premolars

5: VESPERTILIONIDAE
  slow, maneuverable flight changed to faster, more enduring flight
  trochiter extends proximally beyond head of humerus for greater distance
      than anteroposterior width of trochiter
  trochiter appreciably larger than trochin
  catchment surface of trochiter on scapula definitely more than half as
      large as glenoid fossa of scapula
  articulation of supragenoid fossa of humerus and supraglenoid process
      of scapula well developed
  head of humerus oval, with oblique axis
  distal tip of coracoid process directed posterolaterally or posteriorly
  epitrochlea of humerus narrow
  capitellum narrow, scarcely external to axis of shaft of humerus
  musculus omocervicalis inserts onto acromion process of scapula, not
      onto clavicle (Strickler, 1978)
  tail somewhat reduced
  allantoic vesicle reduced
  no thermoregulation during day

6: RECENT VESPERTILINIDAE
  palatal part of premaxilla absent, leaving gap between I^2s
  epitrochlea of humerus obsolete (except Miniopterinae)
  shaft of ulna much reduced
  sperm stored during hibernation, where this occurs (except Miniopterinae)

7: MYSTACINIDAE
  catchment surface of trochiter on scapula nearly as large as glenoid
      fossa of scapula
  capitellum tilted diagonally
  epitrochlear process long
  incipient bridge of bone over infraspinous fossa of scapula
  uropatagium short, propatagium reduced
  foot short and broad; claws enlarged; pelvis robust
  fibula secondarily enlarged
  last cervical and first dorsal vertebrae fused
  I^3, $P^{?2}_{?3}$ lost
  postcingulum M^{1-2} moderately large

8: RECENT MYSTACINIDAE
  New Zealand
  trochin enlarged
  very terrestrial habits (Dwyer 1960, 1962)
  phalanx 1 of finger 3 folded inwards beneath wing at rest (Dwyer 1960, 1962)
  claws of thumb and toes with accessory basal talon
  eat fruit in season
  7 sacral vertebrae
  velvet- or shrew-like fur
  tail reduced
  pelvis elongate
  complete bridge of bone over infraspinous fossa of scapula

9: MOLOSSIDAE
    wing narrowed
    greater trochanter of femur larger than lesser trochanter and with
      hook-like process
    coracoid process of scapula faces medially
    musculus coracobrachialis lost and coracoid head of musculus biceps
      brachii enlarged
    some hairs on muzzle have spoon-shaped tips
    phalanx 1 on finger 3 folded above wing at rest
    palatal part of premaxilla reduced
    tragus reduced
    toes 1 and 5 with fringe of bristles
    hemochorial placenta (Starck, 1959)

10: PHYLLOSTOMATIA, Rhinopomatoidea, undiscovered family
    preorbital region of skull reduced
    protocone lost P^3
    hypocone (or at least relatively large postcingulum) M^{1-2}
    pair of pubic nipples

11: Emballonurid-rhinolophoid stem
    distal epitrochlear process present
    phalanx 2 of finger 2 lost
    tail somewhat reduced
    musculus brachialis inserts on radius, ulna being too reduced

12: RHINOLOPHOIDEA
    Old World
    trochiter extends past head of humerus into shoulder-joint capsule and
      forms catch with scapula
    thoracic ring (presternum, first rib, last cervical and first thoracic
      vertebrae) incipient
    capitellum displaced outwards
    dorsal part of premaxilla short or absent
    postcingulum M^{1-2} enlarged
    musculus latissimus dorsi with double insertion (Strickler, 1978)
    musculus subclavius arises partly from episternum

13: MEGADERMATIDAE
    upper C procumbent and with large secondary cusp
    M_1 paralophid relatively anteroposterior
    carnivorous, usually now and probably primitively so
    premaxilla lost
    tragus bifid

14: NYCTERIDAE
    fibula lost completely
    tail with skeletal crossbar at end
    premaxillae fused to maxillae and to each other
    skull with large depression between orbits
    musculus subclavius inserts onto coracoid process of scapula
    partitioned chamber in flesh of nose, possibly derived from nose leaf

15: RHINOLOPHIDAE
     trochiter forms well-developed catch with scapula
     supraglenoid fossa in proximal end of humerus
     postorbital process lost
     premaxilla spatulate, with large lateral gap in palate between it and
        maxilla
     phalanx 1 of finger 2 lost
     ilium shortened
     tragus lost
     musculi omocervicalis and omohyoideus lost

16: RHINOPOMATIDAE
     Old World
     calcar lost
     slight scapulohumeral catch (fide Winge and Hill)
     large auditory bulla
     muzzle swollen, with ridges
     mostrils slitlike, with valves
     postorbital process lost
     I^3_3, P^{2-3} lost
     small noseleaf-like structure

17: Emballonurid-noctilionoid stem
     slow, maneuverable flight changed to faster and more enduring flight
     fibula-calcaneum articulation lost (Walton and Walton, 1970)
     sacrum resembles urostyle
     pelage hairs lack medullae (Benedict, 1957)

18: EMBALLONURIDAE (family should perhaps extend as far back as 11)
     palatal process of premaxilla short or absent
     space between I^2s
     postprotocrista of M^{1-2} lost

19: RECENT EMBALLONURIDAE
     basioccipital pitted
     phalanx 1 of finger 2 lost
     phalanx 1 of finger 3 folded above wing at rest
     head of humerus oval
     P^3_3 lost (retained in Oligocene Vespertiliavus)
     pubic nipples lost

20: CRASEONYCTERIDIDAE
     southeast Asia
     apparently hovering flight
     deltopectoral crest of humerus nearly lost
     calcar lost
     postorbital process lost
     trochiter extends past head of humerus and is caught by scapula
     capitellum slightly offset from axis of humerus
     very long finger 3
     muzzle swollen
     minute size
     pelvis reduced
     I^3_3, P^{2-3}_3 lost
     proximal half of fibula lost, distal half threadlike

21:   NOCTILIONOIDEA, perhaps early Mormoopidae
      New World
      trochiter extends past head of humerus
      trochin enlarged
      head of humerus oval
      capitellum at least slightly offset from axis of humerus
      infraspinous fossa of scapula divided by sharp ridge
      postorbital process lost
      premaxillae fused to maxillae and to each other
      I_3, P^2 lost
      pubic nipples lost
      posterior part of musculus pectoralis profundus inserts together with
          anterior part and with musculus clavodeltoideus
      dermal bumps below lips

22:   NOCTILIONIDAE
      although smaller than trochin, trochiter extends into shoulder-joint
          capsule and forms slight catch with scapula
      feet very large
      take prey (fish or insects) from water
      cheek pouches
      postcrista bypasses hypoconulid to reach entoconid (myotodonty)
      palatal part of premaxilla reduced
      I_2, P^3_3 lost
      ischia fused together and to sacrum
      proximal half of fibula cartilaginous

23:   MORMOOPIDAE
      supraglenoid fossa in proximal end of humerus
      postprotocrista of M^{1-2} obsolete or lost

24:   RECENT MORMOOPIDAE
      femoral trochanters reduced
      musculus brachialis, intrinsic muscles of hand, and muscle elasticity
          reduced
      lips with well-developed folds
      pinna extends anteriorly beneath eye
      prolonged flight

25:   PHYLLOSTOMATIDAE
      enlarged trochiter extends past head of humerus into shoulder-joint
          capsule and forms catch with scapula
      distal epitrochlear process reduced
      nose leaf present (absent, apparently secondarily, in a few)
      allantoic vesicle reduced

26:   RECENT PHYLLOSTOMATIDAE
      nose leaf enlarged
      distal epitrochlear process lost
      uterine horns joined to form simplex uterus
      most are plant-feeders (not a basal adaptation here)

27: DESMODONTIDAE
    feeding and digestive adaptations for vampirism
    fibula secondarily enlarged
    ischia fused together
    femur laterally compressed, its trochanters enlarged
    head of humerus secondarily round
    thumb enlarged
    calcar and tail lost, uropatagium reduced
    musculus omohyoideus lost
    allantoic vesicle lost (fide Starck, 1959)

APPENDIX 2: Predicted features of an ancestral bat

A. Common to most or all bats but differing from ancestral Insectivora:
    1. Forelimbs modified into wings (with many associated aspects in forelimbs
        and elsewhere).
    2. Hind limbs rotated laterally for support of wings (with several
        associated aspects).
    3. Body short and broad.
    4. Cervical ganglia enlarged.
    5. Calcar present.
    6. Scaphoid and lunar fused.
    7. I^1 and $P^{?1}_{?1}$ lost.
    8. Caecum small.
    9. Gestation time 6 weeks or longer.

B. Primitive states of some characters varying among bats:
    1. Phalangeal formulae 2-3-3-3-3 for manus and pes.
    2. Finger 2 separate from finger 3 in wing, its last phalanx or two not
        in membrane.
    3. Slow flight; wing relatively broad anteroposteriorly.
    4. Ulna unreduced.
    5. Humerus straight.
    6. Humerus lacks epitrochlear process.
    7. Epitrochlea of humerus relatively wide.
    8. Trochlea at distal end of humerus not well developed or displaced outwards.
    9. Humerus lacks supraglenoid fossa.
    10. Pectoral and deltoid ridges of humerus separate.
    11. Trochiter (greater tuberosity) and trochin (lesser tuberosity) of humerus
        small for bats; no scapulohumerus catch.
    12. Head of humerus round.
    13. Coracoid process of scapula extends laterally.
    14. Infraspinous fossa of scapula undivided.
    15. Musculus brachialis inserts on ulna.
    16. Musculus pectoralis abdominalis inserts proximal to apex of "deltopectoral
        crest" of humerus.
    17. Musculus omocervicalis inserts onto clavicle.
    18. Musculus omohyoideus present.
    19. Ischia not fused together.
    20. Fibula articulates with calcaneum.
    21. Tail long.
    22. All vertebrae unfused except for sacrum of 1 to 3 vertebrae.
    23. Sternebrae unfused.
    24. Ribs unfused.
    25. Mesosternum unkeeled.

26. Postorbital processes present.
27. Skull relatively elongate.
28. External ear simple, its margin forming a complete ring around meatus.
29. Premaxillae complete and discrete, unfused.
30. Temporalis musculature strong.
31. Angle of mandible discrete, hook-shaped.
32. Insectivorous diet.
33. Tooth formula $I_{123}^{23} C_1^1 P_{234}^{234} M_{123}^{123}$
34. Canines projecting, caniniform; incisors chisel-like or spatulate, unlobed.
35. DP_{3-4}^{3-4} and P_4^4 semimolariform; P^3 with protocone and lingual root.
36. Molars rather like those of Ageina Russell, Louis, and Savage 1973.
37. No echolocation; middle-ear muscles and cochlea normal for mammals.
38. Auditory and visual regions of brain of normal size for mammals.
39. Tragus absent.
40. Vision unreduced.
41. Nose leaf absent.
42. Crepuscular habits.
43. Spinal cord relatively long.
44. Dorsal roots of spinal nerves enter spinal cord dorsolaterally.
45. Pelage hairs with medullae.
46. Small size.
47. Tropical habitat.
48. Pubic nipples absent.
49. Duplex (bicornuate) uterus.
50. Moderate or large allantoic vesicle.
51. Endotheoliochorial placenta.

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