Evolution of Bats

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Bats (order Chiroptera) are the second largest group of living mammals (after rodents), comprising more than 20% of the class Mammalia. Of the 5,416 species of mammals, 1,116 are bats (Wilson & Reeder, 2005; Simmons, 2005). Flight, echolocation, and diet are the most important factors in bat evolution.

Bats are the only mammals capable of true (= sustained or powered) flight, all other “flying” mammals are gliders (“flying” squirrels, “flying” lemurs, sugar gliders).

The majority of bats are insectivorous, using echolocation to locate prey and to navigate in their nocturnal and often subterranean (cave) environments. However, many species of bats feed on fruit, nectar, and pollen, and others prey on small vertebrates (other bats, birds, and fish). The vampire bats from Middle and South American feed exclusively on vertebrate blood.

Bats have a rather poor fossil record. Bat bones are delicate, and the majority of species live in the tropics where the chances of fossilization are greatly reduced. Because many bats roost in caves, their fossils are most common in caves, fissures, and other paleokarst deposits. Bat fossils also are found in lake sediments.

An extensive area of limestone and karst topography in the Florida peninsula has numerous cave, fissure, and sinkhole deposits, which preserve the largest fauna of Cenozoic bats in North America, covering the past 30 million years.
Bat Skeletal Anatomy

Humerus of Karstala
Miocene bat from Florida

Skeleton of Icaronycteris
Eocene bat from Wyoming

Skeleton of extant tree bat Lasiurus
Ear Region (petrosal and cochlea) of modern (L) and fossil (R) bats

Basicranial region of extant Noctule Bat *Nyctalus*
Showing ear region (petrosal) with coiled cochlea

Radiographs of skull of Eocene bat *Palaeochiropteryx*

Fig. 28. *Nyctalus noctula* (Vespertilionidae; redrawn from Henson, 1970: fig. 9). Ventral view of the basicranium and auditory region showing major osteological features, blood vessels, and muscles. The ectotympanic and malleus have been reflected laterally on the right side of the skull. APP, anterior process of petrosal; B, basioccipital fissure; BO, basioccipital; BOR, basioccipital pit; CO, cochlea; ECT, ectotympanic; ETR, epitympanic recess; FC, fenestra cochleae (= round window); FM, foramen magnum; FO, foramen ovale; FV, fenestra vestibuli (= oval window); GF, glenoid fossa; I, incus; ICA, internal carotid artery; M, malleus; MS, m. stapedius; MTT, m. tensor tympani; OAM, orbital aperture of malleus; OC, occipital condyle; PF, pyriform fenestra; PGF, postglenoid foramen; PP, paroccipital process; PT, pterygoid hamulus; SF, stapedial fossa; ST, stapes; STA, stapedial artery; T, tendon of m. tensor tympani; TM, tympanic membrane; Z, zygomatic arch.

Petrosal (ear bone) showing cochlea
*Primonatalus*: Miocene bat from Florida

Fig. 27. *Palaeochiropteryx tapinozoon*, positive prints of radiographs, from Novacek (1987: fig. 44). A, Dorsal view of the skull of SMF ME 798b; B, Lateral view of SMF ME 1127. An, angular process of dentary; Co, cochlea; Cp, coronoid process of dentary; Ect, ectotympanic; SI, stylohyal; Z, zygomatic arch.
Major Events in Bat Evolution

- Thomas Farm, Florida, early Miocene, 18 Ma
- Brooksville, Florida, late Oligocene, 26 Ma
- Slaughter Canyon Cave, NM, 400 ka

- Living species of bats first appear
  Pliocene, 5 Ma
- Living genera of bats first appear
  Middle Miocene, 15 Ma
- Thomas Farm, Florida, early Miocene, 18 Ma
- Brooksville, Florida, late Oligocene, 26 Ma

- Living families of bats first appear
  Middle Eocene, about 45 Ma

- First bats appear, early Eocene, about 52 Ma
  (True flight and echolocation both present in earliest known bats, e.g. *Icaronycteris*)

- "Ancestor" of bats unknown from Paleocene
Where are Fossil Bats Found?

Surprise Cave, Florida

Haile Quarries, Florida

Carlsbad Caverns, New Mexico

Suwannee River, Florida

Sandia Cave, New Mexico

Brooksville, Florida

Fossil Butte, Wyoming

Panama Canal
How are Fossil Bats Preserved?

- Underwater blue hole, Bahamas
- Carlsbad Caverns, NM
- Green River Fm., WY, Eocene
- Slaughter Canyon Cave, NM
- Pleistocene
- Thomas Farm, FL
- Miocene
Skeletons of Early Eocene Bats
Green River lake deposits, Wyoming

Holotype of *Icaronycteris index* (YPM-PU 18150) (Simmons and Geisler, 1998).

Holotype of *Onychonycteris finneyi* (ROM 55351). Skeleton in dorsal view (L); Skull in ventral view (R). Scale bars, 1 cm. All elements are preserved on a single slab with the skeleton exposed on one side, and the skull and sternum on the reverse. Features labelled: 1, calcar; 2, cranial tip of stylohyal; 3, orbicular apophysis of malleus (Simmons et al., 2008).
Specimen of *Hassianycteris messeleensis* (SMF ME 1414a) from Messel Oil Shale, middle Eocene, Germany (photo courtesy of J. Habersetzer, imagine taken by E. Pantak (Gunnell & Simmons, 2006))

*Palaeochiropteryx tupaiodon* (SMF ME 10) Messel Oil Shale, middle Eocene Germany
Slaughter Canyon Cave
Carlsbad Caverns National Park
Slaughter Canyon Cave stratigraphic section

- Flowstone (>206 ka)
- Level 1
- Level 2-richest layer for bat fossils
- Level 3

Estimated age of bat fossils from Slaughter Canyon Cave is middle Pleistocene ~400 ka
Fossil bones of extinct Free-tailed Bat *Tadarida constantinei*
Slaughter Canyon Cave
Collecting cave sediment for screenwashing
Screenwashing and Sorting Bat Fossils
Slaughter Canyon Cave
Screenwashed concentrate with bat bones
*Tadarida constantinei* fossils
(arrows indicate where bones belong on bat skeleton at right)
Slaughter Canyon Cave
Fossil bones of *Tadarida constantinei*
skulls (top) & humerus (bottom)
Slaughter Canyon Cave
Sample (N=50) of *Tadarida constantinei*
complete humeri (Test Pit 2, 1 bag of sediment)
*Tadarida brasiiliensis*—modern (L)
*Tadarida constantinei*—fossil (reddish bones)
*Nyctinomops femorosaccus*—modern (R)
(skull-top row; humerus-bottom row)
*Tadarida brasiliensis* skull (left)
*Tadarida constantinei* skull (right)
Tadarida constantinei upper teeth & skull (left)
Dental morphology of bat teeth (right)
**Tadarida constantinei** and *T. brasiensis*  
Comparative cranial measurements

<table>
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<tr>
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<th>Cranial Measurements (in mm) of two species of <em>Tadarida</em></th>
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<tr>
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<td>total length of skull</td>
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Early and Middle Pleistocene records of large *Tadarida* from North America
1) Slaughter Canyon Cave, NM; 2) Mammoth Cave, KY; 3) Hamilton Cave, WV; 4) Macasphalt, FL
Thomas Farm, Florida
Collecting Miocene Bats
Thomas Farm Miocene Bats
Funnel Eared Bats (Family Natalidae)
*Primonatalus prattae*

Illustrations by Nicholas Czaplewski (Morgan & Czaplewski, 2003)
Miocene natalid bat from Thomas Farm

*Primonatalus prattae*

Lower jaw with three molars
Type specimen of *Primonatalus prattae*
Funnel Eared Bats
Family Natalidae

*Natalus stramineus*
Mexican funnel-eared bat

Modern distribution of Natalidae
(Hill & Smith, 1984)
Thomas Farm Miocene Bats
Sac-winged bats (Family Emballonuridae)
*Floridopteryx poyeri*

Lower Jaw

Lower Molar

Emballonurid Bats from Central America
Sac-winged Bats
Family Emballonuridae

*Saccopertyx leptura*
White-lined bat

Modern distribution of Emballonuridae
(Hill & Smith, 1984)
Brooksville Fauna, Florida
Late Oligocene Bats

- Mormoopidae
- Emballonuridae
- Phyllostomidae

- Humerus
- Lower jaw
- Speonycteridae
- Mormoopidae

Lower jaw
Ghost-faced Bats
Family Mormoopidae

Ghost-faced Bat
*Mormoops megalophylla*

Modern distribution of (Mormoopidae)
(Hill & Smith, 1984)
Free-tailed bats (Family Molossidae)
Fossil molossids from Florida

A-C Upper molars of Oligocene and Miocene species
D-G. Distal humerus of large *Tadarida* from Pliocene

Modern distribution of Molossidae
(Hill & Smith, 1984)
Miocene Bats from Panama*
(*New discovery yesterday—not pictured)

Lower jaw of *Speonycteris*-like bat
early Miocene of Panama

Lower jaw of *Speonycteris*
late Oligocene of Florida

Phylllostomus hastatus
Greater Spear-nosed Bat

Panama Canal
Great American Interchange

Groups from North America that dispersed to South America between the early Miocene and late Pliocene (~5-20 Ma)

Groups from South America that dispersed to North America in the late Pliocene (~5 Ma)

Phyllostomidae
*Desmodus*
(Vampire Bat)

Molossidae
*Eumops*

Emballonuridae

Mormoopidae

Noctilionoidea

Natalidae

Molossidae near *Tadarida*
A strict consensus of four equally parsimonious trees (791 steps each) derived from analysis of our new morphological dataset. Numbers above the branches are decay values; those below the branches are bootstrap values. In each pair of numbers, the first number represents the support value calculated using the complete dataset; the second number represents the support value calculated in an analysis including all taxa except *Tanzanycteris*, a relatively poorly known fossil. Most decay and bootstrap values were generally unaffected by removal of *Tanzanycteris*. However, support for some nodes in the middle of the tree increased markedly when *Tanzanycteris* was removed (i.e., for the crown group Microchiroptera the decay value increased from one to four, and the bootstrap from 37 to 76%). (Gunnell and Simmons, 2005)
Molecular Phylogeny of the Chiroptera

The maximum likelihood tree (–ln likelihood = 92127.3772) for the concatenated data set under the GTR + Γ + I model of sequence evolution. Numbers at the nodes are the (ML unconstrained bootstrap values)/(ML constrained bootstrap values)/Bayesian (single model posterior probabilities shown as percentages)/Bayesian (partitioned model posterior probabilities shown as percentages). 100* signifies clades that received 100% bootstrap support in all analyses and had posterior probabilities of 1.000. The genera are color coded according to the superfamilial groups identified by the most recent morphological phylogenetic study. (Teeling et al., 2005)
Molecular time scale (“clock”) for the Chiroptera

Molecular time scale for the order Chiroptera based on the divtime analyses (11), using the ML topology depicted in Fig. 1, six fossil constraints, and a mean prior of 65 Mya for the base of the ingroup root. Numbers at the nodes are the molecular dates in millions of years; values in parentheses are the 95% credibility intervals. Letters along the branches refer to the fossil constraint age (Mya) imposed on that particular node: [a] 0.37; [b] 0.55; [c] 0.37; [d] 0.34; [e] 0.30; [f] 0.37. Maximum constraint is an arrow pointing up; minimum constraint is an arrow pointing down. Red circles indicate the age of the oldest fossil representing that lineage or "off-shoots" from that lineage (table S5). Red numbers in brackets to the left of the slash indicate the percentage sum missing of the fossil record for that clade, (total sum missing per lineage)/(sum age of lineage). Numbers in brackets in red to the right of the slash indicate the average percentage missing of that fossil record for that clade or the average of the percentage missing per lineage (11) (table S5). A blue square indicates the time of separation between the New World Rhynchonycteris and the Old World Emballonura (Teeling et al., 2005).
Phylogeny of the Chiroptera and Outgroups (Laurasiatheria)

1, Chiroptera; 2, Yangochiroptera; 3, Yinpterochiroptera; Emballonuroidea; 5, Vespertilionoidea; and 6, Noctilionoidea. Outgroups in yellow (Laurasiatheria) Teeling et al., 2005)
Molecular Phylogeny of the Mammalia

Figure 1: Partial representation of the mammalian supertree showing the relationships among the families (following ref. 23). All orders are labelled and major lineages are coloured as follows: black, Monotremata; orange, Marsupialia; blue, Afrotheria; yellow, Xenarthra; green, Laurasiatheria; and red, Euarchontognires. Families that were reconstructed as non-monophyletic are represented multiple times and numbered accordingly. Branch lengths are proportional to time, with the K/T boundary indicated by a black, dashed circle. The scale indicates Myr. The base tree was drawn using FigTree v1.0 (http://evolve.zoo.ox.ac.uk/software.html?id=figtree).

(Bininda-Emonds et al., 2007)
Another Molecular Phylogeny of the Mammalia

(Meredith et al., 2010)
Bat origins!

Highly derived bats with the ability to fly and echolocate had already appeared worldwide in the early Eocene by about 50 million years ago. Bats must have originated during the Paleocene, between 55 and 65 million years ago. Field work in search of early bats is ongoing worldwide, including New Mexico where paleontologists are screenwashing Paleocene sediments in search of small mammals, hopefully including ancestral bats.
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Photos of Living Bats by Merlin Tuttle; Paintings of Living Bats by Fiona Reid