OLDEST PLACENTAL MAMMAL FROM SUB-SAHARAN AFRICA: EOCENE MICROBAT FROM TANZANIA – EVIDENCE FOR EARLY EVOLUTION OF SOPHISTICATED ECHOLOCATION

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ABSTRACT

A partial skeleton of a new fossil microbat, **Tanzanycteris mannardi,** is the oldest placental mammal found in sub-Saharan Africa. It came from early Lutetian (46 Ma) lake sediments in north-central Tanzania. **T. mannardi** has enlarged cochleae indicating it was capable of a highly derived form of echolocation. Modern bats sharing similar morphology are capable of precise navigation in dense forest undergrowth. The phylogenetic relationships of **T. mannardi** are unclear. It shares character states with Eocene Hassianycterididae, with extant Microchiroptera, and with Rhinolophoidea within Microchiroptera. **T. mannardi** is important in documenting early evolution of sophisticated bat echolocating abilities and demonstrating that Tanzanian crater lakes offer an opportunity for future discoveries of Eocene mammals from the African interior.

INTRODUCTION

Africa has a rich mammalian fossil record, but early Cenozoic mammals are only known from northern Africa (Lavocat 1953; Pickford 1986; Rasmussen et al. 1992). Discovery of Paleocene-Eocene mammals from other parts of the continent offers the potential to broaden understanding of the origin and diversification of many modern mammalian groups (Krause and Maas 1990; Bowen et al. 2002), the origin and maintenance of endemicity in African faunas (Gheerbrant 1990; Holroyd and Maas 1994), and the biogeographic and phylogenetic implications of Afrotheria (Liu and Miyamoto 1999; Springer et al. 1999; Murphy et al. 2001). Here we report the oldest Cenozoic mammal discovered in sub-Saharan Africa. The specimen was found in crater lake sediments at Mahenge (Harrison et al. 2001) in north-central Tanzania and represents a partial skeleton of an echolocating bat. It has extremely large cochleae, indicating that it was capable of specialized high-duty-cycle constant-frequency (CF) echolocation like that seen in extant rhinolophid bats (Fenton et al. 1995).

Eocene microbats are known from North America, Europe, Australia, Africa, Asia, and possibly Antarctica (Schlosser 1910; Jepsen 1966; Russell and Gingerich 1981; Habersetzer and Storch 1987; Sigé 1985, 1991; Hand et al. 1994; Woodburne and Case 1996; Simmons and Geisler 1998). Four taxa, **Icaronycteris** (Early-Middle Eocene, North America), **Archaeonycteris, Palaeochiropteryx,** and **Hassianycteris** (Middle Eocene, Europe) are represented by virtually complete skeletons. All other Eocene bats are known only from fragmentary dental, cranial, and postcranial remains.

Four Eocene microbats have been described from Africa, **Provampyrus** (?=**Vampyrus**), **Philisis** and **Dizzya** (vespertilionids), and an indeterminate rhinolophoid (Schlosser 1910; Sigé 1985, 1991). **Honrovits** (North America) and **Ageina** (Europe) may represent a vespertilionoid and nataloid, respectively (Beard et al. 1992; Simmons and Geisler 1998). **Australonycteris** (Hand et al. 1994) (Australia) may share affinities with vespertilionids or molossids while **Eppsinycteris** (Hooker 1996) (Europe) may be an emballonurid. If the higher level relationships of these Eocene taxa are correct, then several modern superfamilies of bats existed by the late early Eocene.

Eocene microbats are more primitive than extant forms in some morphological features but possess fully developed wings and specializations of the shoulder, axial skeleton, and hind limbs indicating that all were capable of maneuverable, powered flight (Jepsen 1966; Habersetzer and Storch 1987; Simmons and Geisler 1998). All of these taxa possess relatively enlarged cochleae and other specialized features of the auditory region indicating that a complex mechanism for echolocation was present in bats by the early Eocene (Novacek 1987; Habersetzer and Storch 1992; Simmons and Geisler 1998).
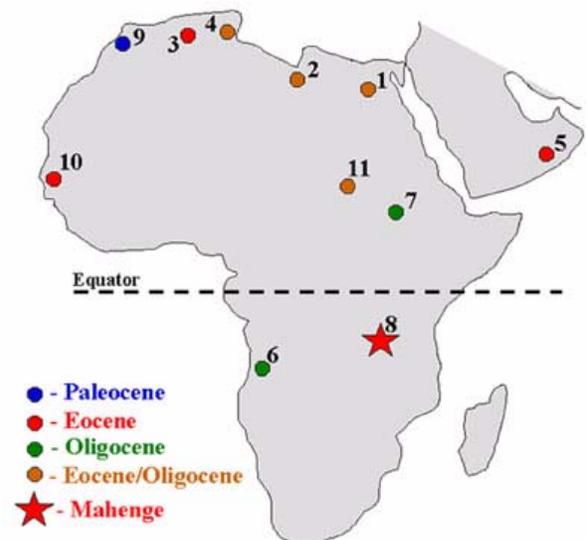

Figure 1. African Paleogene mammal producing localities. Note that Mahenge is the only known locality in Africa that has produced an Eocene mammal from south of the equator. 1 – Egypt (Rasmussen et al. 1992; Simons 1992, 1995). 2 – Libya (Arambourg and Magnier 1961; Savage 1969, 1971). 3 – Algeria (Coiffait et al. 1984; Mahboubi et al. 1986; Godinot and Mahboubi 1994). 4 – Tunisia (Hartenberger et al. 1985, 2001). 5 – Oman (Thomas et al. 1988). 6 – Angola (Pickford 1986). 7 – Ethiopia (Muldoon et al. 2002; Sanders and Kappelman 2002). 8 – Tanzania (Harrison et al. 2001). 9 – Morocco (Sigé et al. 1990; Gheerbrant 1995; Gheerbrant et al. 1993, 1998). 10 – Senegal (Sudre, 1979). 11 – Sudan (Lavocat, 1953).

MAHENGE BAT

The specimen reported here was found at the Mahenge locality, Singida Region, north-central Tanzania, and represents the oldest placental mammal ever found south of the equator on the African continent (Figure 1). The Mahenge fossiliferous deposits (Figures 2, 3) are composed of alternating mudstones and variably silicified shales (Harrison et al. 2001) and represent crater lake sediments deposited in the top of a kimberlite pipe. A diversity of plants and lower vertebrates is preserved at Mahenge (Herendeen and Jacobs 2000; Harrison et al. 2001). The fish assemblage from Mahenge suggests an early middle Eocene (Lutetian) age (Murray 2000). A Pb-U date of

Figure 2. Photograph of Mahenge locality. Red flags in lower part of section indicate crater lake sequence.

Figure 3. Stratigraphic section through Mahenge lacustrine sequence. The holotype specimen of **Tanzanycteris mannardi** was discovered in mudstone horizon 3.

45.83 Ma (+/- 0.17) was recently obtained from a zircon crystal at the base of the Mahenge sequence (Harrison et al. 2001). Based on studies of crater lakes in Europe and Africa, it is likely that sediments began to accumulate rather quickly in the Mahenge pipe after initial formation of the crater (Lorenz 1973; Smith 1986; Rayner 1987; Giresse et al. 1991; Cornen et al. 1992). Given sedimentation rates and compaction factors documented in modern maars, it can be argued that the crater at Mahenge would have been filled by sediments in 0.2-1.0 million years (Harrison et al. 2001). Conservatively, this would place an upper age limit of approximately 45 Ma for the Mahenge sequence.

The bat consists of the anterior half of a skeleton (Figure 4) including skull, lower jaws, vertebral column, both shoulder girdles, and portions of both humeri and the left radius. The wrists, wing elements, most of the pelves, and the hind limbs are missing. Despite repeated attempts, we were unable to locate any teeth. It may be that the expected (high) X-ray absorption of teeth is reduced in this specimen by demineralization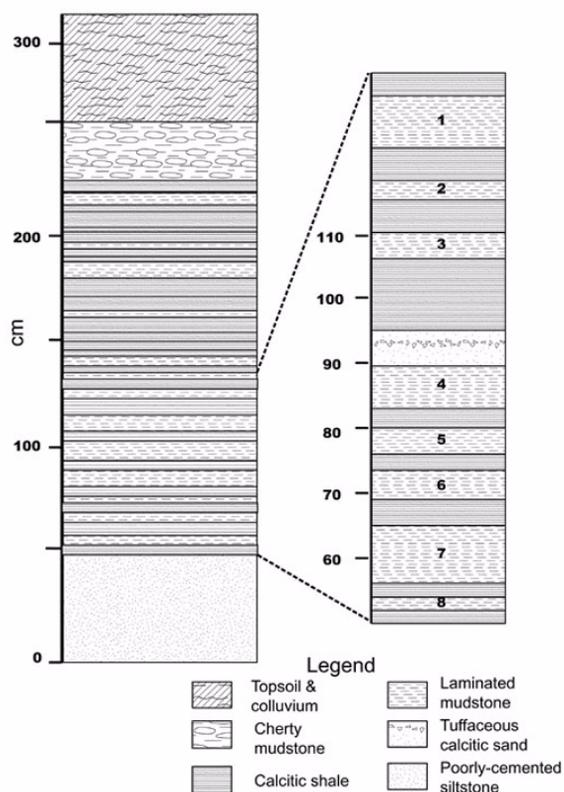 in such a way that density differences between teeth and the surrounding matrix are minimal. The lack of any available tooth morphology limits our comparisons with other Eocene taxa to those that preserve comparable anatomical parts.

Higher level taxonomy follows Simmons (1998) and Simmons and Geisler (1988). However, Springer et al. (2001) and Teeling et al. (2002) have recently presented molecular evidence supporting microchiropteran paraphyly. If this interpretation is true, then **Tanzanycteris** may be included in the suborder Yinpterochiroptera (Springer et al. 2001).

Systematic Paleontology

Order CHIROPTERA Blumenbach, 1779
Suborder MICROCHIROPTERA Dobson, 1875
Family TANZANYCTERIDIDAE, fam. nov.
Tanzanycteris gen. nov.

Type Species. Tanzanycteris mannardi sp. nov.
Etymology. Tanzania and **nykteris,** Greek for bat.
Diagnosis. Differs from all comparable Eocene bats (**Icaronycteris, Palaeochiropteryx, Archaeonycteris,** and **Hassianycteris**) in having a much larger cochlear diameter relative to basicranial
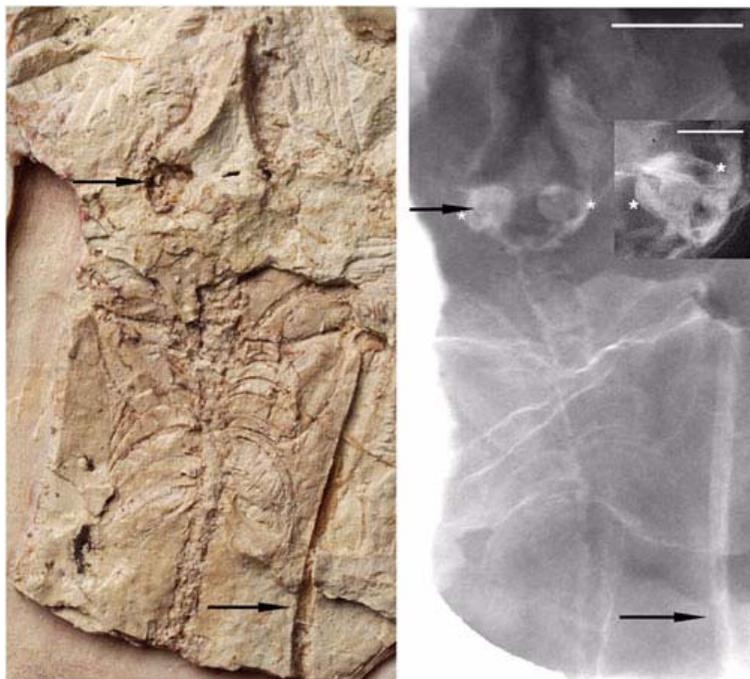
Figure 4. Photograph (left) and X-ray images (right) **Tanzanycteris mannardi** (TNM MP-207). Top arrows in each image indicate right ear region, bottom arrows point to distal shaft of left humerus. Asterisks on large X-ray image indicate basicranial width. Asterisks on close-up (inset) image of left ear region indicate width of cochlear turn. Scale bars in upper right = 1 cm for larger images and 2 mm for inset image.

width (Figures 4, 5). Differs from **Icaronycteris** and **Palaeochiropteryx** in having a first rib that is relatively broader than other ribs, and from **Icaronycteris** in having a clavicle that articulates with (or is in direct contact with) the coracoid (Figure 6). Differs from all but **Hassianycteris** in having the trochiter (=greater tuberosity) of the humerus extending proximally well beyond the humeral head (Figure 6). Further differs from **Icaronycteris** and **Archaeonycteris** in having anterior laminae on ribs and a manubrium with a bilaterally compressed ventral keel. Further differs from **Palaeochiropteryx** in having a narrow scapular

infraspinous fossa and from **Hassianycteris** in having anterior laminae on ribs (Figure 7).

Differs from all extant bats, except Rhinolophidae and **Pteronotus parnellii,** in having an extremely enlarged cochlea (Figure 5). Differs from Rhinolophidae in having an enlarged cochlear fenestra, anterior laminae on ribs, and two facets in the infraspinous fossa. Differs from **P. parnellii** in having a first rib that is relatively broader than other ribs, two facets in the infraspinous fossa, a coracoid with a blunt (not flared) tip, and an iliac blade
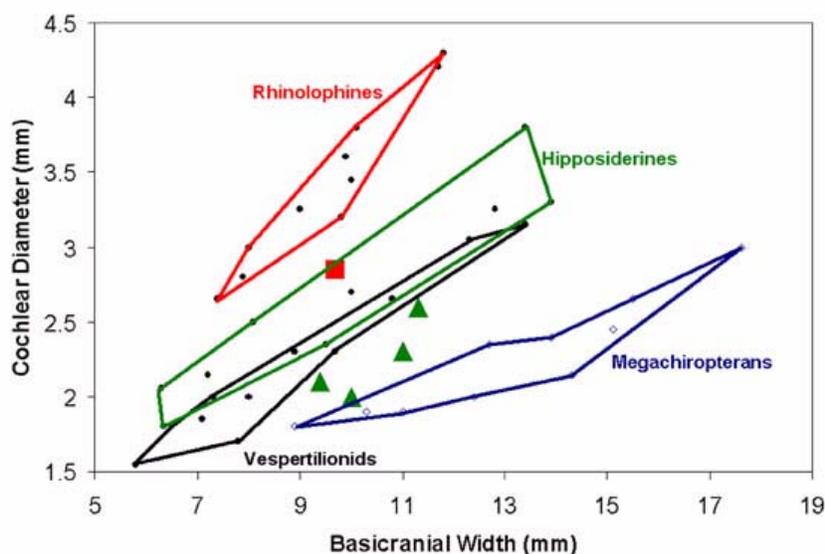

Fig. 5. Bivariate plot of basicranial width (X axis) vs. oblique diameter of first cochlear turn (Y axis) in several extant and fossil bats. Polygons enclose distributions for megachiropterans (blue diamonds) and three extant microbat groups (black circles). Note that **Tanzanycteris mannardi** (large red square) falls at the extreme range of hipposiderines and near rhinolophines. Other Eocene bats designated by large green triangles include (from left to right) **Palaeochiropteryx, Icaronycteris, Archaeonycteris,** and **Hassianycteris.** Note that these taxa all fall between megachiropterans and vespertilionids.
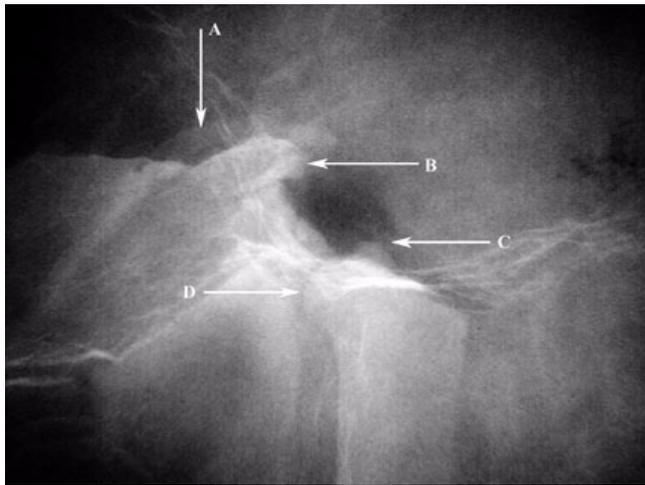
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Figure 6. X-ray image of left proximal humerus and shoulder girdle of **Tanzanycteris mannardi.** A) Clavicle. B) Scapular coracoid – note that clavicle and coracoid contact one another. C) Trochiter. D) Humeral head – note that trochiter extends proximally beyond humeral head.

Figure 7. Close-up photograph of rib-cage of Tanzanycteris mannardi. A) Impression of right scapular spine. B) Impression of left clavicle.

that extends dorsally beyond the level of the iliosacral articulation (Figure 8).

We have chosen to place **Tanzanycteris** in a new family, Tanzanycterididae, to emphasize the derived nature of its basicranial structures in comparison with all other Eocene microbats.

Tanzanycteris mannardi sp. nov.

Holotype. Tanzanian National Museum (TNM) MP-207, partial skeleton including skull, axial skeleton anterior to sacrum, partial left and right humeri, and partial left radius. Only known specimen.

Locality. Mahenge, north-central Tanzania, approximately 50 km west of Singida. The coordinates of the Mahenge kimberlite pipe are 4º 47' 50.2" S; 34º 15' 54.5" E.

Age and Distribution. Middle Eocene, Lutetian, approximately 46 Ma (Harrison et al. 2001).

Diagnosis. Only known species, as for genus.

Etymology. For George W. Mannard who explored the Singida Kimberlite Field and made the first excavation at the type locality in 1957 (Mannard 1962).

Discussion. Tanzanycteris mannardi is a relatively small bat (Table 1) about the size of **Palaeochiropteryx tupaiodon** from the Lutetian of Europe (Habersetzer and Storch 1987). **T. mannardi** (Figures 6-8) has unfused vertebrae throughout the column, an iliac blade that extends dorsally beyond the level of the iliosacral articulation, a

Table 1. Tanzanycteris skeletal measurements.

| Tanzanycteris	mm
Estimated skull length	16.30
Basicranial width	9.70
Cochlear oblique diameter	2.85
Estimated clavicle length	13.00
Estimated humerus length	30.00
Cervical vertebral series length	7.60
Thoracic vertebral series length	12.00
Lumbar vertebral series length	8.50
Mediolateral width scapular blade	5.20
Anteroposterior length scapular blade	12.10
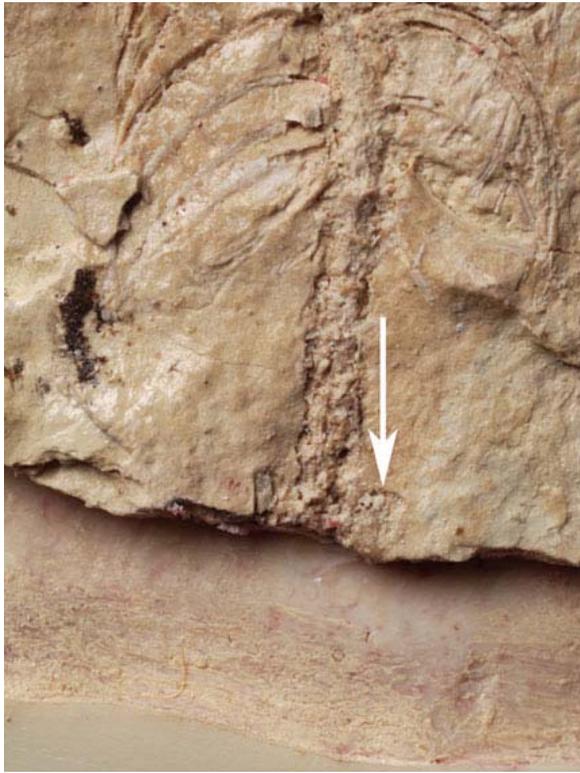
Figure 8. Close-up photograph of posterior axial skeleton showing flaring tip of left iliac blade (arrow).

scapula with a double-faceted infraspinous fossa, a ventrolaterally curving coracoid with a blunt tip, and ribs with posterior laminae. Among Eocene bat taxa, **Tanzanycteris** is most similar to **Hassianycteris**, but differs in the size of the cochlea (much larger in **Tanzanycteris**) and presence of anterior laminae on ribs (absent in **Hassianycteris**).

In other features **T. mannardi** differs from archaic bats and resembles several extant echolocating bats. Among extant Old World bats, **T. mannardi** is most similar to rhinopomatoids and rhinolophoids (excluding Nycteridae) (Simmons 1998; Simmons and Geisler 1998; Teeling et al. 2002). Features shared in common between rhinopomatoids and **Tanzanycteris** include an enlarged cochlear fenestra (also shared by mystacinids and noctilionoids), a clavicle that articulates with the coracoid (craseonycterids only, also shared by emballonurids, phyllostomatids, and mormoopids), and a trochiter that extends proximally well beyond the humeral head (craseonycterids only, also shared by rhinolophoids and most yangochiropterans). None of these shared character states are exclusive to **Tanzanycteris** and rhinopomatids.

Character states shared by **Tanzanycteris** and rhinolophoids include: extremely enlarged cochlea (absent in megadermatids, present in one mor-

moopid); first rib broader than all other ribs; clavicle that articulates with the coracoid (also craseonycterids, emballonurids, phyllostomatids, and mormoopids); trochiter that extends proximally well beyond the humeral head (also craseonycterids, most yangochiropterans, and **Hassianycteris**); and iliac blade that flares dorsally resulting in a well-developed iliac fossa (rhinolophids and **Icaronycteris, Hassianycteris,** and **Archaeonycteris**). Of these character states, the presence of a broad first rib is uniquely shared between **Tanzanycteris** and rhinolophoids. Among other characteristics shared between **Tanzanycteris** and rhinolophoids, all but the flaring iliac blade are present in other extant groups and several other Eocene taxa. The flaring iliac blade with a well-developed iliac fossa is likely primitive for bats.

ECHOLOCATION

The extremely enlarged cochlea (Figure 5) indicates that **Tanzanycteris** had developed sophisticated echolocation abilities (Habersetzer and Storch 1987, 1992; Novacek 1987; Fenton et al. 1995; Simmons and Geisler 1998). Among extant forms only rhinolophids and **Pteronotus parnellii** have comparable cochlear enlargement – no other Eocene bat had a cochlea in this size range. Extant bats characterized by similar relative cochlear dimensions uniformly use a highly derived type of sonar navigation known as high-duty-cycle constant-frequency echolocation. This system employs the Doppler shift to avoid self-deafening– the echolocation call pulse and echo are separated in frequency (Fenton et al. 1995). The majority of extant microbats use low-duty-cycle echolocation in which emitted pulses and returning echoes are separated in time. Bats that use the high-duty-cycle system can forage for fluttering insects in dense forest close to vegetation or the ground (Fenton et al. 1995; Simmons and Geisler 1998), behavior beyond the capability of most low-duty-cycle bats (Fenton et al. 1995). This type of echolocation is consistent with the presence of vegetation that is structurally similar to modern-day miombo woodlands as indicated by Mahenge plant fossils (Herendeen and Jacobs 2000).

The apparent presence of high-duty-cycle echolocation in **Tanzanycteris** indicates that this specialized form of echolocation originated by the middle Eocene. Echolocation apparently evolved in the common ancestor of all bats and was subsequently lost in megachiropterans (Springer et al. 2001). However, it is likely that rhinolophids and mormoopids acquired high-duty-cycle echolocation independently (Teeling et al. 2002).

Table 2. Microchiropteran and fossil microbat comparisons.

Character State	Icaronycteris	Archaeonycteris	Palaeochiropteryx	Hassianycteris	Tanzanycteris	Microchiroptera	Megachiroptera
Cochlea moderately enlarged	X	X					*
Cochlea larger			X	X		#	
Cochlea greatly enlarged					X	#	
Phanerocochlear cochlea	?	?	X	X	?	#	
Periotic loosely attached to basisphenoid	?	X	X	?	?	#	
Orbicular apophysis on malleus enlarged	X	X	X	X	?	X	
Stylohyal with moderately expanded tip	X	X	X	?	?	#	
Stylohyal with greatly expanded tip				?	?	#	
Stapedial fossa deep and constricted	?	?	X	?	?	#	
P3 with two or fewer roots		X	X	X	?	*	X
Nyctalodont dentition			#	X	?	#	
Cervicals 2-3 with ventral accessory processes	X	X	X	X	?	X	#
Cervical 4 with ventral accessory process		X	X	X	?	X	
Cervical 5 with ventral accessory process			X		?	X	
Ventral process of manubrium compresed			X	X	X	#	X
Ribs with posterior laminae	X	?	X	X	X	#	X
Ribs with anterior laminae		?	X	?	X	#	#
Suprascapular process absent	X	X	X	X	X	#	#
Scapular dorsal articular facet present		?	X	X	X	*	
Trochiter extends proximally to humeral head	X	X	X			#	
Trochiter extends proximally beyond humeral head				X	X	#	
Wing digit II distal phalanx absent			X	X	?	X	
Wing digit III distal phalanx absent		X	X	X	?	#	X
Fibula thin and thread-like			X	X	?	#	
Calcar present			X	X	?	*	#

PHYLOGENY

The phylogenetic affinities of **Tanzanycteris** remain unclear at this time. Many of the crucial character states important in bat phylogeny (Simmons and Geisler 1998) are not preserved in the single known specimen of **Tanzanycteris**. Table 2 presents a compilation (Simmons and Geisler 1998) of key microbat character states and their distribution among **Icaronycteris, Archaeonycteris, Palaeochiropteryx, Hassianycteris, Tanzanycteris,** and extant microchiropterans. Of these 21 characteristics (some with multiple states) only seven can be accurately scored for **Tanzanycteris**.

Based on the characteristics that can be scored for **Tanzanycteris**, several alternative phylogenetic hypotheses can be supported. If microchiropterans are monophyletic (Figure 9A), then **Tanzanycteris** could either be a sister taxon to **Hassianycteris** or to the extant microchiropteran clade. If Microchiroptera is paraphyletic (Figure 9B), then **Tanzanycteris** could be the sister taxon of **Hassianycteris**, or of all extant bats (including Megachiroptera), or of rhinolophoid microchiropterans. Further evidence is required before a more definitive statement can be made about the relationships of **Tanzanycteris**.

The discovery of **Tanzanycteris** is significant for bat paleobiogeography and evolutionary history, but the ramifications of the first mammal found in the Eocene of sub-Saharan Africa exceed the origin and diversification of Chiroptera. The crater lakes of the Singida region, which have not yet been studied in detail, offer the first real opportunity to discover Eocene floral and faunal samples from the interior of Africa.
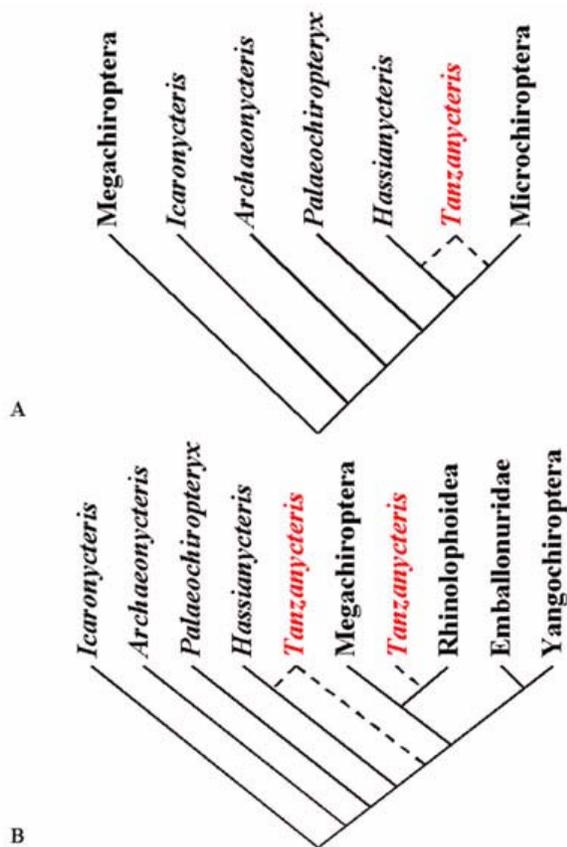
Figure 9. Possible phylogenetic relationships of **Tanzanycteris** with (A), microchiropteran monophyly or (B) microchiropteran paraphyly. In A, megachiropterans are the sister taxon to all fossil microbats and extant microchiropterans. In B, megachiropterans are the sister taxon to extant rhinolophoids rendering Microchiroptera paraphyletic. Possible synapomorphies supporting nodes (see Table 2): 1,3 – trochiter extends proximally beyond humeral head; suprascapular process absent; ribs with posterior laminae; distal ventral process of manubrium laterally compressed; 2 – cochlea greatly enlarged; ribs with anterior laminae; 4 – cochlea greatly enlarged.

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