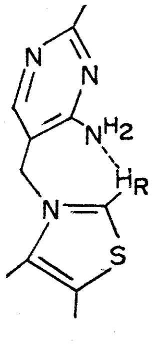
A comparison of the structures of thiamine (*6*), thiamine monophosphate (*4*), and thiamine pyrophosphate indicates that there is some flexibility in the preferred orientation between the two rings since the dihedral angles (the angle between the normals to the planes of the two rings) in these structures are 76°, 90°, and 84°, respectively. However, since the conformation of the rings in the three structures is basically similar, this is the likely conformation in the catalytically active molecule. According to Breslow's mechanism (*7*) the initial step in the reaction is the loss of a proton from the thiazolium ring. Part of the support for this mechanism rests on the observed acidic nature of this thiazolium ring hydrogen. In all three crystal structures containing the thiamine moiety, the thiazolium carbon which contains the active hydrogen participates as a hydrogen bond donor, an unusual role for carbon, which demonstrates its acidic character. In the subsequent steps of the proposed mechanism the substrate reacts with the resulting carbanion to form several different intermediates before the final product is released. By the use of space-filling models it is possible to build these intermediates with the rings in the abovementioned conformation. From these models it can be shown that formation of the intramolecular hydrogen bond is possible between the amino group and the substrate group as is illustrated diagrammatically below.



In order to achieve the most favorable spatial relationships for this intramolecular hydrogen bond formation, it is necessary to rotate the rings slightly (~10° to 15°) about both bonds to the methylene carbon and also to rotate the amino group slightly. The amount of rotation required depends upon the nature of the intermediate attached to the thiazolium ring and the specific hydrogen involved in the hydrogen bond formation. The structural possibility of forming these intramolecular hydrogen bonds may be significant in light of the suggestion by Breslow and McNelis (*8*) that several of the steps in the reaction sequence may be assisted by internal proton removal. The main conformational difference in the three structures is found in the dimethylene side chain to which the pyrophosphate group is attached. In thiamine pyrophosphate the dimethylene group extends to the opposite side of the thiazolium ring from that found in the other two structures.

Another structural feature of the thiamine pyrophosphate molecule worth noting is that the three nonprotonated pyrophosphate oxygens are directed away from the same side of the molecule. If a model of the molecule is supported on a flat surface by these three atoms, the remainder of the molecule is directed away from that surface (Fig. 3). In particular, the reactive site on the thiazolium ring points away from this surface. Since the pyrophosphate group apparently serves to bind the molecule to the enzyme, the structural arrangement observed here would allow the coenzyme to be bound to the protein surface and yet permit the reactive site to be freely accessible to the substrate. Also, small relative conformational shifts between the two rings can be readily accomplished as may be required for the various different intermediates in the reaction.

Because the crystals used in this analysis were very small, only about two-thirds of the reflections within the copper sphere could be measured. With this data it was possible to refine the structure anisotropically to a final agreement index (R factor) of 12 percent. At this stage of the refinement the estimated standard deviation in the P—O bond lengths is 0.010 Å whereas for the C—C and C—N bonds the average value is approximately 0.015 Å. Since it is desirable to know the structural parameters more accurately, the intensity data are being remeasured with a diffractometer from a somewhat larger crystal. The complete structure analysis utilizing the improved data will be published later.

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9. We thank F. Rial for his assistance in preparing the illustrations. Supported by NIH grant HE-09068.

14 October 1966

Early Eocene Bat from Wyoming

Abstract. *A fossil skeleton of an early Eocene bat, the oldest known flying mammal, was found in southwest Wyoming. The bat is assigned to the new species* Icaronycteris index *of the suborder Microchiroptera. It was apparently of a young male whose body was buried in varved marls of the Green River Formation, on the bottom of Fossil Lake, about 50 million years ago. The bones, some as slender as a human hair, show a few "primitive" characteristics such as a clawed index finger and a complete phalangeal formula, but the bat was fully developed —an anatomically precocious contemporary of the dog-sized polydactylous horse.*

Remarkably complete and beautifully preserved, the skeleton of an early Eocene bat (see cover) from southwest Wyoming represents the oldest-known genus and species, here named *Icaronycteris index,* within the order Chiroptera. Found about 33 years ago (*1*) in the fossil-fish marlstones of the Green River Formation, the specimen is one of the most extraordinary vertebrate fossils in both the superb completeness of the bony skeleton and the rare preservation of remnants of structures such as wing membranes, abdominothoracic diaphragm, and cartilages of the ribs and throat—even of fragmentary residues of ingested food.

I now report for the first time some of its unique characteristics. Living bats are so numerous, in contrast with the rarity of fossil bats, and have such diversified variations in functional adaptations (*2*) that every bone in this specimen, especially the carpus, may give information about the origin and evolution of bats.

Dorsal (Fig. 1) and ventral (Fig. 2) aspects of the specimen show some of the extensive cracking and crushing that attended postdepositional compaction of the investing sediments. The film-thin top of the skull is so shattered and flattened that the relative development (size) of the midbrain colliculi—one of the most significant and diagnostic traits of microchiropterans—cannot be determined. The right lower jaw has been pressed into and through the skull so far that some tips of the cusps of the lower teeth have pierced the palate and the skull roof; this penetration was favorable in that the crowns of the lower teeth could be further exposed in the laboratory without much additional destruction of skull bone.

Fortunate also was the movement of the left dentary from a vertical to a horizontal position: as a result, the entire external side of this jaw, and its teeth, could be exposed when the matrix was removed from the ventral side of the head (Fig. 2). Figure 2 also shows several delicate and minute skeletal structures (hyoid bones, No. 76; baculum?, No. 88) that are not frequently preserved in fossil vertebrates.

Extreme fragility and delicacy and the smallness of parts of the bat make study difficult: A flat area of the left scapula, now free of matrix on both sides, is translucently thin; and the gracile bony bar lateral to the vertebroarterial canal of the second cervical vertebra is only 0.07 mm thick. Excavation was tedious, and such sharp points were needed for removing the matrix that the steel digging needles had to be sharpened under the microscope (*3*).

The specimen's taxonomy follows:

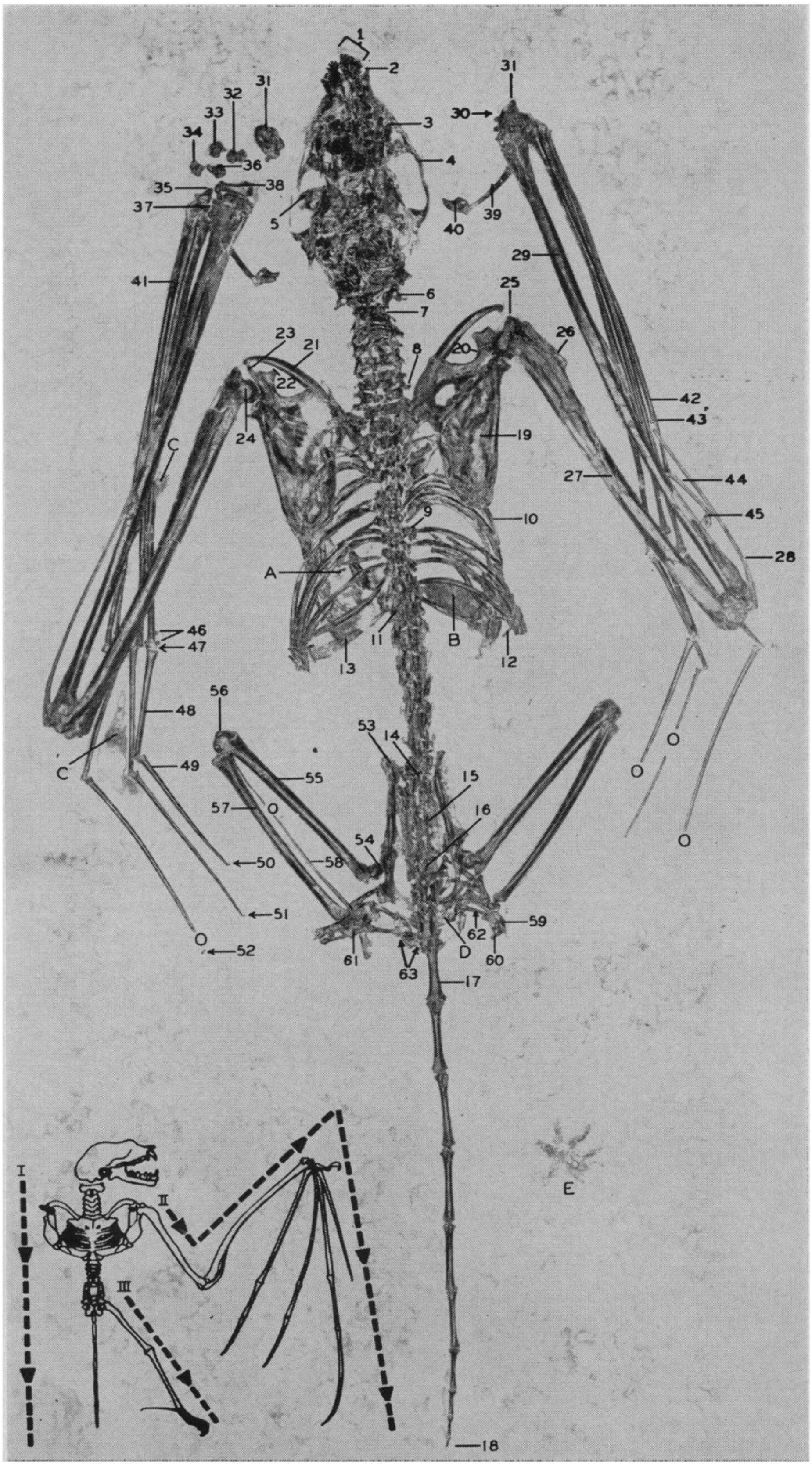
Order Chiroptera Blumenbach 1779
Suborder Microchiroptera Dobson 1875
Icaronycteridae, new family
Icaronycteris index (*4*), new genus and species; Figs. 1 and 2; Tables 1–4

Type: Princeton University Museum of Natural History No. 18150; skeleton lacking right fibula and several toe bones.

Known distribution: Early Eocene; Green River Formation of ancient Fossil Lake; about 21 m above Wasatchian Knight Formation; northwest quarter section 13, Township 21 North, Range 117 West, 8 km west of Kemmerer, southwest Lincoln County, Wyoming. 41°48′15″N, 110°39′W.

Previously illustrated: *Time* **37**(1), 44 (6 Jan. 1941).

Anatomy: Many of the vertebrate anatomists who have examined PU 18150, perhaps the smallest complete Tertiary mammalian skeleton, have remarked upon similarities in size and general structure to members of the *Myotis* group, probably because this genus of microbat is so well known and because it has a wider distribution than any other vertebrate genus except *Homo*.

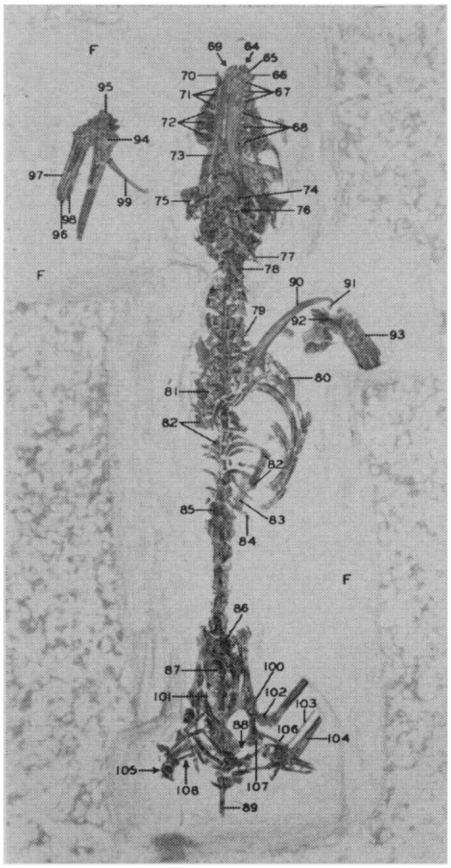


If the skull is counted as a single element, *I. index* had at least 254 bones and 38 teeth in its solid skeleton; all except a few of the 44 sesamoids in the wings and feet have been studied on one side or the other (or both) of PU 18150.

From head to tail and from limb girdles to limb ends *I. index* has the following distinctive combination of qualities, with the few that are especially characteristic of Megachiroptera indicated by *M*: long narrow head; premaxillaries not united at midline (*M*); dental formula, (2.1.3.3.)/(3.1.3.3.) = 38; diastema between upper incisors; one root on P2 and p2, two on p3 and p4, three on P3 and P4; W-shaped labial wall of upper molars; metaconid and long, deep talonid basin ("postfossid") on p4; long nasal bones (*M*); shallow eye orbits; no postorbital processes on frontals or jugals; zygomatic arch, slender, long, and complete; very small sagittal and occipital ridges; palate projected rearward beyond posterior molars; stylohyals, long, slender, and articulating with bullae; dentary body, long, low, and slender; mental foramina below i3 and p2; ascending process of dentary, broad anteroposteriorly, with high, rounded superior border (*M*); condyle of dentary, well above line of tops of molar cusps; angle of dentary, hook-shaped and pointed; vertebral formula, 7-12-7-3-13 or 14; no vertebral fusion except in sacrum; no coalesced ribs; segments of sternum (*5*), not fused; mesosternum, not keeled; pubic bones, loosely united at symphysis; pubic spine, short and robust; long and free tail; 5th to 7th caudal vertebrae, larger than others; tail tapers abruptly near tip; large supraglenoid tuberosity on scapula; coracoid process of scapula, long and slender—not bifid; clavicle, heavy and not expanded at ends; trochiter of humerus, large and articulates with scapula; high flange-like deltoid crest on straight, slender humerus; relatively short radius; no trace of sesamoid at end of ulna; large scapholunar; very flexible metacarpophalangeal joint; claw on thumb, not hooded; claw on index finger (*M*); digital formula, 2-3-3-3-3 (wing) and 2-3-3-3-3 (foot); all claws of wings and feet, compressed laterally; decreasing order of finger length, 3-4-5-2-1; femur comparatively robust; femur has a distinct, very short neck between head and shaft; femur head and neck, at angle to shaft; fibula, slender and well developed; fibula, slightly longer than tibia; tibia, shorter than femur; metatarsal I, shorter and heavier than others; big toe, shorter than other toes; no calcar; decreasing order of toe length, 4-3-2-5-1.

Characteristics of *I. index* that might be called "primitive" or "generalized," or lacking specialization among bats, are the (i) large number of teeth, (ii) shapes of teeth, (iii) uncoalesced ribs, vertebrae, and sternal segments, (iv) lack of prominent keel on the mesosternum, (v) long tail, (vi) shape of scapula, (vii) relatively short radius, (viii) index claw, (ix) complete phalangeal formula, (x) head and neck of the femur being at an angle to the shaft, (xi) big toe being shorter than the others, (xii) absence of calcar, and (xiii) low aspect ratio of the wings (see *5*).

Attempts to reconstruct the taphonomic (death-to-discovery) history of PU 18150 draw upon several areas of geobiotic information and upon experiments based on the assumption that



Figs. 1 (left) and 2 (right). Fig. 1. Dorsal aspect of *Icaronycteris index* (Princeton Museum of Natural History No. 18150; about 8:5 true size). Sketched at lower left is the skeleton of a greater horsehoe bat [redrawn from Hooper (*22*)] to indicate numbering sequence: *I*, axial bones of skeleton, anterior to posterior; *II*, wing bones, proximal to distal; *III*, leg and foot bones, proximal to distal. Fig. 2. Ventral aspect of *I. index;* about 5:4 true size. Bones and features, Figs. 1 and 2:

1, right upper and lower incisors; *2*, right upper canine; *3*, right orbit; *4*, right zygomatic arch; *5*, ascending ramus of left dentary; *6*, right lateral process of atlas; *7*, axis (No. 78, Fig. 2); *8*, seventh cervical vertebra (No. 79, Fig. 2); *9*, second segment of mesosternum (anterior part of No. 82, Fig. 2); *10*, fourth right rib; *11*, first lumbar vertebra (No. 85, Fig. 2); *12*, costal cartilage; *13*, twelfth left rib (No. 84, Fig. 2); *14*, seventh lumbar vertebra (No. 86, Fig. 2); *15*, sacrum (No. 87, Fig. 2); *16*, first caudal vertebra; *17*, fourth caudal vertebra (No. 89, Fig. 2); *18*, thirteenth caudal vertebra; *19*, right scapula; *20*, suprascapular notch; *21*, left clavicle (No. 90, Fig. 2); *22*, supraglenoid tuberosity of left scapula; *23*, acromion process of left scapula (No. 91, Fig. 2); *24*, head of left humerus; *25*, trochiter (greater tuberosity) of right humerus; *26*, pectoral ridge of right humerus; *27*, shaft of right humerus; *28*, right ulna; *29*, shaft of right radius; *30*, sesamoid of right wrist; *31*, right and left scapholunars (No. 95, Fig. 2); *32*, left magnum; *33*, left trapezoid; *34*, left cuneiform; *35*, left unciform; *36*, left trapezium; *37*, left pisiform; *38*, metacarpal of left digit *I*; *39*, first phalange of right digit *I* (No. 99, Fig. 2); *40*, second phalange (claw) of right digit *I*; *41*, left metacarpal *IV*; *42*, right metacarpal *II* (index finger); *43*, first phalange of right digit *II* (index finger); *44*, second phalange of right digit *II* (index finger); *45*, third phalange (claw) of right digit *II* (index finger); *46*, sesamoids; *47*, metacarpophalangeal joint of left digit *V*; *48*, first phalange of left digit *V*; *49*, second phalange of left digit *V*; *50*, third phalange of left digit *V*; *51*, third phalange of left digit *IV*; *52*, third phalange of left digit *III*; *53*, left iliac crest of pelvis; *54*, head of left femur (No. 102, Fig. 2); *55*, shaft of left femur; *56*, left patella; *57*, left tibia (No. 104, Fig. 2); *58*, left fibula (No. 103, Fig. 2); *59*, right calcaneum; *60*, right astragalus; *61*, left cuboid; *62*, right metatarsals; *63*, claws; *A*, fish scale; *B*, diaphragm?; *C*, remnants of wing membranes?; *D*, coprolite; *E*, flower; *F*, varves; *O*, bone missing; *64*, left lower incisors; *65*, left lower canine; *66*, left upper canine; *67*, left lower premolars; *68*, left lower molars; *69*, shattered symphysis of right dentary; *70*, right upper canine; *71*, right upper premolars; *72*, right upper molars; *73*, ventral border of right dentary; *74*, angle of left dentary; *75*, right postglenoid foramen; *76*, left stylohyal; *77*, left lateral process of atlas; *78*, axis (No. 7, Fig. 1); *79*, seventh cervical vertebra (No. 8, Fig. 1); *80*, second left rib; *81*, manubrium (episternum); *82*, mesosternal segments (see No. 9, Fig. 1); *83*, xiphisternum; *84*, twelfth left rib (No. 13, Fig. 1); *85*, first lumbar vertebra (No. 11, Fig. 1); *86*, seventh lumbar vertebra (No. 14, Fig. 1); *87*, sacrum (No. 15, Fig. 1); *88*, baculum; *89*, fourth caudal vertebra (No. 17, Fig. 1); *90*, left clavicle (No. 21, Fig. 1); *91*, end of acromion process, left scapula (No. 23, Fig. 1); *92*, coracoid process of left scapula; *93*, pectoral ridge of left humerus; *94*, distal end of right radius; *95*, right scapholunar (No. 31, Fig. 1); *96*, right metacarpal *II*; *97*, right metacarpal *III*; *98*, right metacarpal *V*; *99*, first phalange of right digit *I* (No. 39, Fig. 1); *100*, rim of left acetabulum; *101*, right pubic spine; *102*, head of left femur (No. 54, Fig. 1); *103*, left fibula (No. 58, Fig. 1); *104*, left tibia (No. 57, Fig. 1); *105*, right ankle; *106*, first phalange of digit *I*, left foot; *107*, second phalange (claw) of digit *I*, left foot; *108*, metatarsals of right foot (No. 62, Fig. 1).

bat behavior, in life and death, and the physical and biotic conditions in nature were about the same in early Tertiary time as they are now.

The following individual characteristics of PU 18150 are pertinent to its preservation:

Age. All permanent teeth of the bat are fully erupted and worn to a degree normal in some 2- to 3-year-old microchiropts (*6*). The lingual slope of each molar parastyle shows comparatively heavy wear and many surficial fractures, perhaps the result of specific but unknown feeding habits. Epiphyses of the long bones are solidly welded to the shafts, and most of the cranial sutures seem to be obliterated.

Sex. A small bone is in the appropriate position at the rear of the pelvis (Fig. 2, No. 88) to be an os penis; it has the tapered-club shape characteristic of the bacula of some small bats (*7*).

Skeletal pose. Experiments indicate that the bone positions (Fig. 1) are normal for a dead bat in water—with the wings folded and the femora at angles to the vertebral column. In a bat having a well-developed uropatagium, however, the tail must be curved forward under the body when the femora are at the angle (about 45° to the body axis) of this specimen; this fact and the apparent absence of calcars are evidence that the bat was free-tailed. The anatomy of dead bats causes them to sink through water back first, with the wings trailing upward, and to rest, on the bottom, belly-side up. PU 18150 was probably buried in the calcitic ooze in this position, although no field records of its attitude were made at the time of its discovery. All minor displacements of the bones (except those of the left wrist) are readily explained by the collapse of the carcass as the muscles and ligaments and other tissues disintegrated, and as the weight of muds accumulating on the lake bottom pressed downward upon its ventral side.

Table 1. Skeletal dimensions of the bat.

Item	Dimensions (mm)
Skull	
Ant. border I2 to post. occipital condyle	20.1
Ant. border premax. to post. border supraoccipital	21.2
Ant. border of premax. to ant. border of orbit	~6.0
Jaw	
Depth below p2	1.5
Depth below m1	1.6
Depth below m3	1.6
Thickness below p3	1.0
Thickness below m3	0.8
Rear border m3 to rear of condyle	6.2
il To tip of angle	15.3
*Body, midline**	
Overall length	125.0
Vertebrae:	
7 Cervicals: dorsal, neural arches	9.3
ventral, centra	9.9
12 Thoracics: dorsal, neural arches	17.2
ventral, centra	18.1
7 Lumbars: dorsal, neural arches	16.4
ventral, centra	16.7
Sacrum: dorsal, neural arches	6.2
ventral, centra	5.8
13 Caudals	52.4
Baculum	0.35

* Dorsal dimensions less than when measured around the curve of the original body.

Ingested material. Within the area of the rib cage, a single scale (Fig. 1, *A*) of a small fish has evoked speculation that it may have been in the intestinal tract of the bat. This inference (supported by the provenience of the skeleton) is more reasonable than the possibility that the scale drifted into this position after the bat's death. Several kinds of bats eat fish (*8*), and some such forms, like *Pizonyx* and *Noctilio leporinus,* use their exceptionally large feet to gaff fish at the surface of the water. The feet of *I. index* are no larger than the feet of many living microbats; nor are special aptitudes for fishing or swimming otherwise indicated.

Constituents of the very small mass of fecal material (Fig. 1, *D*) near the posterior border of the pelvis have not been fully identified; it may include bits of insect chitin and fragments of bacteria, algae, pollen, spores, and arthropods.

Cause and place of death. No sign of disease, functional (respiratory, neural, or circulatory) failure, or injury is clearly manifest in the skeleton, although the slight displacement of bones in the lumbar, left carpal, and sternal areas may have resulted from attack by bird or fish; either of these predators, however, would probably have consumed the bat. Perhaps, but improbably, it was killed by lightning or hail.

Neither can one determine where the bat died: on land (with subsequent transportation into the lake), above the water, or in it. Bats frequently drink water to compensate the great evaporation from their wings; some scoop up water with their mouths from streams and lakes during crepuscular and nocturnal flight.

Sediments enclosing PU 18150 were deposited in quiet water, with little or no current at the bottom, but the body may have been carried to its site from shore (perhaps a few kilometers to the east) by surficial currents. The longer it drifted on the surface or in the water of the epilimnion, the more remarkable became the fact that it was not destroyed by fish or other predators before it sank into the near-sterile hypolimnion.

Flower. Near the midpoint of the bat's tail is a small, delicate, unidentified flower (Fig. 1, *E*) having six petaloid structures and a stem; it presumably reached the lake floor about 1 year later than the bat, because it is enclosed in the tan carbonate layer of the varve that was originally the next one above that enveloping the skeleton.

All flying mammals are formally classified in the ordinal taxon Chiroptera, which has no nonvolant mem-

Table 2. Dental dimensions of the bat; measurements are of elements of the right side, except where indicated by (L).

Item		Dimensions (mm)	
Upper			
I2–rear M3		9.3	
M1–3 (midline)		3.7	
Ant.–post. diam.: I2		0.5	
I3		0.6	
C		1.1	
Midline length:	P2	0.5	
	P3	0.9	
	P4	1.3	
Midline:	M1	1.1	
	M2	1.1	*
	M3	1.0	
External border length:	M1	1.3	
	M2	1.4	†
	M3	1.3	
Width:	M1	2.1	
	M2	2.4	‡
	M3	2.2	
Lower			
il–Rear m3		9.3 (L)	
il–Rear of condyle		15.3 (L)	
il–Tip of angle		15.3 (L)	
c–m3		8.3	
Ant.–post. length			
c		0.8	
p2		0.7	
p3		1.1	
p4		1.2	
m1		1.5	
m2		1.5	
m3		1.5	
p2–p4		3.3	§
m1–m3		4.5	
p2–m3		7.7	

* Total less than the midline length of M1–3 together, because the teeth are wasp-waisted. † Total of external labial border lengths is greater than midline length of M1–3 because labial styles overlap. ‡ Parastyle to innermost (lingual) base of cingulum, a diagonal dimension. § Total is greater than p2-m3 because of overlap.

bers. It is usually divided into two suborders: (i) Megachiroptera, large Old World tropical fruit bats (all in the family Pteropidae), having a clawed ungual phalanx on the index finger and teeth of simple crown pattern, and (ii) Microchiroptera, almost worldwide in distribution and in many families, that lack an index claw and have diversified tooth forms that correlate with feeding habits. Upper molars of most of the insect-eating bats have a W-shaped external wall. (These statements grossly oversimplify the complexity of bat structure, but retain a classic, nearly true, and useful simplicity.)

Icaronycteris index differs from all other known bats by combining the megabat characteristic of clawed index finger with the typical insectivorous microchiropteran structure of W-shaped labial crests on the upper molars. Allocation of this new form to either the Microchiroptera or Megachiroptera therefore makes it an exception to the long-serviceable generality that in bats an index claw is associated with simple teeth and that lack of that claw usually accompanies W-form molars. One could retain this old quality-pair criterion by continuing to ignore the few minor and inconvenient exceptions to it and to create a third suborder, Mesochiroptera, for the reception of the family Icaronycteridae and subordinate taxa in a taxonomic hierarchy for the species *I. index.*

Clearly, however, this species is more similar, and hence presumably more closely allied phylogenetically, to living microchiropterans (in teeth, "advanced" type of shoulder articulation of humerus and scapula, long tail, and many other anatomical features) than it is to megachiropts; therefore I tentatively classify it within the suborder Microchiroptera. It has not been possible to compare PU 18150 with the bones of all other Tertiary bats, but all described fossil bats are apparently more recent (mid-Eocene to Recent), and none has this combination of skeletal structures (*9*).

Recently I have examined a partial skeleton (axial elements, limb girdles, and proximal segments of the limbs) of a bat (*10*) from a level of rock (*11*) apparently higher and less ancient (mid-Eocene, Bridgerian) than the level (early Eocene, Wasatchian) yielding PU 18150. A dense, hard matrix covers most of the soft bone of this specimen but study of the exposed parts, and of x-ray photos of the whole, shows that it is smaller than PU 18150 and different in many proportions (*12*).

A few other American specimens of early Tertiary age (Paleocene and Eocene), once believed to represent taxa of bat ancestors, have been lost physically or by reallocation to nonbat orders (*Vesperugo anemophilus, Zanycteris paleocena, Nyctitherium, Picrodus*). Search in American pre-Eocene rocks has not found fossil bones that certainly pertain to bats. Thousands of man-hours of work on the eroded Paleocene rocks in the Bighorn Basin of Wyoming have discovered many thousands of fossil vertebrate specimens (many of them as small as analogous parts of most bats) but not a single fragment that is clearly related to bats. Paleocene sediments in other western states have been explored with similar results. Traces of early bats may have been sought in the wrong places; filled ancient crevices and fissures may be more favorable sites.

Tilly Edinger (*13*) recently discussed a fossil, Princeton University No. 16494, from the late-Paleocene Silver Coulee beds in the Polecat Bench Formation of northwest Wyoming. This specimen, the cracked and incomplete rear part of a head and about 25 mm long, lacks the front half of the skull and all teeth, the conventional basis for most paleomammal classifications. Edinger believes that the development of the large midbrain acoustic colliculi (posterior corpora quadrigemina), clearly preserved in the flattened clay endocast, indicate that the animal was a chiropteran.

Regretfully (as discoverer of the specimen) I cannot confirm Edinger's conclusion; the bones of the skull show that it was not the cranium of a flying animal: They are heavy, unlike the gracile and delicate analogous regions in heads of bats. Detailed osteologic analysis of the skull is here out of place, but all its observable structures closely resemble those of some larger contemporary miacid carnivores from the same quarry.

One such specimen (Princeton University No. 16495), with a midbrain endocast sufficiently well preserved to reveal the colliculi also, shows that the posterior ones are bigger than the anterior pair. The teeth of this specimen place it in or near the miacid genus *Protictis,* and many details of its posterior cranial structures ally it closely with PU 16494: in both crania the position of the fossa subarcuata is similar, and the mastoid process is similar in position and shape—as is the stylohyoid fossa, the fenestra ovale, the foramen lacerum medium, the glenoid pedicle, and many another feature. Several lower jaws almost certainly represent the species to which cranium PU 16495 pertains, and one dentary (PU 16523), with the diagnostic first lower molar in place, is of proper size and structure to be part of the same individual as PU 16494. Unfortunately,

Table 3. Dimensions of elements of limbs of the bat; unless indicated by (L), they are of elements of the right side.

Item	Dimensions (mm)
Wing	
Spread	~310.0
Length:	
Humerus	34.3
Radius	48.0
Ulna	28.0
Metacarpal I	3.5
II	28.5
III	40.1
IV	39.0
V	38.0
Phalanx: 1, digit: I	5.7
1 II	4.9
1 III	10.9
1 IV	11.5
1 V	10 1 (L)
2 I	2.7 (claw)
2 II	4.9
2 III	18.8 (L)
2 IV	16.1 (L)
2 V	12.2 (L)
3 II	1.5 (claw)
3 III	0.4 (clawlet?) (L)
3 V	.3 (clawlet?) (L)
Hind limb	
Total length of pelvis	13.9
Iliac crest to center of acetabulum	9.2
Center of acetabulum to rear border of ischium	4.7
Length:	
Femur	19.8
Tibia	18.3 (L)
Fibula	18.4 (L)
Calcaneum to tip of claw on digit IV (length of composite foot)	14.0
Metatarsal: I	2.8
II	3.2
III	3.3
IV	3.4 (L)
V	3.1
Calcaneum (L)	2.7
Cuboid (L)	0.9
Phalanx: 1, digit: I	3.4
1 II	2.4
1 III	2.5
1 IV	2.5
1 V	2.6 (L)
2 I	2.5 (claw)
2 II	2.5
2 III	2.5
2 IV	2.7
2 V	2.7
3 II	2.3 (claw)
3 III	2.3 (claw)
3 IV	2.1 (est.)*
3 V	2.1 (est.)

* Taken from deepest part of concavity of proximal articular surface to tip, for calculating length of foot.

Table 4. Ratios of various dimensions (lengths) of the bat. R, right; L, left.

Item	Ratio (× 100)
p2–p4 : p2–m3	42.9
m1–m3 : p2–m3	58.4
Humerus : radius	71.5 (R), 72.8 (L)
Femur : humerus	57.7 (R), 53.2 (L)
Foot : tibia	72.9 (R), 76.5 (L)
Aspect ratio of wing	~2.75 to 2.84

no other known cranial parts are assignable to the specific taxon of this jaw.

Thus at least two Paleocene carnivores possessed comparatively large acoustical colliculi that may possibly indicate advanced ability to echolocate or some other auditory specialization. Land-living animals known to be capable of echolocation (or audioresponse) include some subterranean shrews, some terrestrial and arboreal members of the family Tenrecidae (*14*), and some cave-frequenting birds—*Steatornis caripensis* (oilbird) and *Callocalia brevirostris* (cave swiftlet). A few other living mammals (certain marsupials, carnivores, and insectivores) apparently have relatively large posterior colliculi but, like most fruit bats, are not known to practice echolocation.

Although remains of most classes of vertebrates are extremely rare in the Green River Formation, it is the source of many thousands of fish skeletons. Sediments of this formation were deposited in the waters of several separate lakes that formed in basins of accumulation in the Wyoming-Colorado-Utah region in early Tertiary time (*15*). Indirect evidences indicate that these lakes were not wholly contemporaneous—that their geologic cycles neither began nor ended at the same time (see *18, 19*).

Rocks of this formation west of Kemmerer, including those at the source of PU 18150, began as sediments on the floor of relatively small Fossil Lake, in a long, narrow depression north of Lake Uinta (Utah) and west of Gosiute Lake, both of which lakes were much larger than Fossil Lake at maximum development in their discrete hydrographic basins. At present the irregular and discontinuous outcrop pattern of the Fossil Lake sediments extends about 27 km in the east–west direction and about 48 km north–south. The bat skeleton was found in these sediments, a kilometer or two west of their eastern border, about 19 km west of the closest mapped sediments of Gosiute Lake. Part of the terrane between the fluctuating borders of these two Eocene lakes was probably as rugged as nearby eroded rock outcrops are today, with small fissures and caves that many bats favor.

Various members and tongues of the Green River Formation in its several basins are interdigitated marginally with fluviatile mudstones that contain Wasatchian (early Eocene) and Bridgerian (mid-Eocene) mammals. Paleontologic evidence, based on fossil mammals collected (*16*) within a few kilometers of the source of the bat, indicates (*17*) that the local red-banded fluviatile rocks immediately below the Green River Formation of Fossil Lake are of Lysite age, representing the time span between the earlier (Gray Bull) and later (Lost Cabin) intervals of tripartite Wasatchian time—all of early-Eocene date (Sparnacian and Ypresian equivalents). About 107 m below the Green River Formation in this area, the gray fluviatile beds underlying the red-banded (Knight) sediments yield late-Paleocene mammals of Tiffanian provincial age.

Evernden *et al.* (*20*) list potassium-argon ages of 49.2×10^6 years for a late Wasatchian "Wind River Formation" locality and 49.0×10^6 years for a late Wasatchian–early Bridgerian site in central Wyoming. These tests, coupled with the evidence from fossils, indicate that the lowest sediments of Fossil Lake are a little older than 49 million years. The entire mass of Fossil Lake sediments has been charted as of early Eocene age (*21*).

Now at an altitude of about 2200 m above sea level, the bat stratum has been elevated tectonically from its original position, which was ". . . probably less than 1000 feet above sea level" (*18*), in early and mid-Eocene time. Analyses of the paleobiotas of the Green River Formation indicate that they developed in a humid subtropical climate like that of Alabama today. From analogies with the Zürichsee and other central-European lakes, Bradley concludes that the water of Fossil Lake was at least 30 and possibly more than 100 m deep.

The marlstone matrix around, and fortunately slightly softer than, the bat's brittle bones is composed of varves or annually deposited pairs of layers of sediment; each year is represented by two laminae of fine-grained clastic material, one being a thin dark-brown layer; the other, thicker, more granular, and light-buff in color. Bradley (letter, 22 March 1965) states that "Such varves form only in lakes that have a permanent, stagnant hypolimnion and that have enough Ca in the surface waters so that it precipitates each summer as calcite particles by reason of the photosynthesis of the phytoplankton and by warming of the surface waters." The thinner brown layers, richer in organic material, reached the floor of the lake between the periods of carbonate deposition.

At present a 1-cm-thick section of bat-quarry rock contains about 100 alternating light and dark layers, or about 50 varves (Fig. 2, *F*), but the original thickness of each uncompacted varve, when it was deposited at the bottom of the lake, was of course much greater than 0.2 mm. Irregularities in the sediments and inequalities of compacting pressures have caused each layer to be undulating in configuration; thus, when the matrix around the bat was flatly planed, the surface transected both light and dark layers of varves and was mottled (cover; Figs. 1 and 2).

Icaronycteris index, highly precocious contemporary of eohippus, prompts much speculation about the natural history of flying mammals. When, from what, where, and how did bats originate? What were their relative rates of evolution? Did they evolve through a glider stage? Was *I. index* ancestral to any, all, or none of the living microbats and megabats? What ecologic-anatomic-temporal comparisons of pterosaurs and birds and bats are significant? Did volitation by mammals originate only once? When and how did bats acquire their highly developed auditory-response system?

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Terpenoid Precursors of Hydrocarbons from the Gasoline Range of Petroleum

Abstract. *2,6-Dimethyloctane and 2-methyl-3-ethylheptane were isolated from petroleum. These hydrocarbons which are present in relatively large amounts appear to be derived from the monoterpenoids.*

The presence in petroleum of hydrocarbons that have skeletal structures or large fragments of the skeletal structures of certain compounds that are also in vegetable and animal products is well established (*1, 2*). Most, if not all, of these hydrocarbons have been isolated from petroleum distillates with a relatively high boiling point.

We have isolated two C_{10}-branched paraffins that appear to be derived from the terpenoids. These hydrocarbons, which are present in relatively large amounts, are 2,6-dimethyloctane and 2-methyl-3-ethylheptane. The finding of a large amount of 2,6-dimethyloctane was not unexpected since higher homologs of this series have previously been shown to be important constituents of petroleum (*1*). This hydrocarbon is probably formed from the acyclic monoterpenoids, though it could also be derived by splitting acyclic terpenoids which have a higher molecular weight. However, the finding, in large amount, of 2-methyl-3-ethylheptane

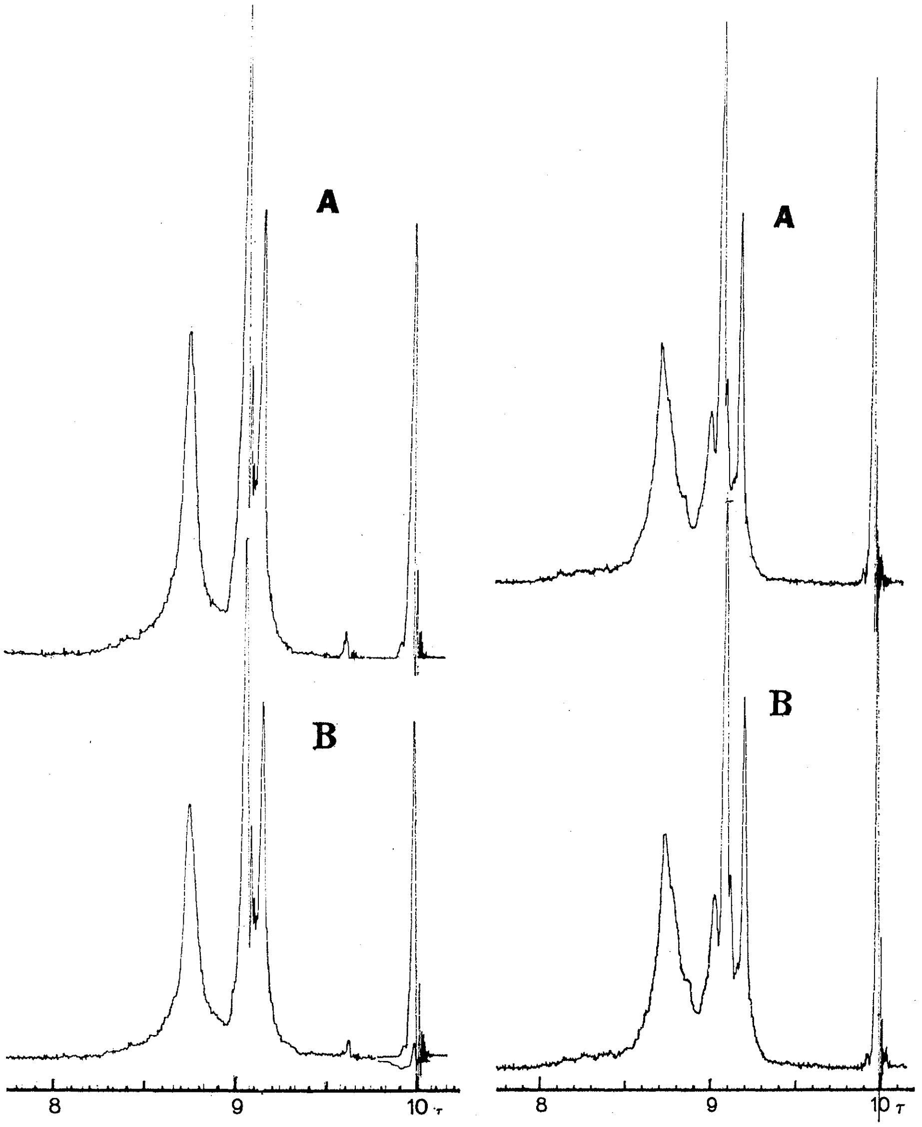

Fig. 1 (left). NMR spectra of two samples of 2,6-dimethyloctane. (A) Synthetic; (B) from petroleum. Fig. 2 (right). NMR spectra of two samples of 2-methyl-3-ethylheptane. (A) Synthetic; (B) from petroleum.