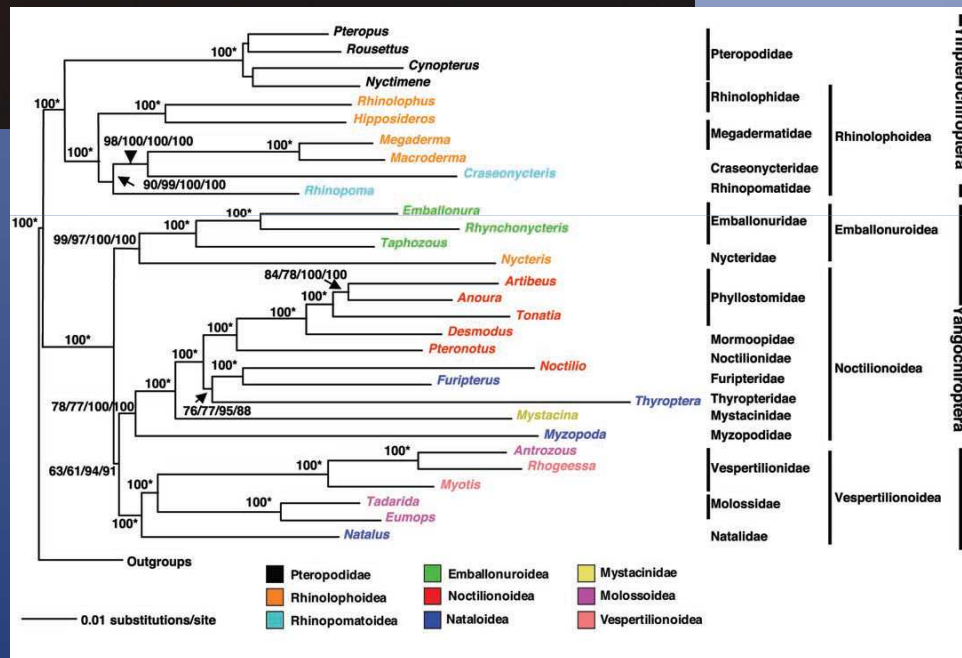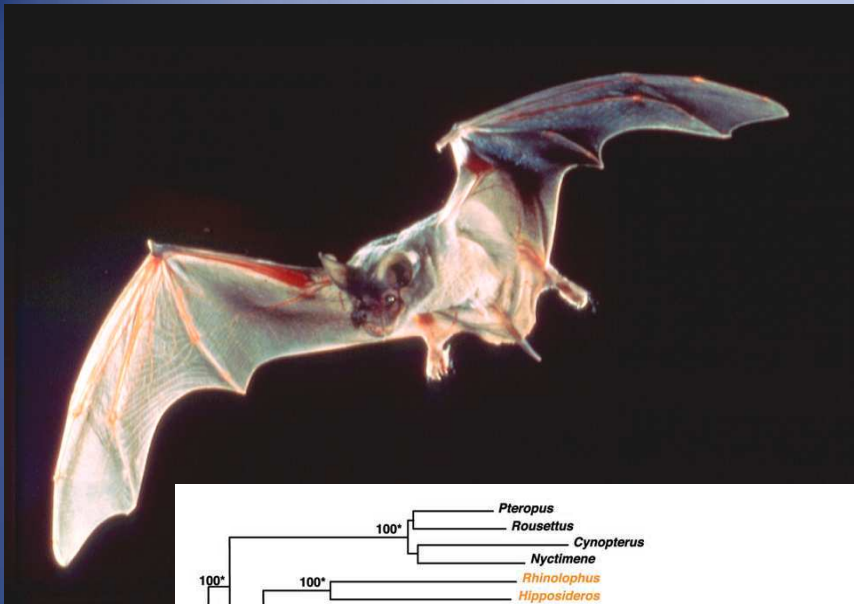# Evolution of Bats

Gary Morgan
New Mexico Museum of Natural History

Bat Facts

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

Skeleton of *Icaronycteris*
Eocene bat from Wyoming
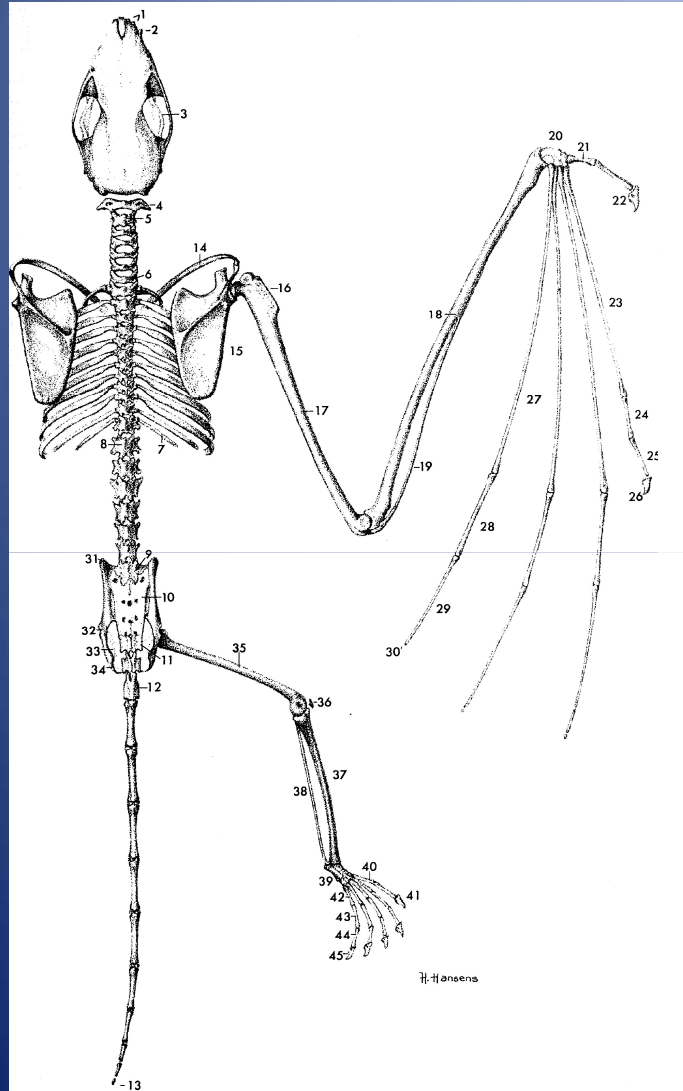
1	second and third upper incisors
2	upper canine
3	coronoid process of dentary
4	lateral process of atlas
5	axis
6	seventh cervical vertebra
7	twelfth rib
8	first lumbar vertebra
9	seventh lumbar vertebra
10	sacrum
11	first caudal vertebra
12	third caudal vertebra
13	thirteenth caudal vertebra
14	clavicle
15	scapula
16	pectoral ridge of humerus
17	shaft of humerus
18	radius
19	ulna
20	carpus (wrist)
21	metacarpal of first digit (thumb)
22	second phalange (claw) of first digit
23	metacarpal of second digit
24	proximal (first) phalange of second digit
25	second (middle) phalange of second digit
26	third (distal) phalange (claw) of second digit
27	metacarpal of fifth digit
28	proximal (first) phalange of fifth digit
29	second (middle) phalange of fifth digit
30	third (terminal) phalange (claw) of fifth digit
31	iliac crest of pelvis
32	acetabulum
33	obturator foramen
34	ischium
35	femur
36	patella
37	tibia
38	fibula
39	tarsus
40	metatarsal of first digit
41	second phalange (claw) of first digit
42	metarsal of fifth digit
43	proximal (first) phalange of fifth digit
44	second (middle) phalange of fifth digit
45	third (terminal) phalange (claw) of fifth digit
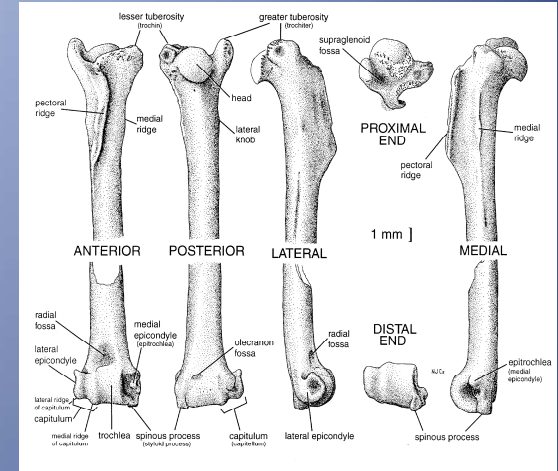
Humerus of *Karstala* Miocene bat from Florida
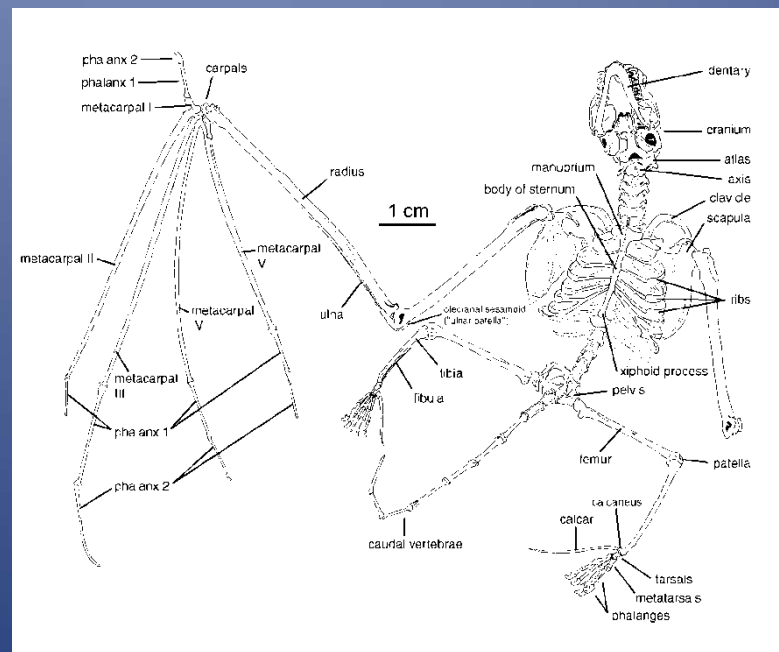
Skeleton of extant tree bat *Lasiurus*

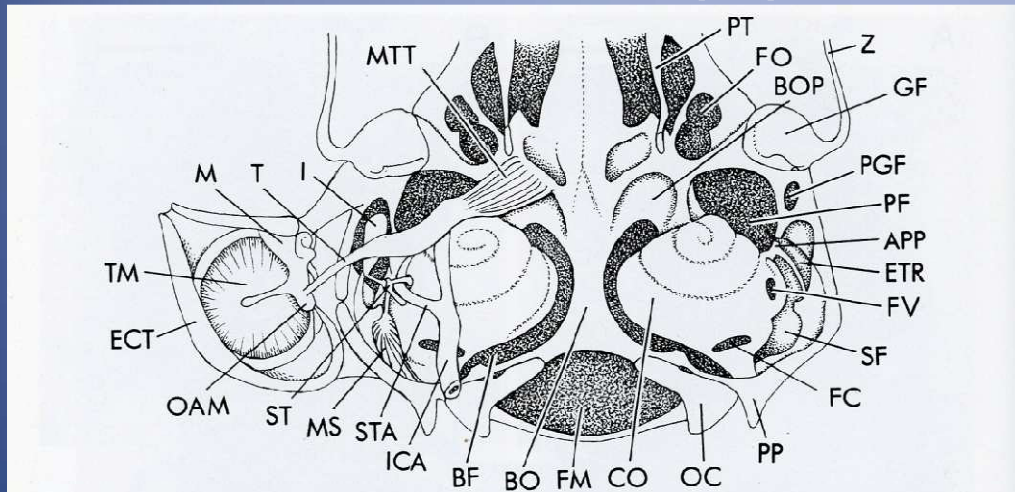# Ear Region (petrosal and cochlea) of modern (L) and fossil (R) bats

Fig. 28. *Nyctalus noctula* (Vespertilioninae; redrawn from Henson, 1970: fig. 9). Ventral view of the basicranium and audtory 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; BF, basicochlear fissure; BO, basioccipital; BOP, 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, orbicular apophysis 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.

Basicranial region of extant Noctule Bat *Nyctalus*
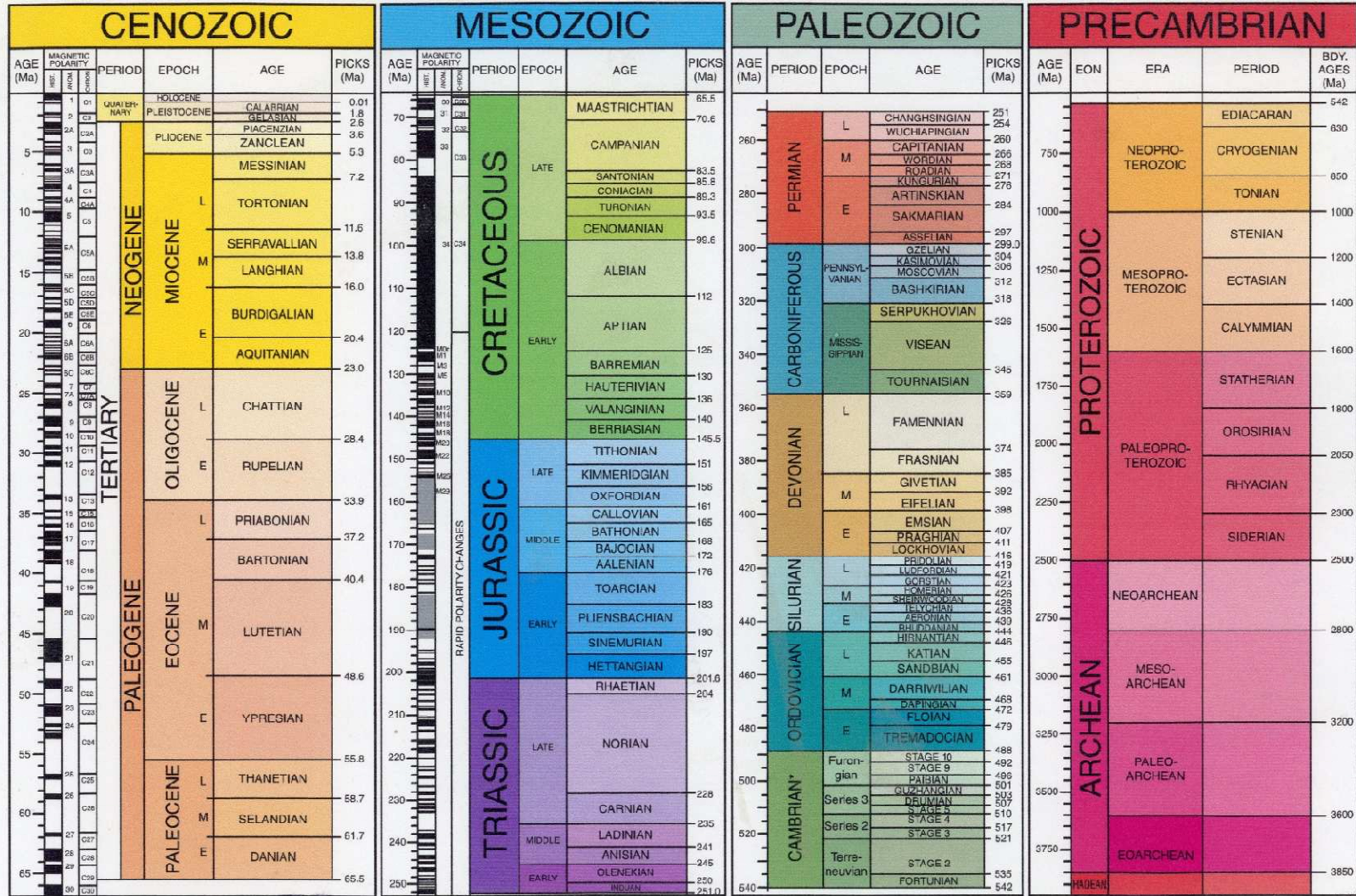Showing ear region (petrosal) with coiled cochlea
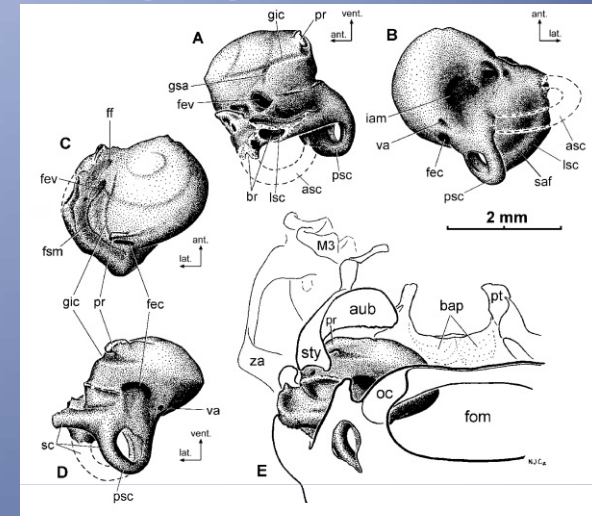
Petrosal (ear bone) showing cochlea
Primonatalus: Miocene bat from Florida

Fig. 27. *Palaeochiropteryx tupaiodon*, positive prints of radiographs; from Novacek (1987: fig. 4). A. Dorsoventral view of the skull of SMF ME 788b. B. Lateral view of SMF ME 1127. An, angular process of dentary; Co, cochlea; Cp, coronoid process of dentary; Ect, ectotympanic; Sl, stylohyal; Z, zygomatic arch.
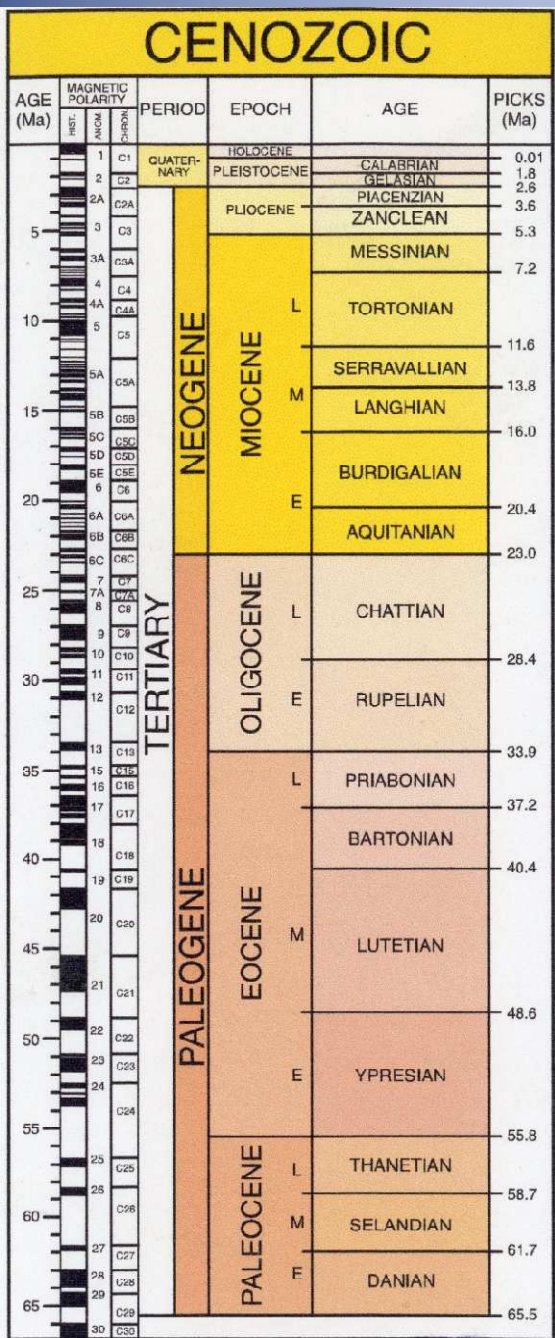
Radiographs of skull of Eocene bat *Palaeochiropteryx*

2009 GEOLOGIC TIME SCALE

CENOZOIC

AGE (Ma)	MAGNETIC POLARITY	PERIOD	EPOCH	AGE	PICKS (Ma)
		QUATER-NARY	HOLOCENE		0.01
			PLEISTOCENE	CALABRIAN	1.8
				GELASIAN	2.6
			PLIOCENE	PIACENZIAN	3.6
5				ZANCLEAN	5.3
				MESSINIAN	7.2
10		NEOGENE	MIOCENE L	TORTONIAN	11.6
				SERRAVALLIAN	13.8
15			M	LANGHIAN	16.0
				BURDIGALIAN	
20			E		20.4
				AQUITANIAN	23.0
25		TERTIARY	OLIGOCENE L	CHATTIAN	28.4
30			E	RUPELIAN	33.9
35			EOCENE L	PRIABONIAN	37.2
40		PALEOGENE		BARTONIAN	40.4
			M	LUTETIAN	
45					48.6
50			E	YPRESIAN	55.8
55			PALEOCENE L	THANETIAN	58.7
60			M	SELANDIAN	61.7
65			E	DANIAN	65.5

MESOZOIC

AGE (Ma)	MAGNETIC POLARITY	PERIOD	EPOCH	AGE	PICKS (Ma)
70			LATE	MAASTRICHTIAN	65.5
					70.6
80				CAMPANIAN	
					83.5
90				SANTONIAN	85.8
				CONIACIAN	89.3
				TURONIAN	93.5
100		CRETACEOUS		CENOMANIAN	99.6
				ALBIAN	
110			EARLY		112
120				APTIAN	125
130				BARREMIAN	130
				HAUTERIVIAN	136
140				VALANGINIAN	140
				BERRIASIAN	145.5
150			LATE	TITHONIAN	151
				KIMMERIDGIAN	156
160				OXFORDIAN	161
		JURASSIC		CALLOVIAN	165
			MIDDLE	BATHONIAN	168
170				BAJOCIAN	172
				AALENIAN	176
180				TOARCIAN	183
			EARLY	PLIENSBACHIAN	190
190				SINEMURIAN	197
200				HETTANGIAN	201.6
			LATE	RHAETIAN	204
210				NORIAN	
220		TRIASSIC			228
230				CARNIAN	235
			MIDDLE	LADINIAN	241
240				ANISIAN	245
250			EARLY	OLENEKIAN	250
				INDUAN	251.0

PALEOZOIC

AGE (Ma)	PERIOD	EPOCH	AGE	PICKS (Ma)
		L	CHANGHSINGIAN	251
			WUCHIAPINGIAN	254
260	PERMIAN	M	CAPITANIAN	260
			WORDIAN	266
			ROADIAN	268
			KUNGURIAN	271
280		E	ARTINSKIAN	276
			SAKMARIAN	284
			ASSELIAN	297
300			GZELIAN	299.0
		PENNSYL-VANIAN	KASIMOVIAN	304
			MOSCOVIAN	306
	CARBONIFEROUS		BASHKIRIAN	312
320			SERPUKHOVIAN	318
		MISSIS-SIPPIAN	VISEAN	326
340				345
			TOURNAISIAN	359
360		L	FAMENNIAN	374
380	DEVONIAN		FRASNIAN	385
		M	GIVETIAN	392
			EIFELIAN	398
400		E	EMSIAN	407
			PRAGHIAN	411
			LOCKHOVIAN	416
420		L	PRIDOLIAN	419
			LUDFORDIAN	421
			GORSTIAN	423
	SILURIAN	M	HOMERIAN	426
			SHEINWOODIAN	428
			TELYCHIAN	429
440		E	AERONIAN	430
			RHUDDANIAN	444
			HIRNANTIAN	446
		L	KATIAN	455
460			SANDBIAN	461
	ORDOVICIAN	M	DARRIWILIAN	468
			DAPINGIAN	472
480		E	FLOIAN	479
			TREMADOCIAN	488
		Furon-gian	STAGE 10	492
			STAGE 9	496
500			PAIBIAN	501
		Series 3	GUZHANGIAN	503
			DRUMIAN	507
	CAMBRIAN*		STAGE 5	510
		Series 2	STAGE 4	517
520			STAGE 3	521
		Terre-neuvian	STAGE 2	535
540			FORTUNIAN	542

PRECAMBRIAN

AGE (Ma)	EON	ERA	PERIOD	BDY. AGES (Ma)
			EDIACARAN	542
				630
750		NEOPRO-TEROZOIC	CRYOGENIAN	850
			TONIAN	
1000				1000
			STENIAN	1200
1250	PROTEROZOIC	MESOPRO-TEROZOIC	ECTASIAN	1400
1500			CALYMMIAN	1600
			STATHERIAN	
1750				1800
2000		PALEOPRO-TEROZOIC	OROSIRIAN	2050
2250			RHYACIAN	2300
			SIDERIAN	
2500				2500
2750		NEOARCHEAN		2800
3000	ARCHEAN	MESO-ARCHEAN		3200
3250				
3500		PALEO-ARCHEAN		3600
3750		EOARCHEAN		3850
	HADEAN			

CENOZOIC

AGE (Ma)	MAGNETIC POLARITY			PERIOD	EPOCH	AGE	PICKS (Ma)
	HIST.	ANOM.	CHRON				
		1	C1	QUATER-NARY	HOLOCENE		0.01
		2	C2		PLEISTOCENE	CALABRIAN	1.8
						GELASIAN	2.6
		2A	C2A		PLIOCENE	PIACENZIAN	3.6
5		3	C3			ZANCLEAN	5.3
		3A	C3A			MESSINIAN	7.2
		4	C4			TORTONIAN	
10		4A	C4A		MIOCENE		11.6
		5	C5	NEOGENE		SERRAVALLIAN	13.8
		5A	C5A			LANGHIAN	
15		5B	C5B				16.0
		5C	C5C			BURDIGALIAN	
		5D	C5D				
		5E	C5E				
20		6	C6				20.4
		6A	C6A			AQUITANIAN	
		6B	C6B				23.0
		6C	C6C				
25		7	C7		OLIGOCENE	CHATTIAN	
		7A	C7A				
		8	C8				
		9	C9				28.4
30		10	C10			RUPELIAN	
		11	C11				
		12	C12				33.9
		13	C13	TERTIARY		PRIABONIAN	
35		15	C15				37.2
		16	C16			BARTONIAN	
		17	C17				
40		18	C18		EOCENE		40.4
		19	C19				
		20	C20	PALEOGENE		LUTETIAN	
45		21	C21				
		22	C22				48.6
50		23	C23			YPRESIAN	
		24	C24				
55							55.8
		25	C25		PALEOCENE	THANETIAN	
		26	C26				58.7
60		27	C27			SELANDIAN	61.7
		28	C28			DANIAN	
65		29	C29				65.5
		30	C30				

Slaughter Canyon Cave, NM **Major Events in Bat Evolution**
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
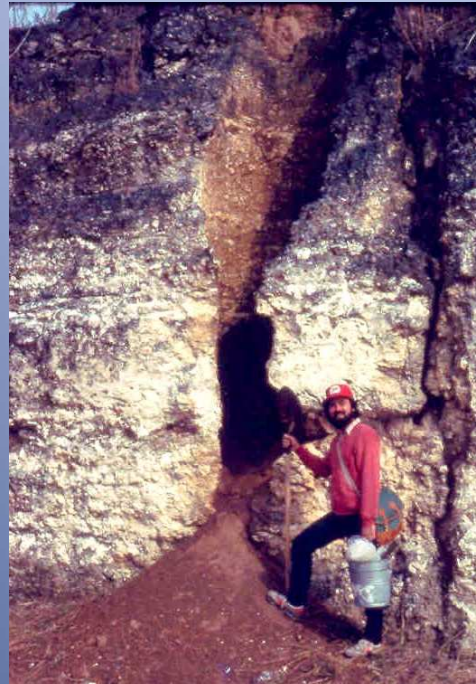
Haile Quarries, Florida
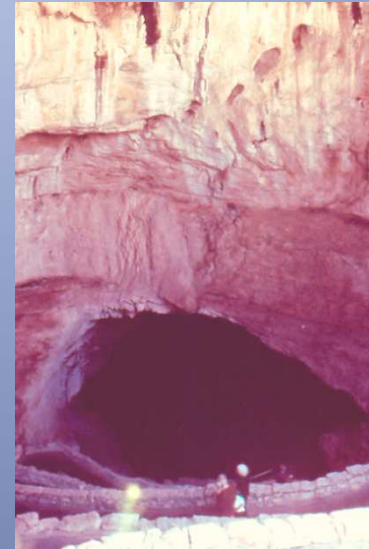
Carlsbad Caverns, New Mexico
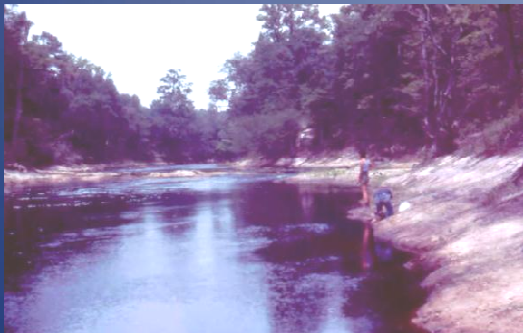
Suwannee River, Florida

Sandia Cave
New Mexico
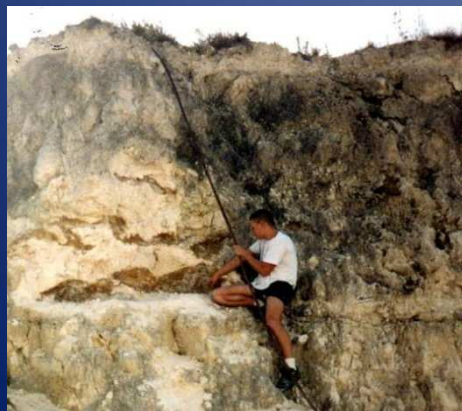
Brooksville, Florida

Fossil Butte, Wyoming

Panama
Canal

How are Fossil Bats Preserved?
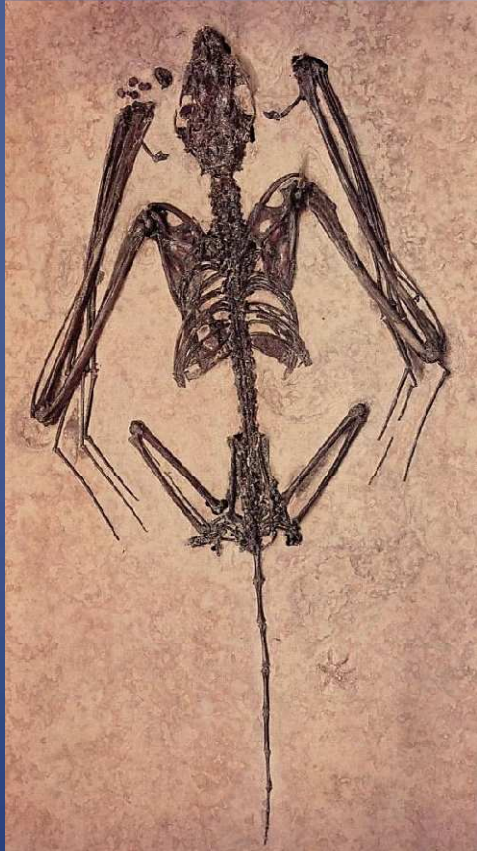
Underwater blue hole, Bahamas

Carlsbad Caverns, NM

Slaughter Canyon Cave, NM Pleistocene

Green River Fm., WY, Eocene
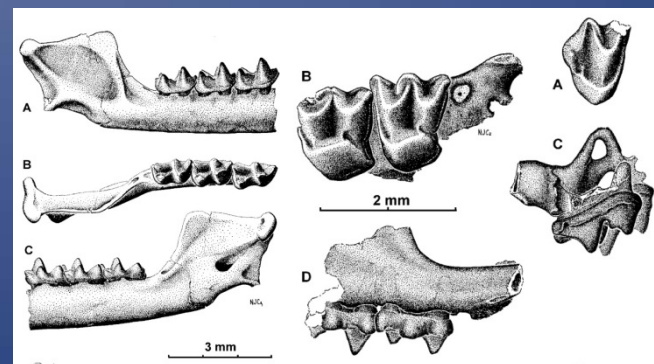
Thomas Farm, FL Miocene

Skeletons of Early Eocene Bats
Green River lake deposits, Wyoming
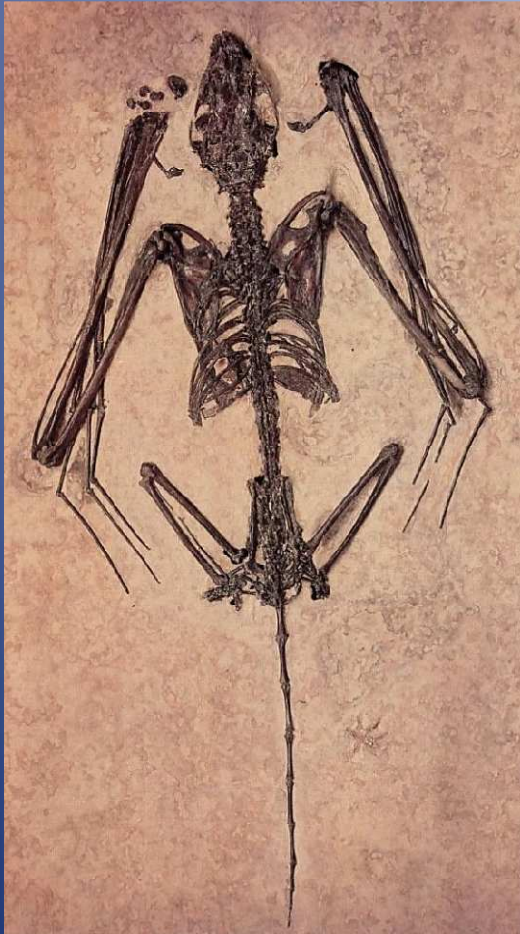
Holotype of *Icaronycteris index* (YPM-PU 18150) (Simmons and Geisler, 1998).
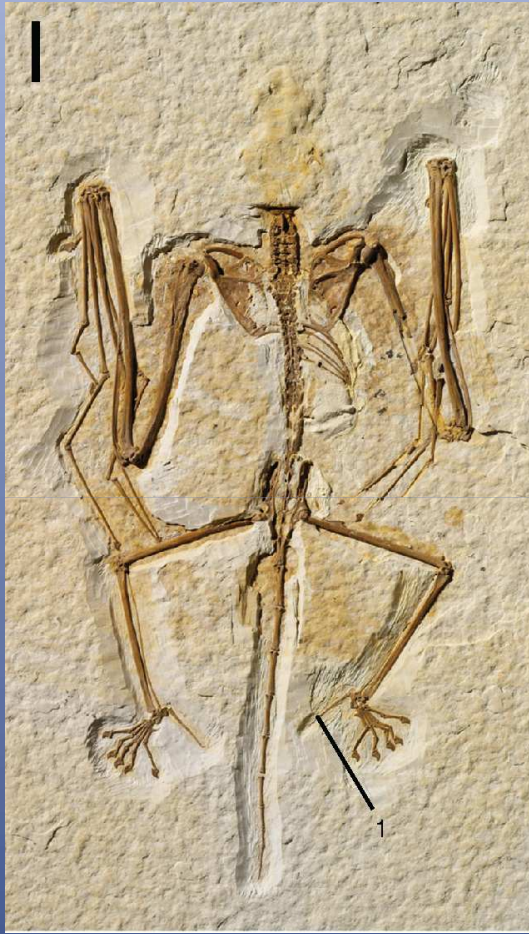
Holotype of Onychonycteris finneyi (ROM 55351). Skeleton in dorsal view (L); Skull in ventral view (R). Scale bars, 1 cm. All elements are preserved on a single slab with the skeleton exposed on one side, and the skull and sternum on the reverse. Features labelled: 1, calcar; 2, cranial tip of stylohyal; 3, orbicular apophysis of malleus (Simmons et al., 2008).
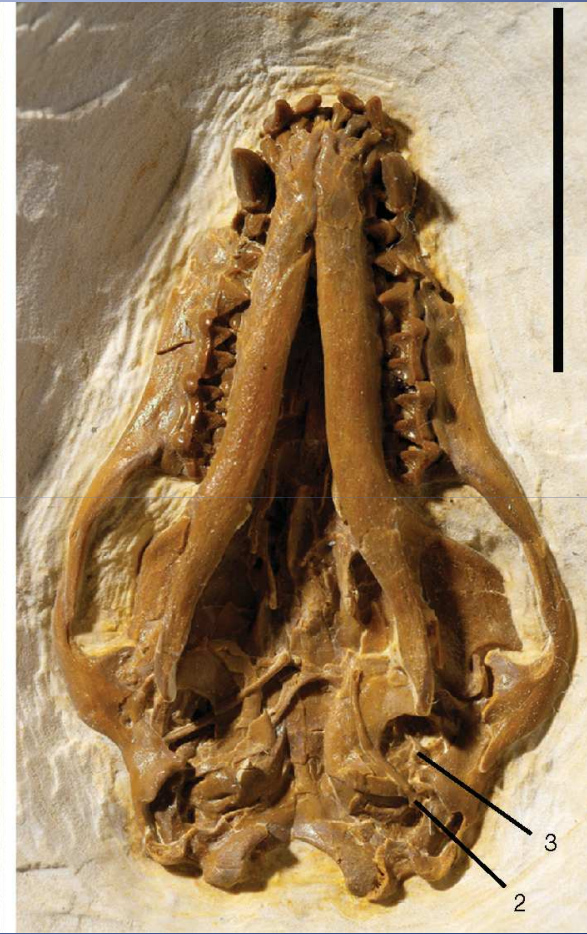
Skeletons of Middle Eocene bats
Messel oil shale, Germany

Specimen of *Hassianycteris messelensis* (SMF ME 1414a) from Messel Oil Shale, middle Eocene, Germany (photo courtesy of J. Habersetzer, imagine taken by E. Pantak (Gunnell & Simmons, 2006)
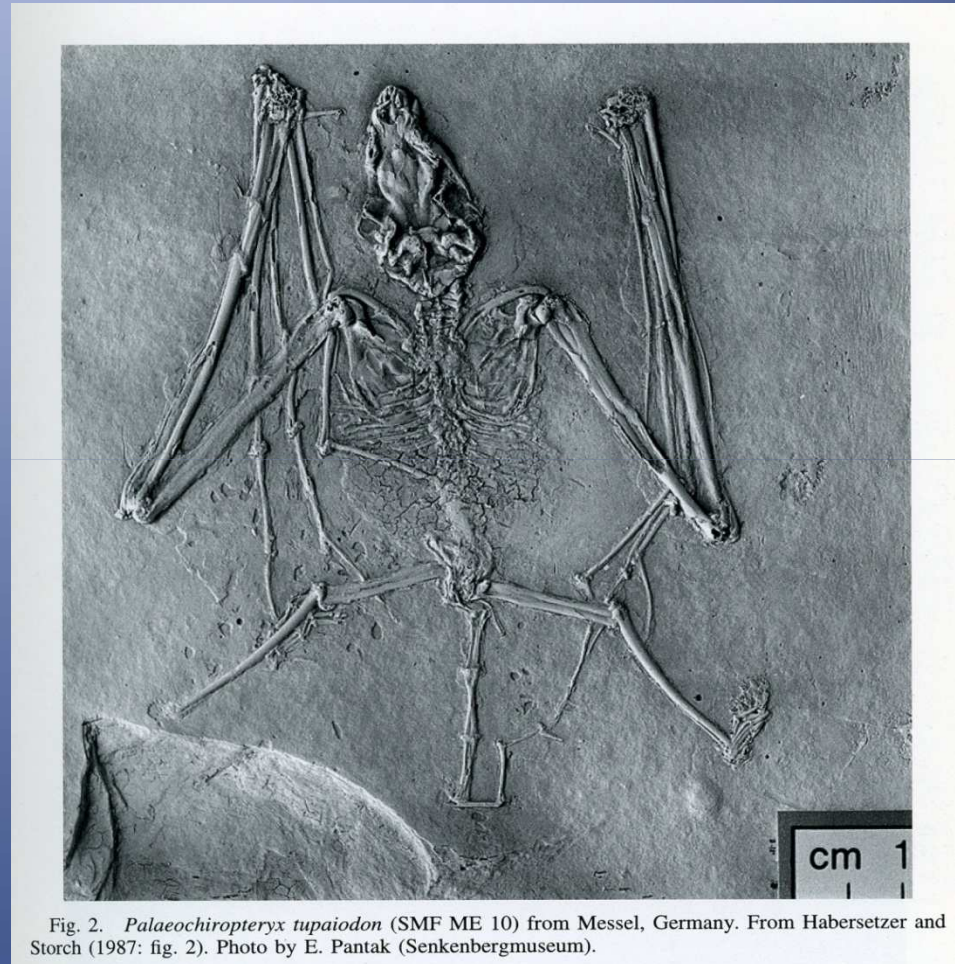
Fig. 2. *Palaeochiropteryx tupaiodon* (SMF ME 10) from Messel, Germany. From Habersetzer and Storch (1987: fig. 2). Photo by E. Pantak (Senkenbergmuseum).

Palaeochiropteryx tupaiodon (SMF ME 10) Messel Oil Shale, middle Eocene Germany

Slaughter Canyon Cave
Carlsbad Caverns National Park
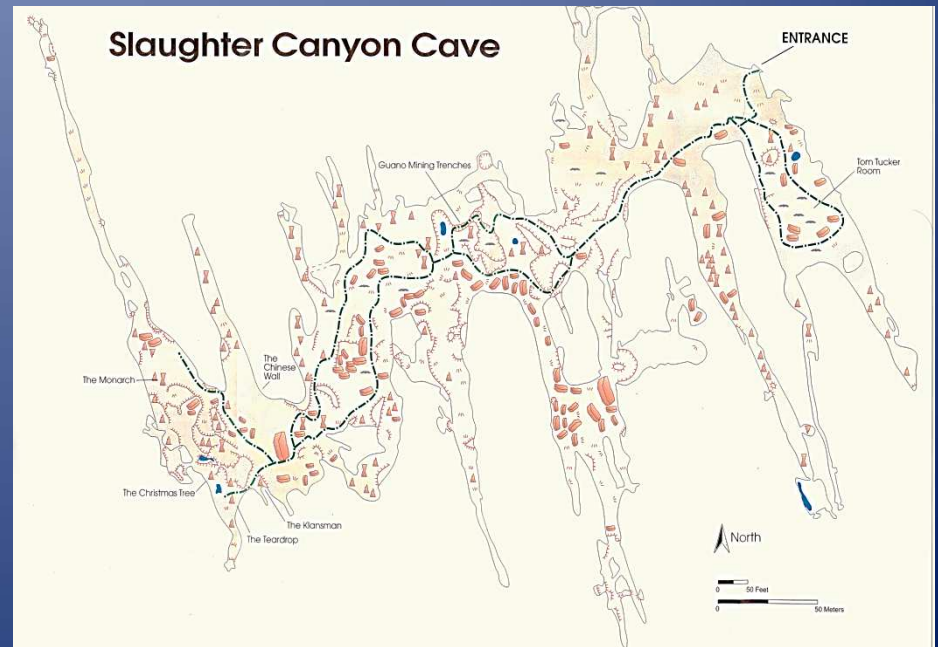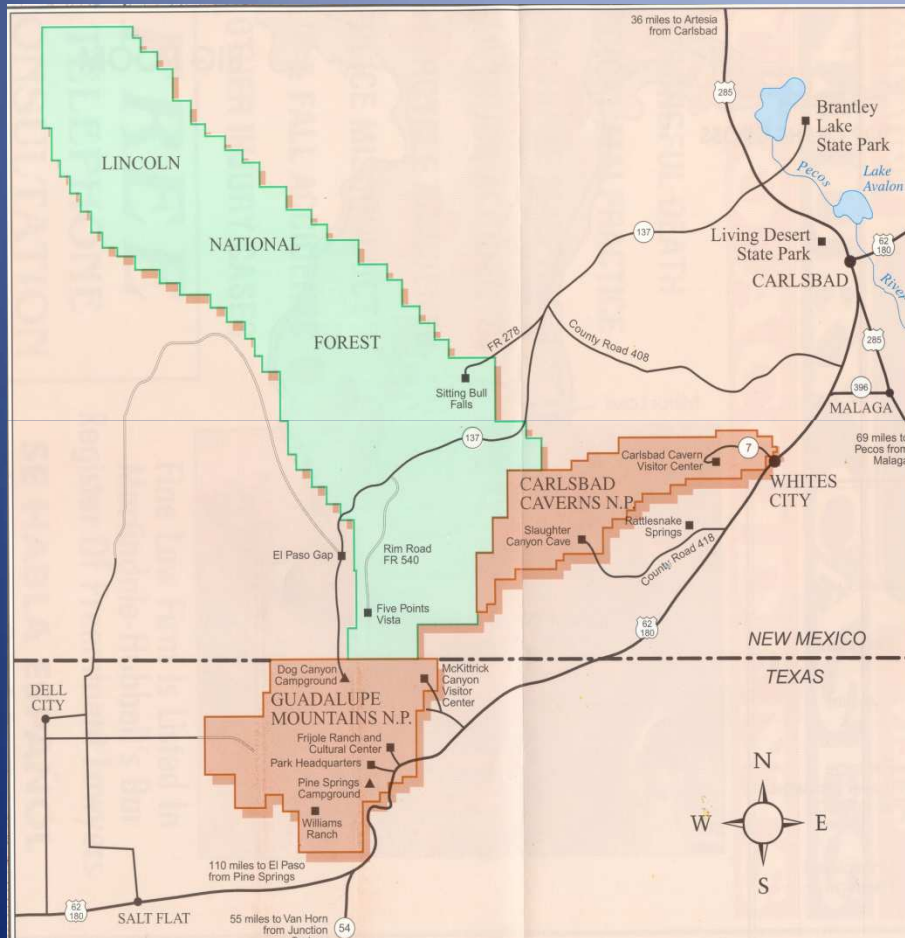
Slaughter Canyon Cave stratigraphic section

- 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*

skulls
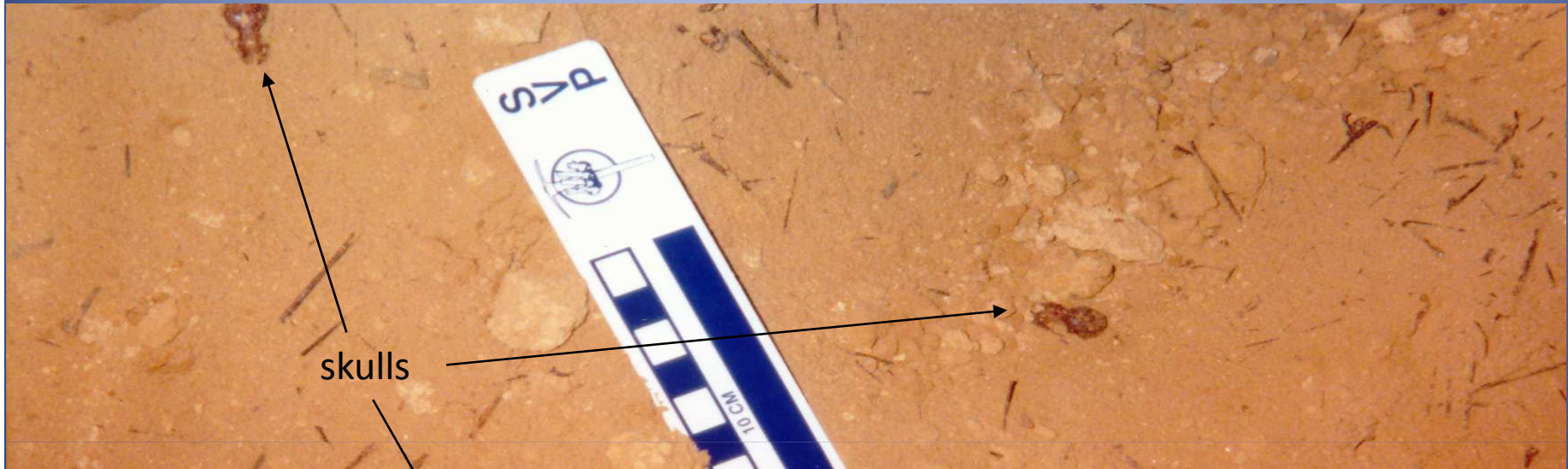
Slaughter Canyon Cave
Collecting cave sediment for screenwashing
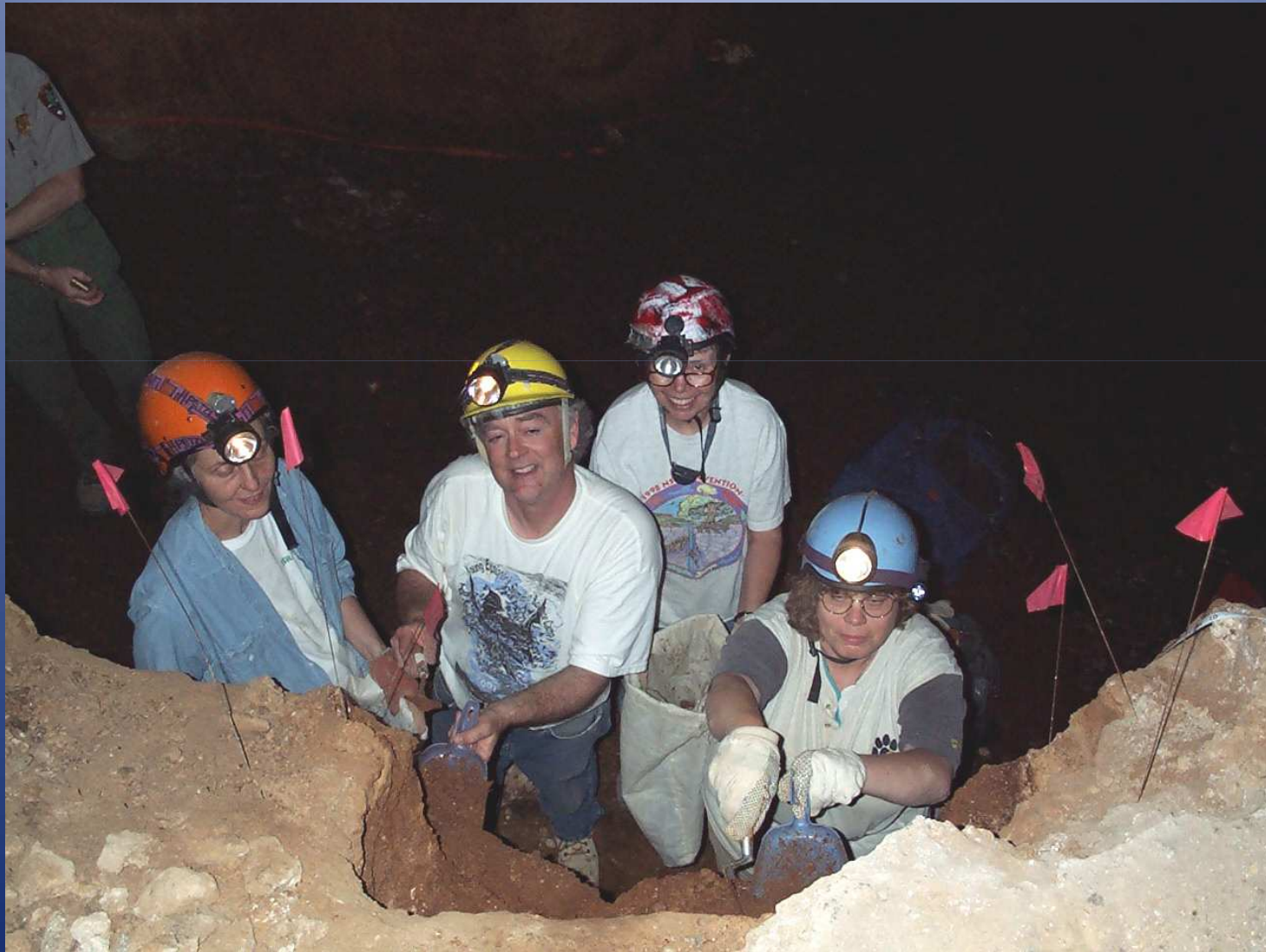
Screenwashing and Sorting Bat Fossils

Slaughter Canyon Cave
Screenwashed concentrate with bat bones

Tadarida constantinei fossils
(arrows indicate where bones belong on bat skeleton at right)
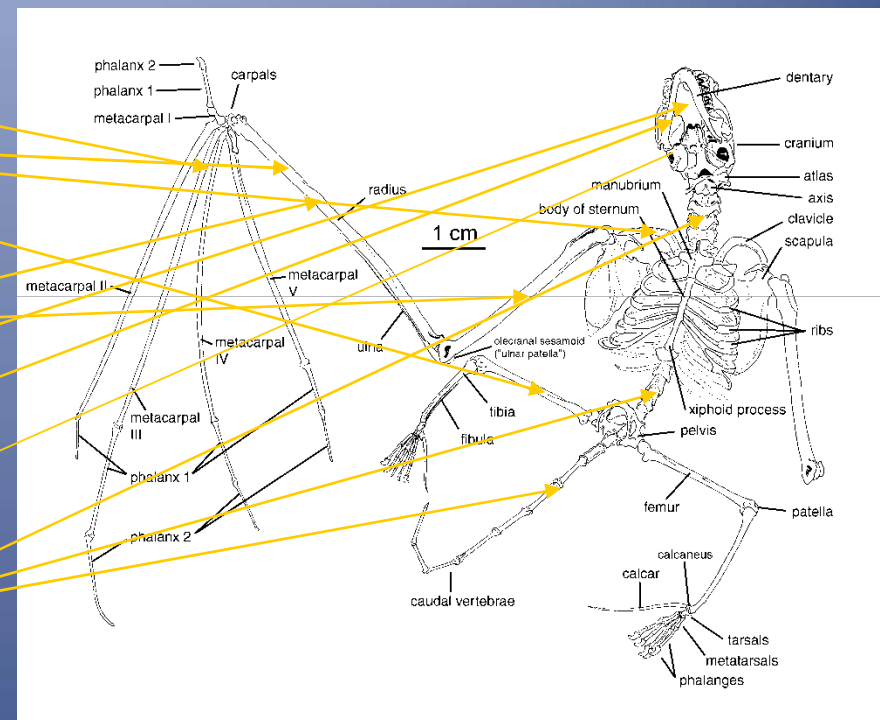
Slaughter Canyon Cave
Fossil bones of *Tadarida constantinei*
skulls (top) & humerus (bottom)

Slaughter Canyon Cave
Sample (N=50) of *Tadarida constantinei* complete humeri (Test Pit 2, 1 bag of sediment)

Society of Vertebrate Paleontolo

Tadarida brasiliensis—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)
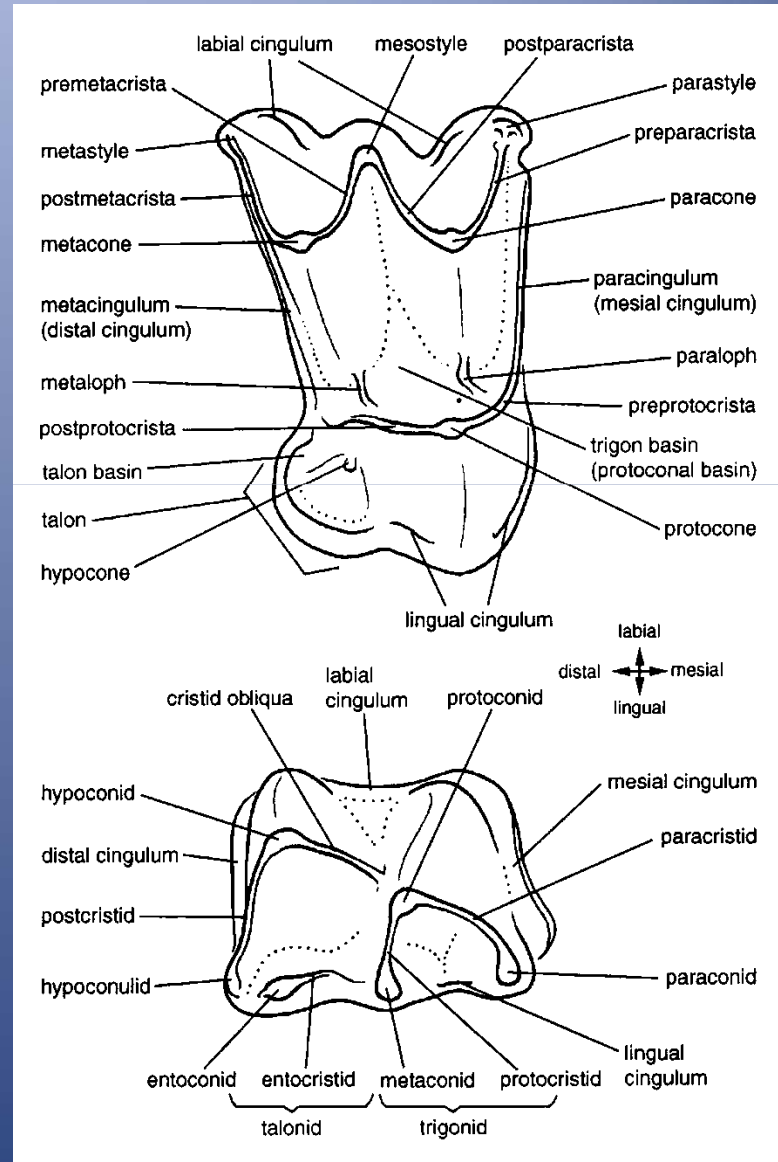
Tadarida constantinei and *T. brasiliensis*
Comparative cranial measurements

Cranial Measurements (in mm) of two species of *Tadarida*

	total length of skull	alveolar length of upper teeth	alveolar width across molars	height of braincase	width of braincase
Tadarida constantinei					
mean	17.0	6.8	7.8	5.8	9.0
observed range	16.5-17.4	6.6-7.1	7.5-8.1	5.6-6.0	8.6-9.3
sample size	20	20	20	20	20
Tadarida brasiliensis mexicana					
mean	15.0	6.1	7.0	5.5	8.3
observed range	14.5-15.6	5.9-6.3	6.6-7.2	5.0-5.8	8.0-8.6
sample size	20	20	20	20	20

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
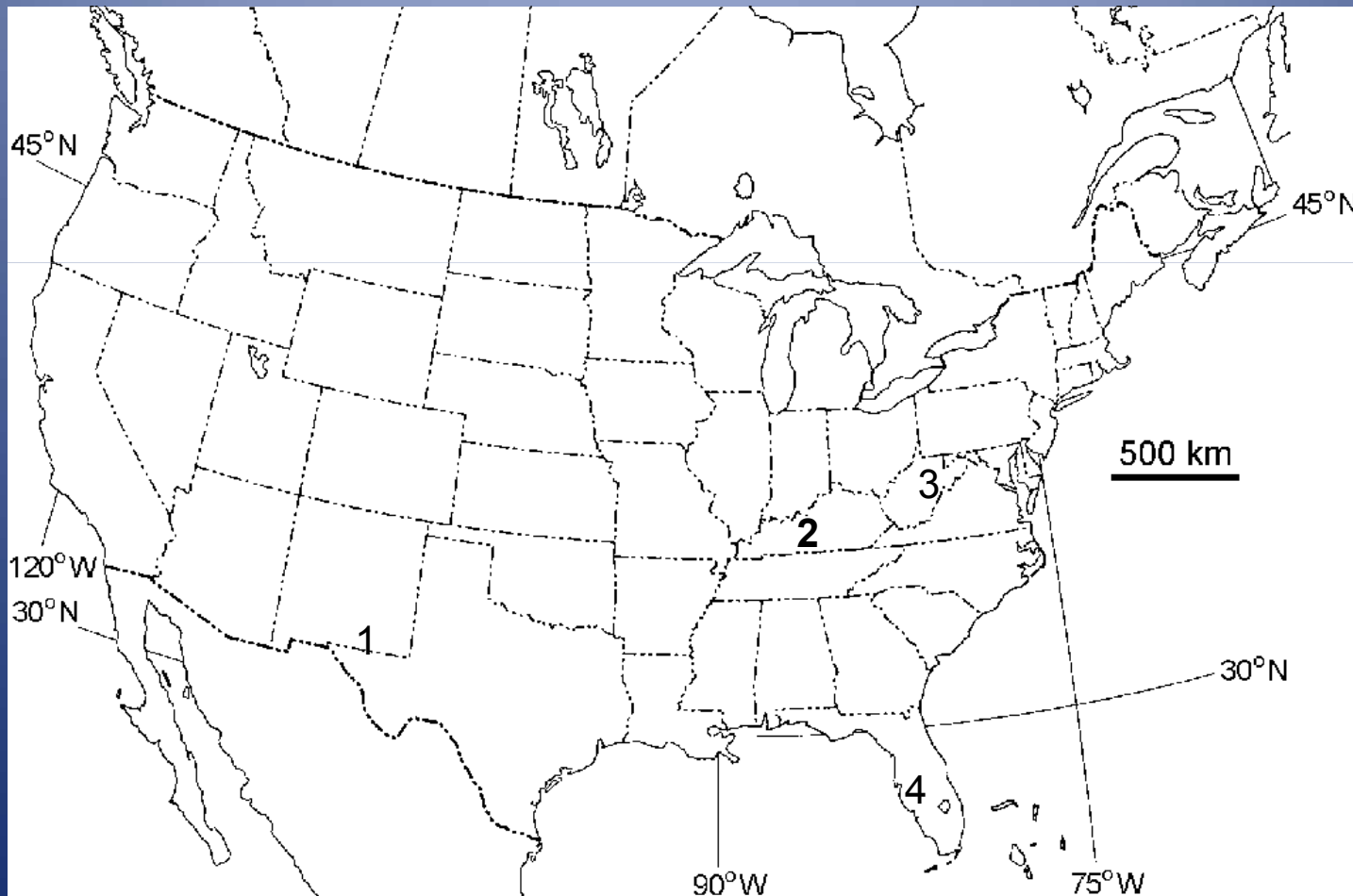
Thomas Farm, Florida
Collecting Miocene Bats

Thomas Farm Miocene Bats
Funnel Eared Bats (Family Natalidae)
Primonatalus prattae
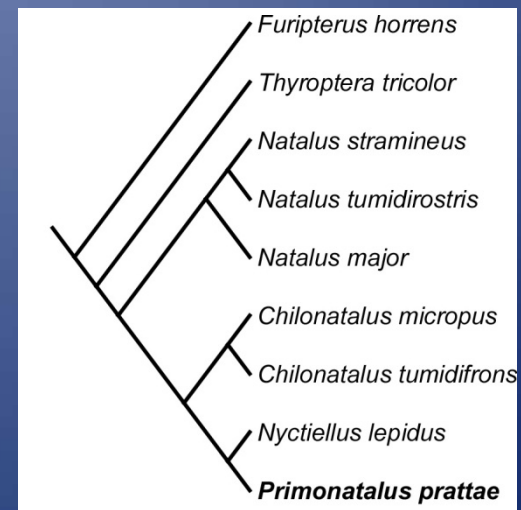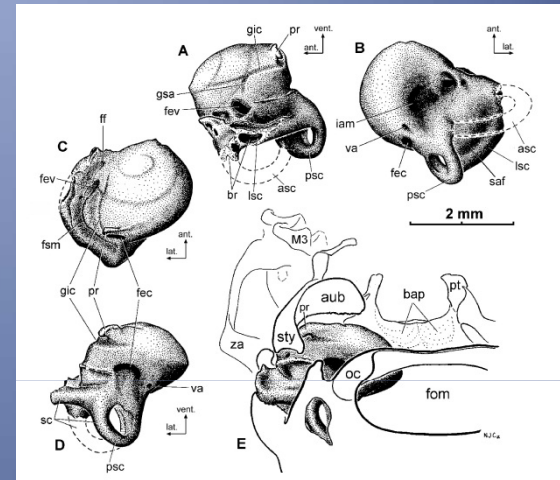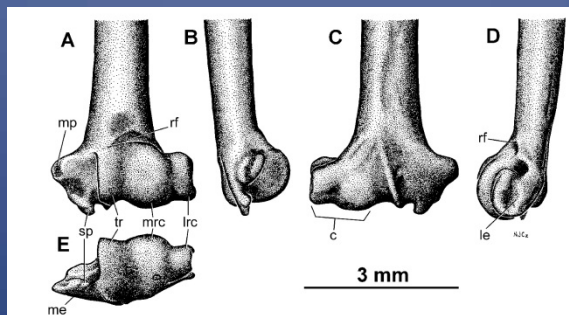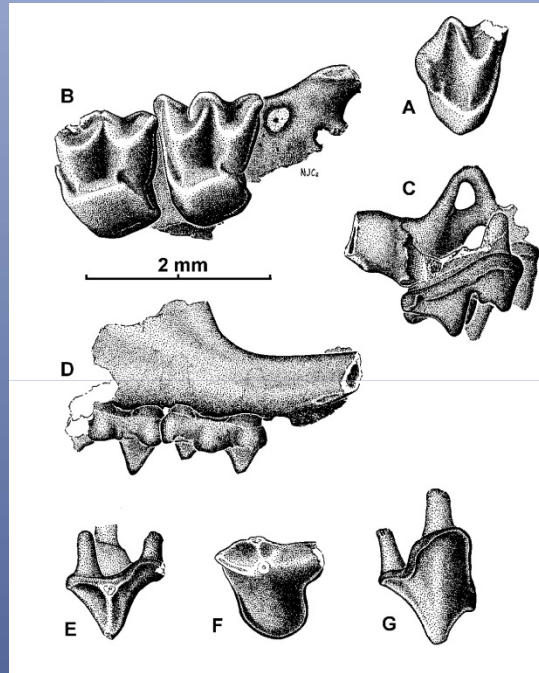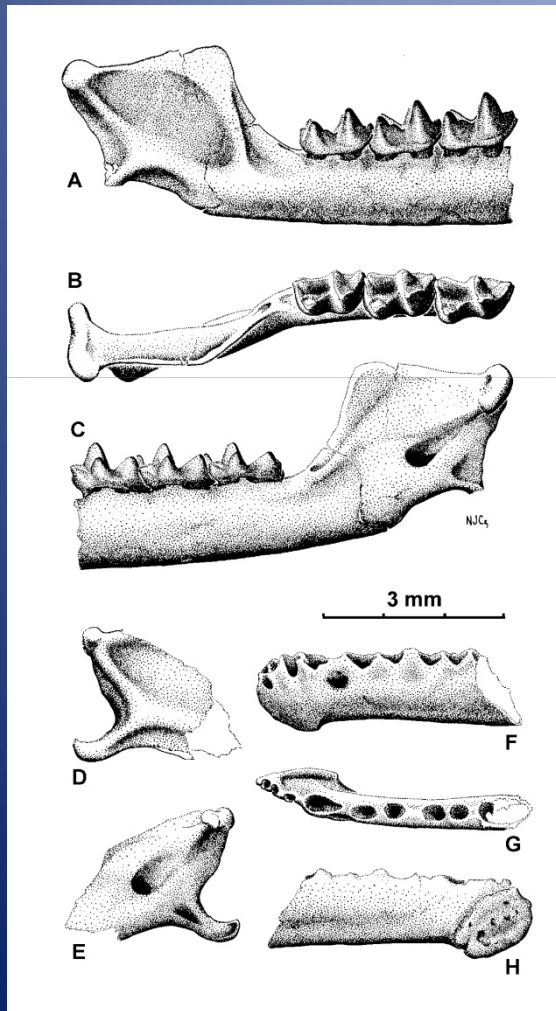
Illustrations by Nicholas Czaplewski (Morgan & Czaplewski, 2003)

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
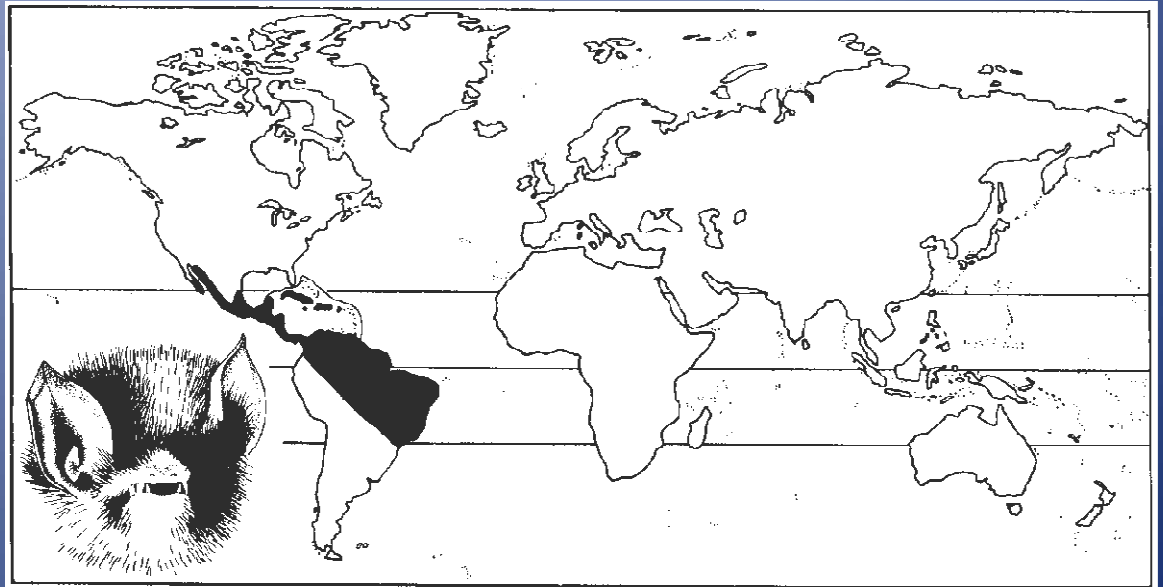
Modern distribution of Natalidae
(Hill & Smith, 1984)

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

Saccopteryx leptura
White-lined bat
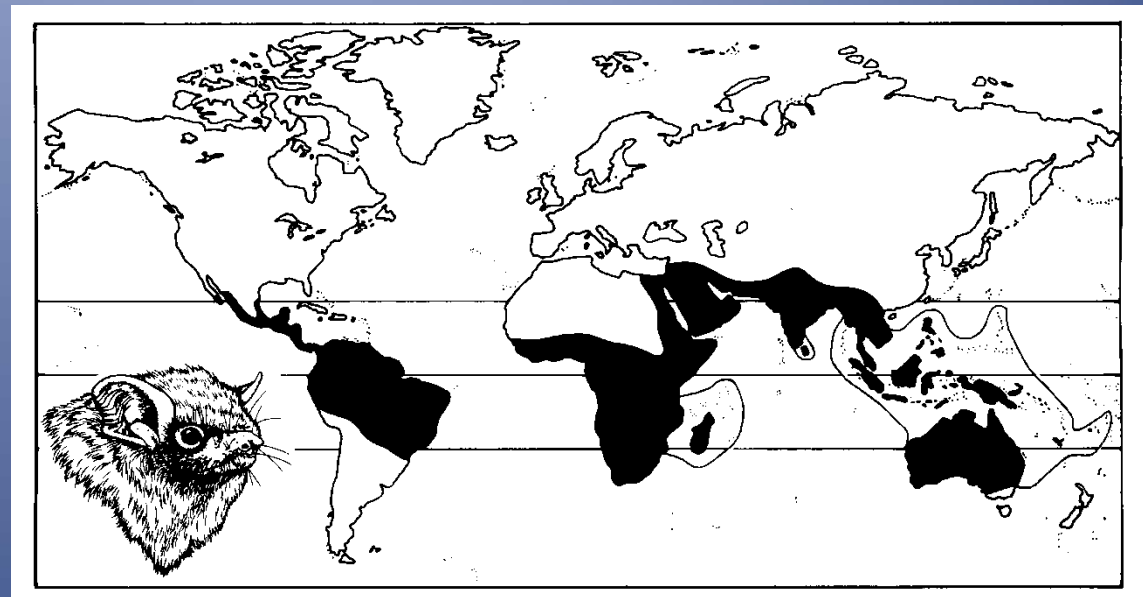
Modern distribution of Emballonuridae
(Hill & Smith, 1984)

Brooksville Fauna, Florida
Late Oligocene Bats

Mormoopidae   Emballonuridae

Lower jaw

Speonycteridae

Mormoopidae

Lower jaw   Phyllostomidae

Humerus

Ghost-faced Bats
Family Mormoopidae

Ghost-faced Bat
Mormoops megalophylla
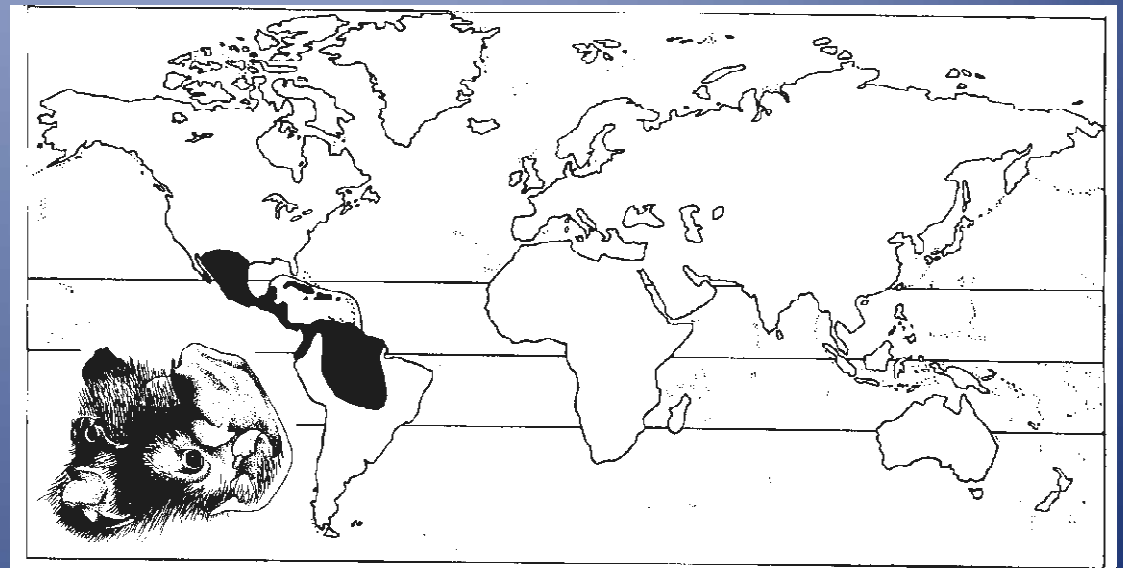
Modern distribution of (Mormoopidae)
(Hill & Smith, 1984)

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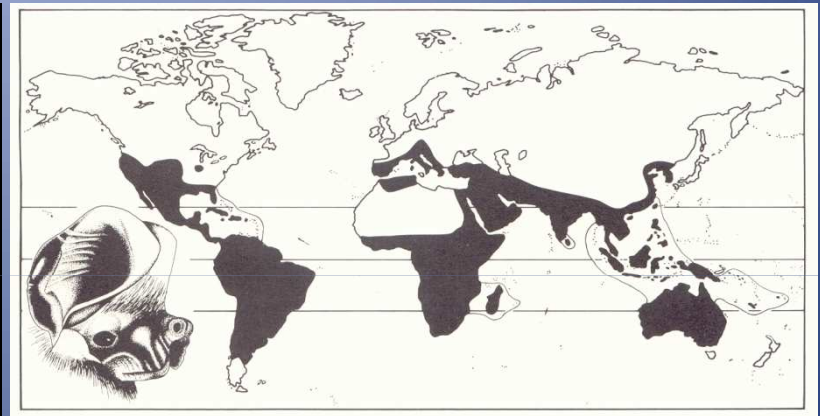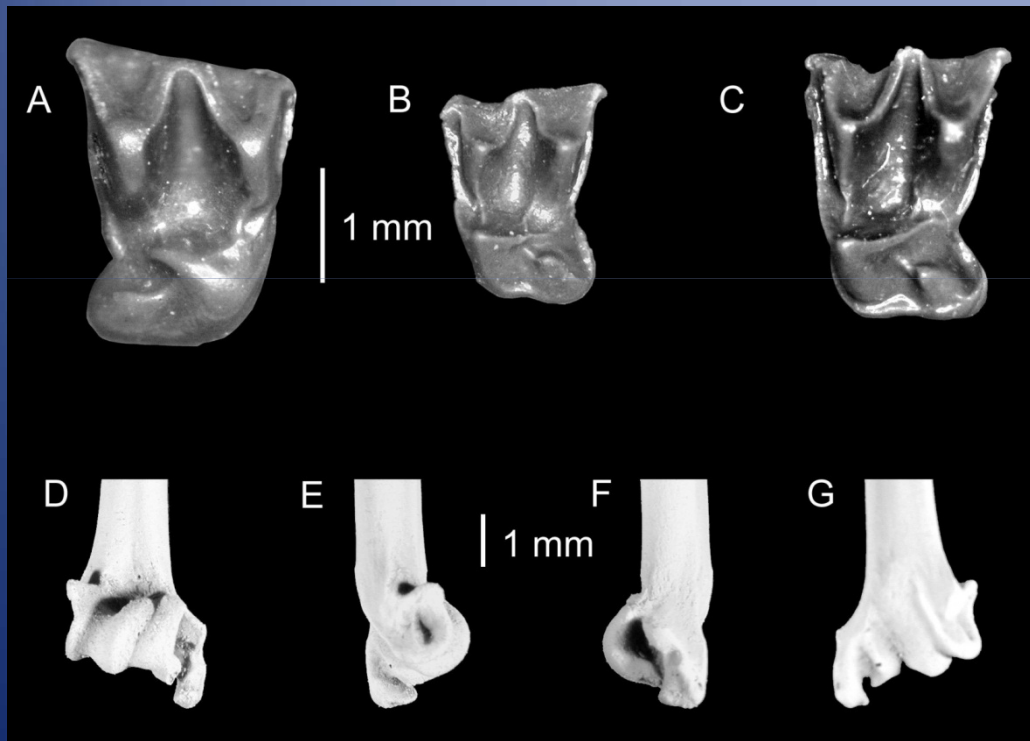
Modern distribution of Molossidae
(Hill & Smith, 1984)

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

Miocene Bats from Panama*
(*New discovery yesterday—not pictured)

Lower jaw of *Speonycteris*-like bat
early Miocene of Panama
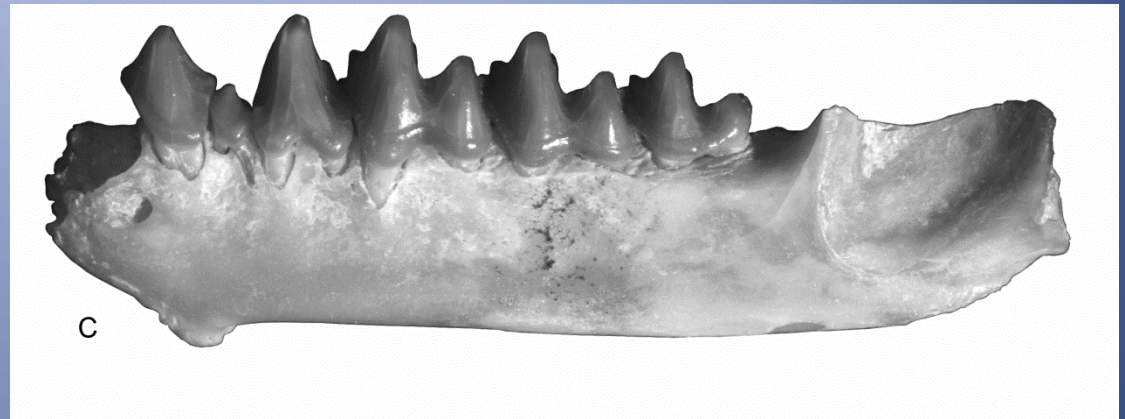
Lower jaw of *Speonycteris*
late Oligocene of Florida

Phylllostomus hastatus
Greater Spear-nosed Bat

Panama Canal

Great American Interchange

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

Phyllostomidae
Desmodus
(Vampire Bat)

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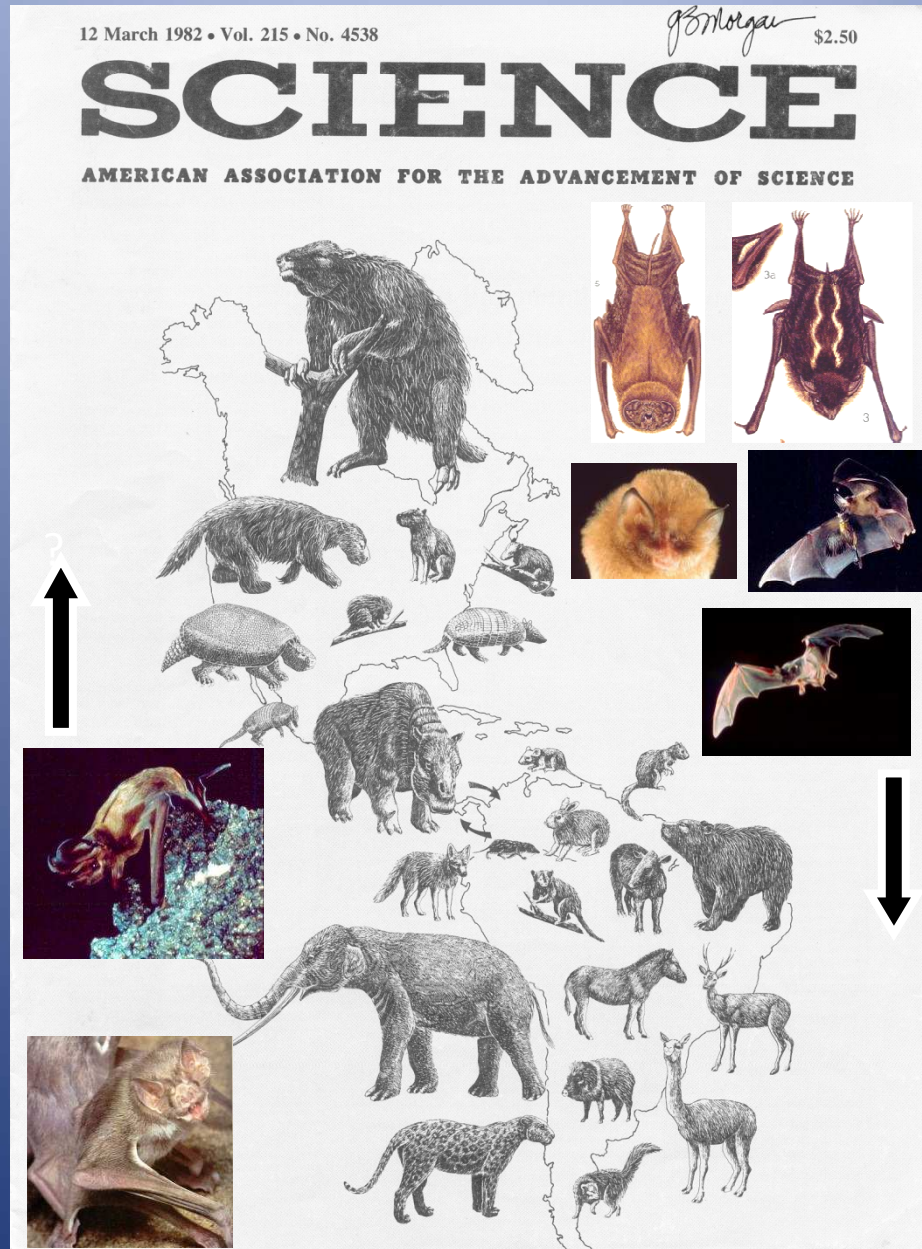
Groups from North America that dispersed to South America between the early Miocene and late Pliocene (~5-20 Ma)

Emballonuridae

Mormoopidae

Noctilionoidea

Natalidae

Molossidae
near *Tadarida*

# Phylogenetic Analysis of the Chiroptera
Morphology & Paleontology
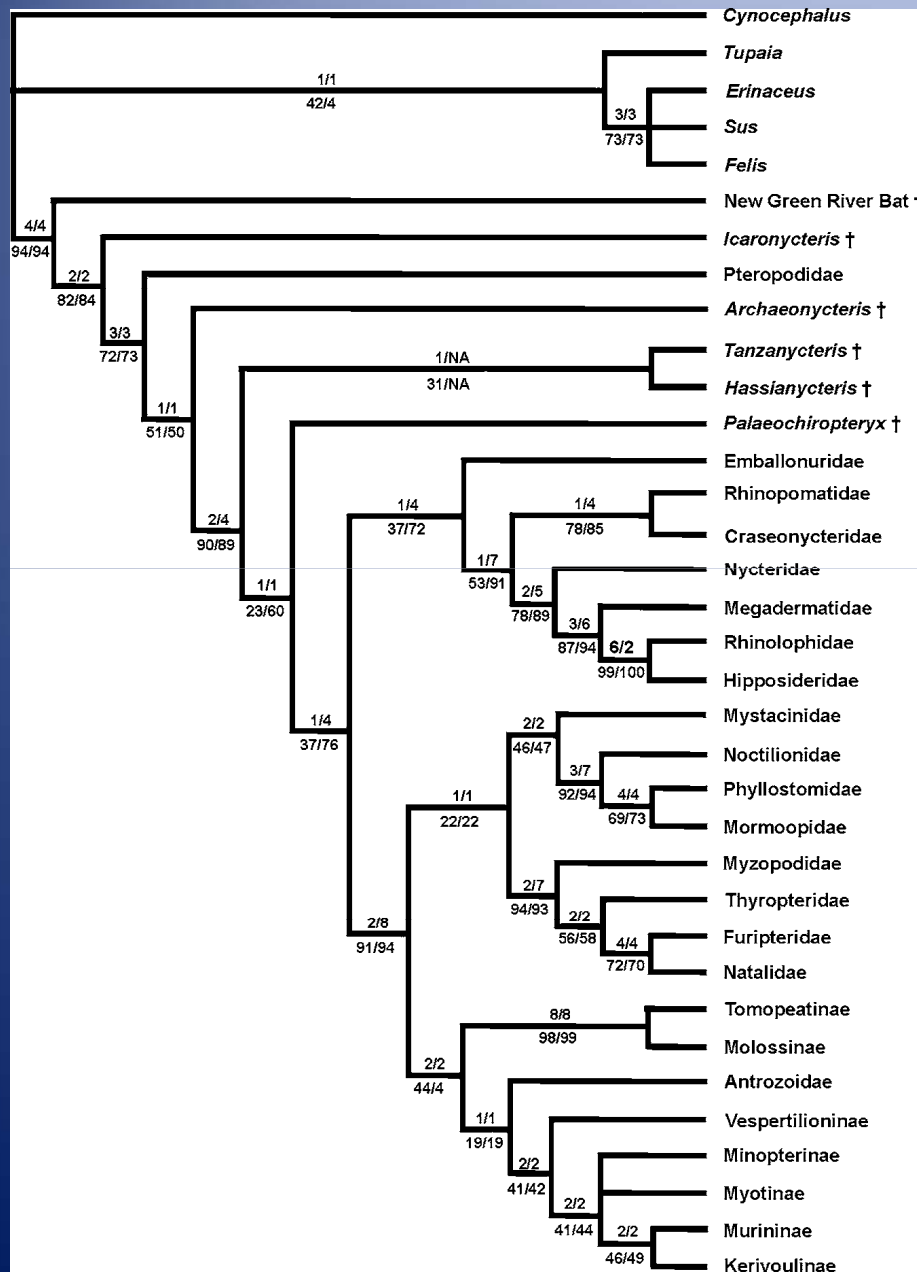
A strict consensus of four equally parsimonious trees (791 steps each) derived from analysis of our new morphological dataset. Numbers above the branches are decay values; those below the branches are bootstrap values. In each pair of numbers, the first number represents the support value calculated 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)
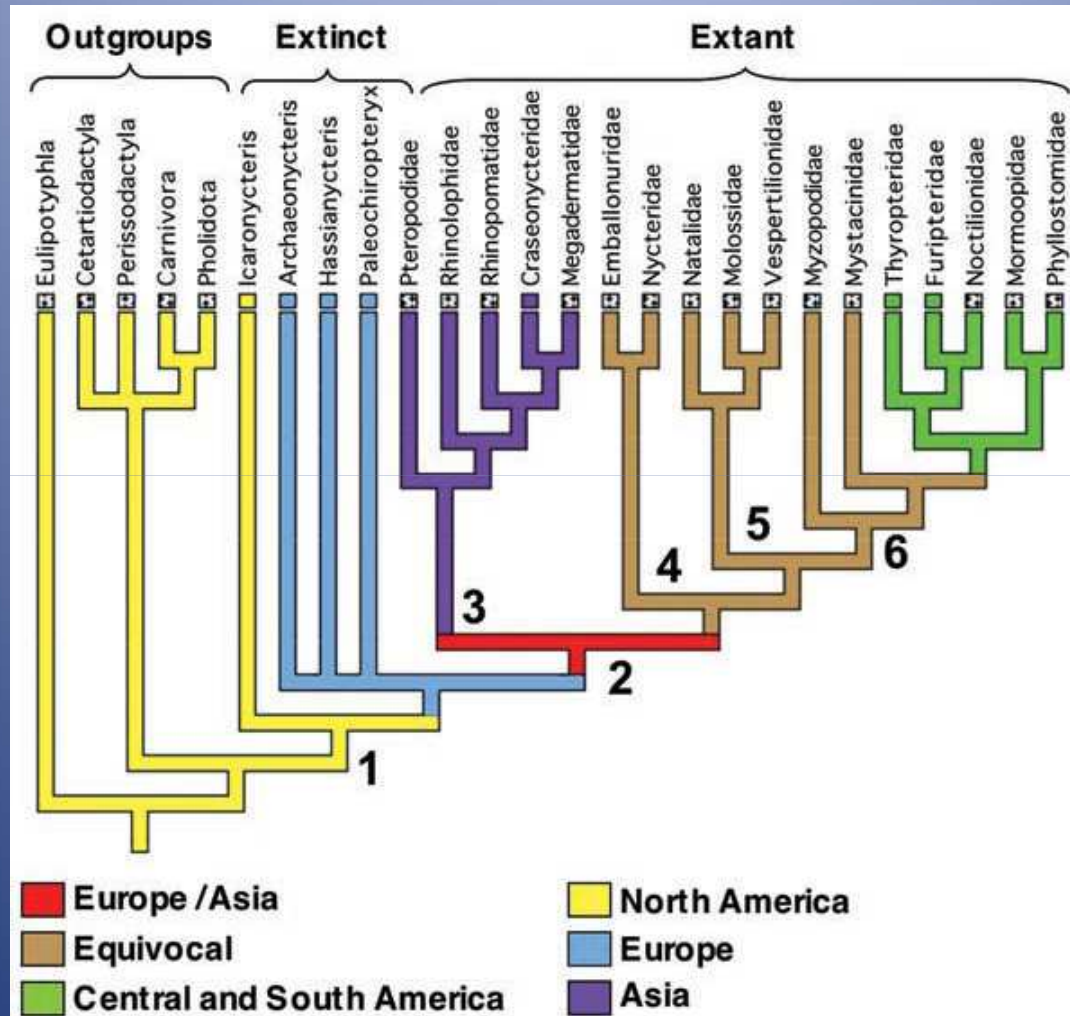
Molecular Phylogeny of the Chiroptera
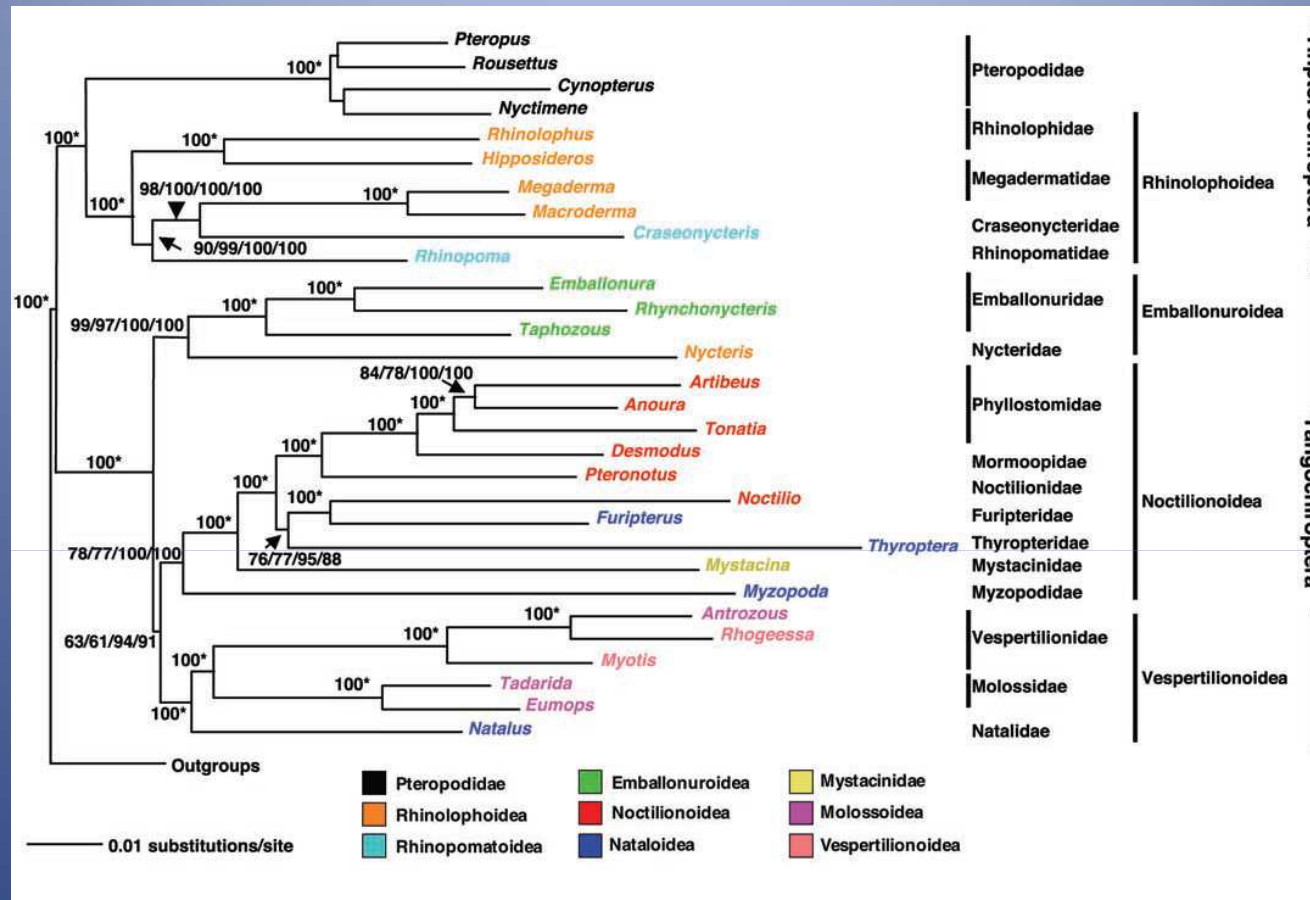
The maximum likelihood tree (–ln likelihood = 92127.3772) for the concatenated data set under the GTR + Γ + I model of sequence evolution. Numbers at the nodes are the (ML unconstrained bootstrap values)/(ML constrained bootstrap values)/Bayesian (single model posterior probabilities shown as percentages)/Bayesian (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
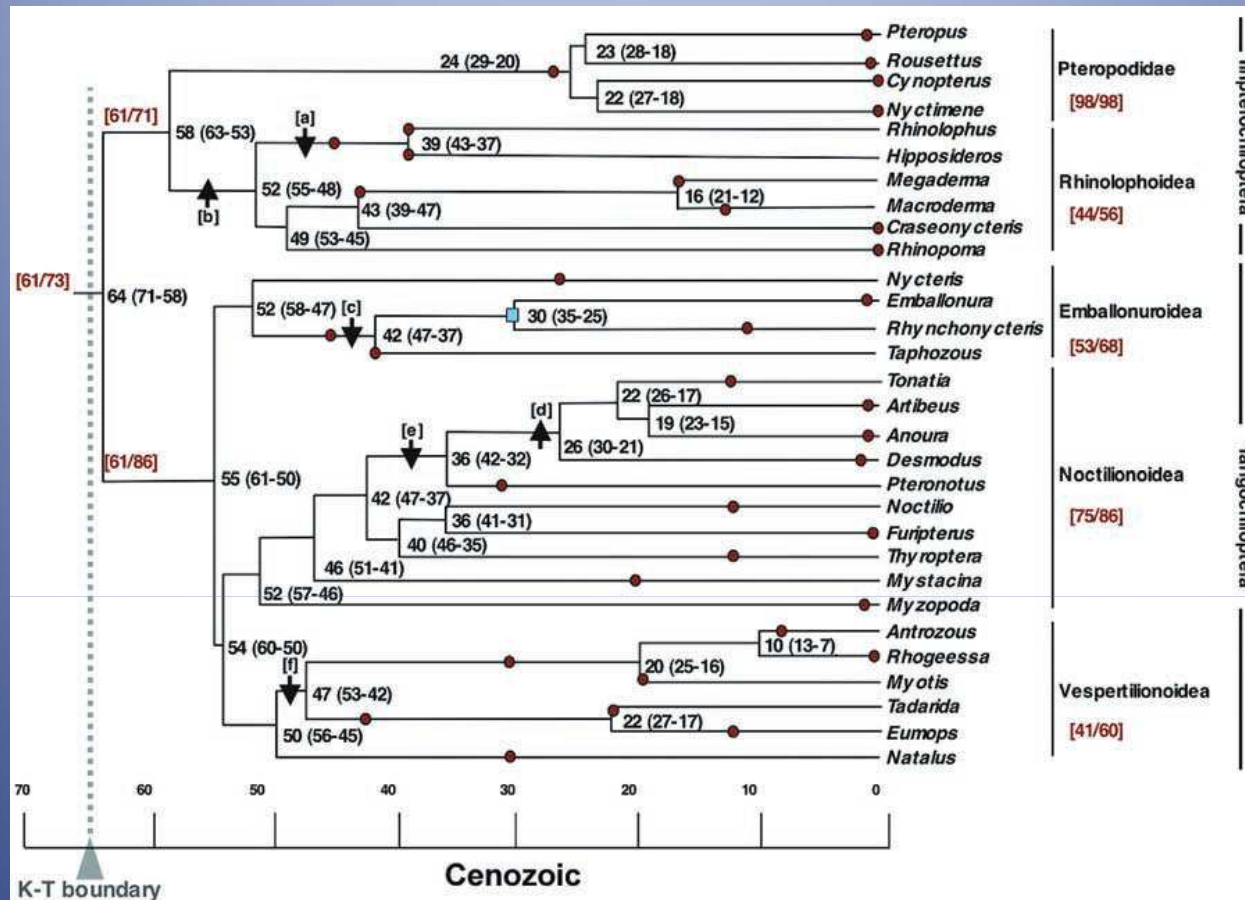
Molecular time scale for the order Chiroptera based on the divtime analyses (11), using the ML topology depicted in Fig. 1, six fossil constraints, and a mean prior of 65 Mya for the base of the ingroup root. Numbers at the nodes are the molecular dates in millions of years; values in parentheses are 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)

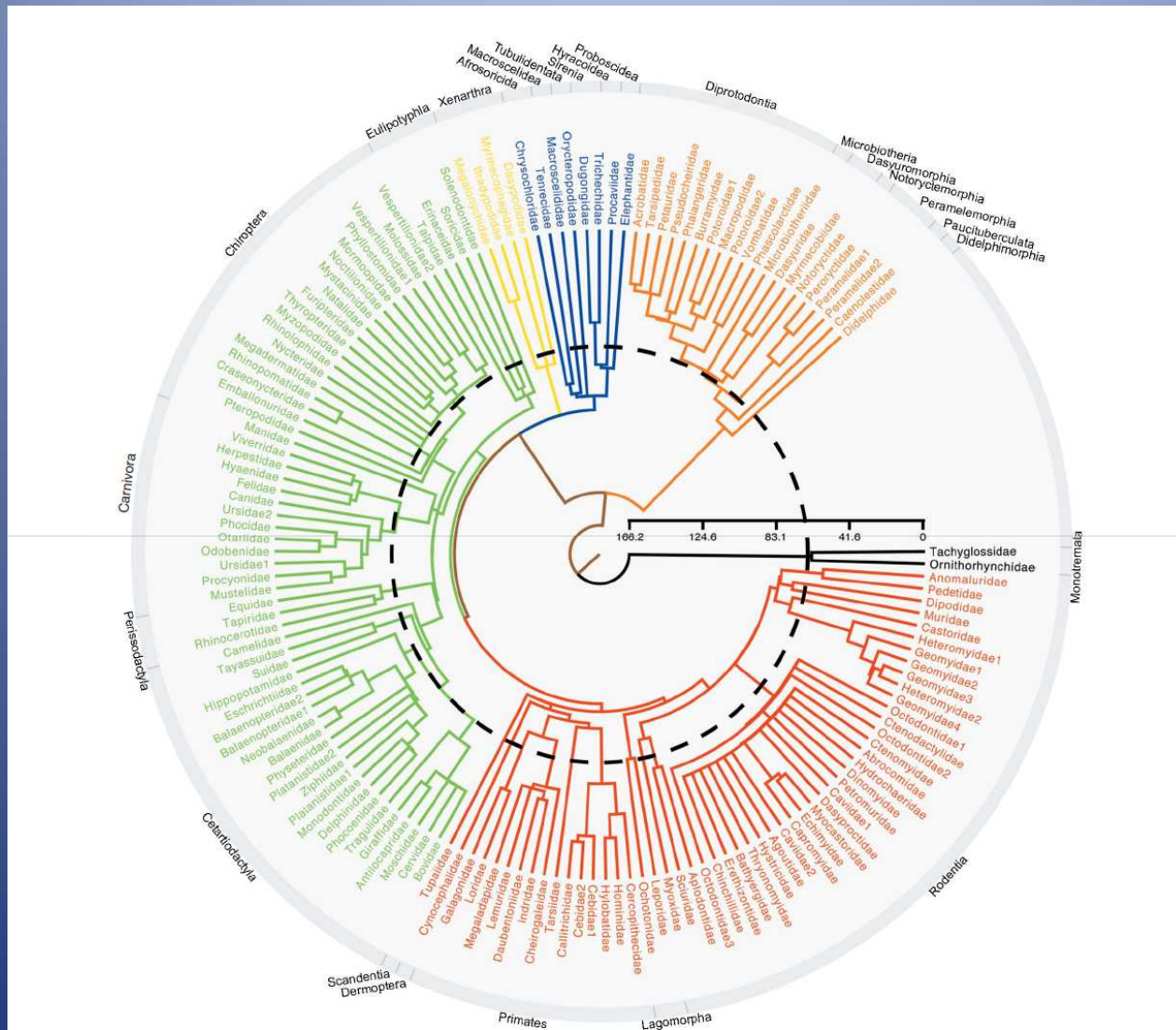# Molcular Phylogeny of the Mammalia

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, Euarchontoglires. 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)

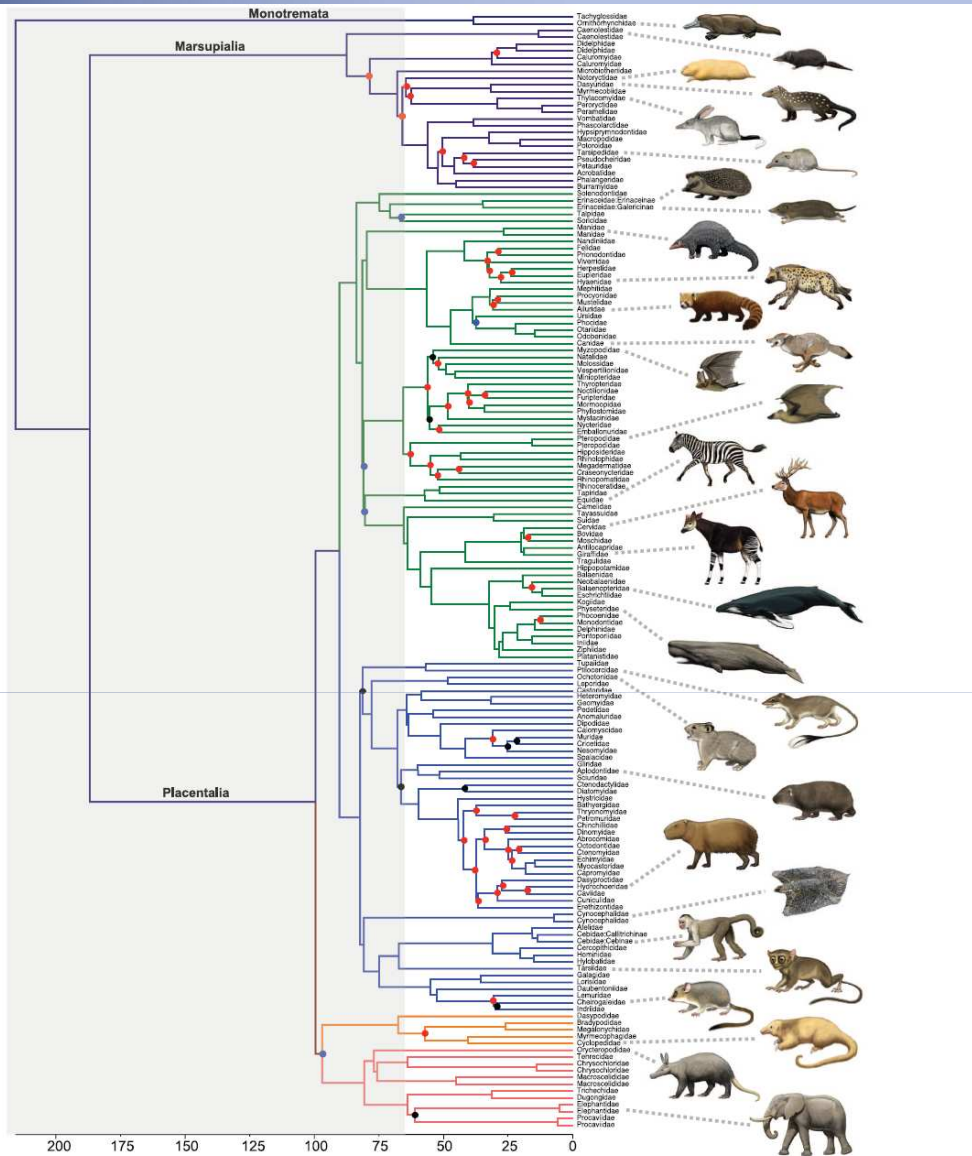# Another Molecular Phylogeny of the Mammalia

Fig. 1. Phylogenetic time tree of mammalian families (*13*) created on the basis of an analysis of the amino acid matrix (autocorrelated rates and hard-bounded constraints) of 164 mammals, rooted with five vertebrate outgroups (chicken, zebrafinch, green anole, frog, and zebrafish; see SOM for trees with outgroups). All nodes were strongly supported (BS ≥ 90%, BPP ≥ 0.95) in amino acid and DNA analyses except for nodes that are denoted by solid blue circles (conflict between DNA and amino acid trees) or solid black circles (DNA and amino acid trees agree, but with BS < 90%). Strongly supported nodes that disagree with Bininda-Emonds *et al.* (*8*) are indicated with solid red ci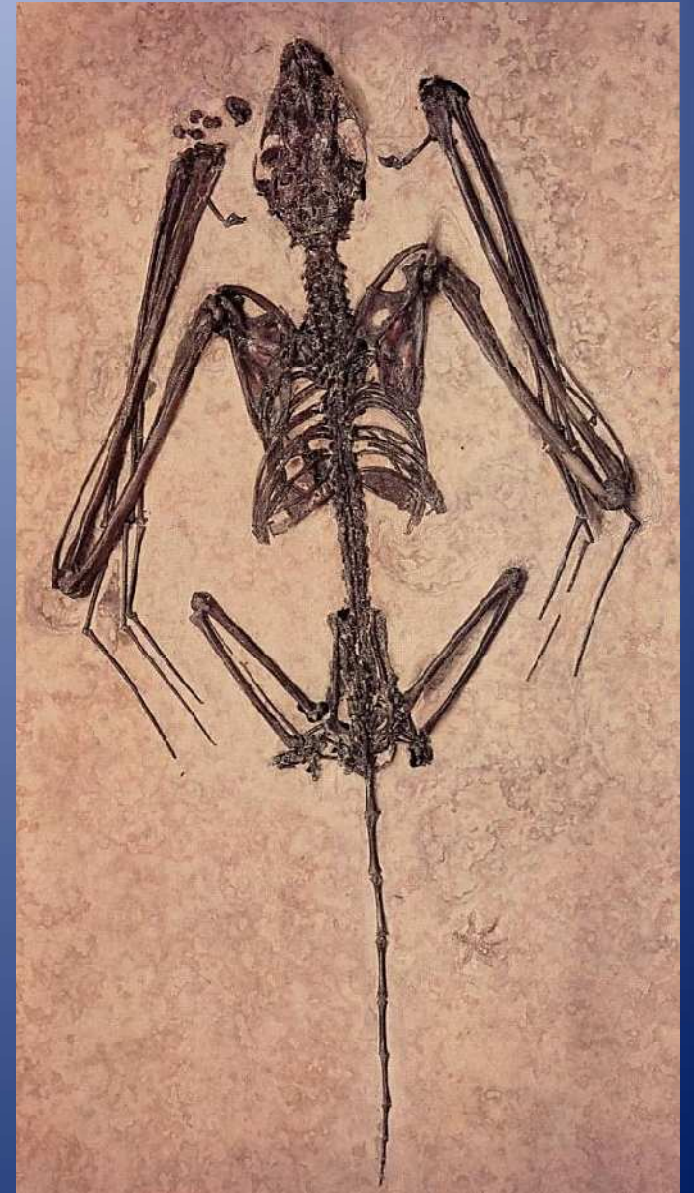rcles. Several nodes that remain difficult to resolve (e.g., placental root) have variable support between studies of rare genomic changes (*29, 30*), as well as genome-scale data sets (*31–33*), which suggest that diversification was not fully bifurcating or occurred in such rapid succession that phylogenetic signal tracking true species relations may not be recoverable with current methods. The KPg boundary is denoted by the transition from gray background (Mesozoic) to white background (Cenozoic). Color-coded branches in Placentalia correspond to Laurasiatheria (green), Euarchontoglires (blue), Xenarthra (orange), and Afrotheria (pink). See table S11 for ordinal affiliations of mammalian families. [Mammal paintings are by Carl Buell]

(Meredith et al., 2010)

Major Question in Bat Evolution?

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.

ACKNOWLEDGMENTS