

Primitive bat from the Early Eocene of Wyoming: flight and the evolution of echolocation

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1. Supplementary Tables

Supplementary Table 1. Skull and limb measurements of Eocene bats including *Onychonycteris finneyi*. MC = metacarpal; PP = proximal phalanx; IP = intermediate phalanx; DP = distal phalanx; ROM = Royal Ontario Museum (Toronto); YPM-PU = Yale Peabody Museum, Princeton University Collection (New Haven); FMNH = Field Museum of Natural History (Chicago); LNK = Landessammlungen für Naturkunde (Karlsruhe); SMF = Forschungsinstitut Senckenberg (Frankfurt am Main); HLMD = Hessisches Landesmuseum (Darmstadt); BE = Institut Royale des Sciences (Brussels). Citations are provided for data taken from the literature; all other measurements were made by the authors.

Onychonycteris finneyi

Specimen	ROM 55351A (Holotype)	ROM 55055 (Cast of Paratype)
Skull	22.6	23.7
Body	55.5	62.6
Tail	56.9	63.8
Femur	26.6	26.3
Tibia	24.6	25.5
Humerus	35.2	36.4
Radius	45.8	45.4
Digit I	----	11.3
MC I	----	4.90
PP I	----	4.00
DP I	2.60	2.40
Digit II	35.1	37.1
MC II	21.2	21.5
PP II	5.20	6.00
IP II	6.40	6.70
DP II	2.30	2.90
Digit III	64.2	66.9
MC III	30.2	30.2
PP III	13.8	15.3
IP III	18.3	20.1
DP III	1.90	1.30
Digit IV	61.8	64.3
MC IV	30.7	31.9
PP IV	13.6	14.5
IP IV	16.2	17.0
DP IV	1.30	0.90
Digit V	63.1	64.5
MC V	34.7	34.9
PP V	14.0	14.7
IP V	13.5	14.2
DP V	0.90	0.70

Icaronycteris index

Specimen	LNK 124/126 ¹¹	YPM-PU 18150 ¹⁹	ROM 52666	FMNH PM 61096
Skull	19.7	20.1	19.7	20.8
Body	42.5	50.5	48.0	46.0
Tail	46.8	52.4	47.3	46.2
Femur	19.6	19.8	17.3	17.4
Tibia	17.4	18.3	17.1	17.8
Humerus	33.9	34.3	30.2	31.8
Radius	46.3	48.0	41.6	43.5
Digit I	9.70	11.9	-----	-----
MC I	3.30	3.50	-----	-----
PP I	4.30	5.70	-----	-----
DP I	2.10	2.70	1.90	-----
Digit II	36.0	39.8	33.0	35.8
MC II	25.8	28.5	23.2	25.4
PP II	4.80	4.90	4.10	4.50
IP II	4.20	4.90	4.50	4.50
DP II	1.20	1.50	1.20	1.40
Digit III	66.0	70.2	65.9	64.3
MC III	36.2	40.1	36.0	35.2
PP III	10.9	10.9	10.4	10.8
IP III	18.6	18.8	19.2	18.3
DP III	0.30	0.40	0.30	-----
Digit IV	61.7	66.7	62.0	-----
MC IV	35.2	39.0	35.6	-----
PP IV	11.3	11.5	10.6	10.9
IP IV	15.2	16.1	15.8	16.6
DP IV	-----	-----	0.20	-----
Digit V	56.1	60.6	57.7	-----
MC V	34.8	38.0	36.6	-----
PP V	9.10	10.1	8.90	-----
IP V	11.9	12.2	12.0	-----
DP V	0.30	0.30	0.20	-----

Archaeonycteris trigonodon

Specimen	SMF Me 963a ¹¹	SMF Me 663 ¹¹	SMF 80/1379 ¹¹
Skull	22.4	23.0	22.4
Body	45.8	46.0	54.1
Tail	52.5	53.6	56.6
Femur	24.7	23.2	24.9
Tibia	25.4	25.0	25.9
Humerus	36.2	38.2	39.6
Radius	52.5	54.4	58.2
Digit I	9.90	-----	12.6
MC I	3.70	-----	4.60
PP I	4.10	-----	5.70
DP I	2.10	-----	2.30
Digit II	39.5	41.2	45.6
MC II	28.1	29.8	32.1
PP II	5.00	5.90	5.30
IP II	4.80	5.50	6.00
DP II	1.60	-----	2.20
Digit III	72.9	82.5	85.1
MC III	39.9	46.1	45.0
PP III	14.3	16.4	17.9
IP III	18.7	20.0	22.2
DP III	-----	-----	-----
Digit IV	69.6	73.8	73.1
MC IV	38.9	45.6	42.5
PP IV	15.5	15.4	15.4
IP IV	15.2	12.8	15.2
DP IV	-----	-----	-----
Digit V	68.0	73.6	74.6
MC V	42.9	46.1	46.4
PP V	12.7	14.0	14.2
IP V	12.4	13.5	14.0
DP V	-----	-----	-----

Specimen	<i>Palaeochiropteryx tupaiodon</i>			<i>Palaeochiropteryx spiegelii</i>	
	SMF Me 207 ¹¹	SMF Me 10 ¹¹	SMF Me 1032 ¹¹	HLMD Me 32/29 ¹¹	SMF Me 1008 ¹¹
Skull	15.7	20.1	18.9	20.5	19.8
Body	26.3	26.8	27.5	31.5	32.1
Tail	34.9	37.1	37.8	39.0	39.6
Femur	14.6	14.7	14.0	19.0	18.6
Tibia	16.5	18.3	17.9	18.8	20.9
Humerus	26.7	27.3	27.6	29.5	29.9
Radius	38.6	42.6	46.0	43.5	48.7
Digit I	6.40	8.20	-----	-----	10.9
MC I	2.10	2.50	3.10	-----	3.70
PP I	2.80	3.70	-----	-----	4.90
DP I	1.50	2.00	-----	-----	2.30
Digit II	33.2	33.9	35.2	36.7	42.1
MC II	27.4	28.6	31.4	-----	36.1
PP II	4.90	4.40	3.20	-----	5.40
IP II	0.90	0.90	0.60	-----	0.60
DP II	-----	-----	-----	-----	-----
Digit III	58.1	65.4	64.7	65.0	71.6
MC III	32.8	36.8	37.7	-----	41.2
PP III	10.7	13.5	10.6	-----	12.6
IP III	14.6	15.1	16.4	-----	17.8
DP III	-----	-----	-----	-----	-----
Digit IV	50.6	54.8	54.5	55.5	62.7
MC IV	31.9	33.3	35.1	-----	37.5
PP IV	9.10	12.1	9.70	-----	12.3
IP IV	9.60	9.40	9.70	-----	12.9
DP IV	-----	-----	-----	-----	-----
Digit V	50.3	52.8	51.3	56.2	55.2
MC V	33.1	35.6	35.6	-----	37.6
PP V	9.60	8.90	8.90	-----	10.2
IP V	7.60	6.80	6.80	-----	7.40
DP V	-----	-----	-----	-----	-----

	<i>Hassianycteris messelensis</i>		<i>Hassianycteris magna</i>	<i>Tachypteron franzeni</i>
Specimen	SMF Me 1469 ¹¹	SMF Me 492 ¹¹	HLMD 7539 ¹¹	BE 4-119 (Holotype) ²⁴
Skull	24.5	26.4	27.0	21.5
Body	44.2	47.6	59.3	39.0
Tail	42.7	46.0	59.1	31.9
Femur	22.7	24.5	24.9	19.4
Tibia	20.2	21.8	26.2	17.5
Humerus	39.3	37.8	44.0	33.5
Radius	64.5	69.5	81.5	53.1
Digit I	12.6	-----	19.7	11.5
MC I	3.50	-----	5.30	3.90
PP I	6.50	7.00	9.40	5.20
DP I	2.60	2.80	5.00	2.40
Digit II	47.8	51.4	38.4	38.5
MC II	44.2	47.6	33.9	38.5
PP II	3.60	3.80	4.50	-----
IP II	-----	-----	-----	-----
DP II	-----	-----	-----	-----
Digit III	89.0	93.8	111.2	82.2
MC III	53.8	56.1	65.5	39.7
PP III	12.5	13.2	17.3	17.0
IP III	22.7	24.5	28.4	25.5
DP III	-----	-----	-----	-----
Digit IV	79.9	83.8	99.2	63.1
MC IV	50.5	52.5	63.1	35.2
PP IV	16.3	17.7	20.4	11.4
IP IV	13.1	13.6	15.7	16.5
DP IV	-----	-----	-----	-----
Digit V	60.4	66.0	72.4	49.2
MC V	37.6	41.1	46.9	21.2
PP V	11.7	13.5	17.6	16.2
IP V	11.1	11.4	7.90	11.8
DP V	-----	-----	-----	-----

Supplementary Table 2. Aspect Ratio Indices (ARI) for Eocene fossil bats with representative values from extant bat families for comparison. $ARI = [\text{length of digit III} + \text{the length of the radius}] / \text{length of digit V}$. Higher values indicate proportionately longer, narrower wings.

<u>Taxon</u>	<u>Aspect Ratio Index</u>	<u>Data Source</u>
<i>Onychonycteris finneyi</i>	1.74	This Paper
<i>Icaronycteris index</i>	1.97	11
<i>Archaeonycteris trigonodon</i>	1.87	11
<i>Palaeochiropteryx tupaiodon</i>	2.04	11
<i>Palaeochiropteryx spiegelii</i>	2.06	11
<i>Hassianycteris messelensis</i>	2.51	11
<i>Hassianycteris magna</i>	2.66	11
<i>Tachypteron franzeni</i>	2.75	24
Pteropodidae	2.16-2.21	40
Rhinopomatidae	2.11	40
Megadermatidae	2.19	40
Rhinolophidae	2.14	40
Emballonuridae	2.39	40
Nycteridae	2.00	40
Noctilionidae	2.53	40
Mormoopidae	2.22	40
Phyllostomidae	1.99-2.20	40

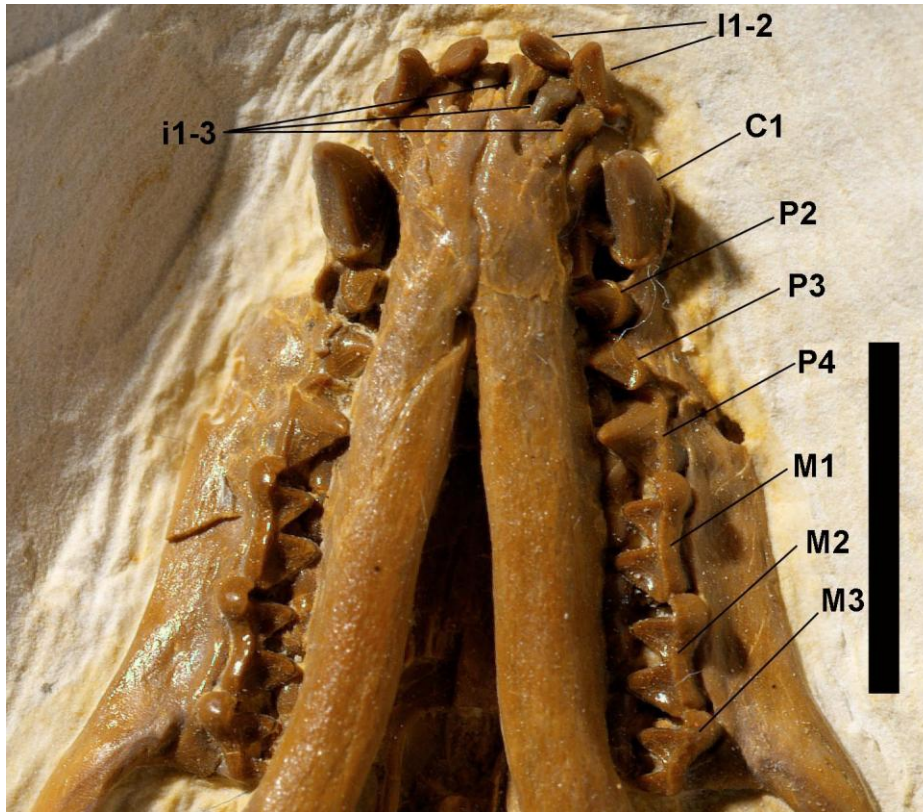
Mystacinidae	2.16	40
Natalidae	2.05	40
Vespertilionidae	1.95-2.33	40
Miniopterinae	2.47	40
Molossidae	2.87	40

Supplementary Table 3. Brachial and Intermembral Indices for Eocene bats and selected non-volant taxa. UM = University of Michigan Museum of Paleontology; UMMZ = University of Michigan Museum of Zoology.

<u>Specimen</u>	<u>Taxon</u>	<u>Brachial</u>	<u>Intermembral</u>
ROM 55351A	<i>Onychonycteris finneyi</i>	130	158
ROM 55055	<i>Onychonycteris finneyi</i>	125	158
LNK 124/126	<i>Icaronycteris index</i>	137	217
YPM-PU 18150	<i>Icaronycteris index</i>	140	216
ROM 52666	<i>Icaronycteris index</i>	138	209
FM PM 61096	<i>Icaronycteris index</i>	137	214
SMF Me 963a	<i>Archaeonycteris trigonodon</i>	145	177
SMF Me 663	<i>Archaeonycteris trigonodon</i>	142	192
SMF 80/1379	<i>Archaeonycteris trigonodon</i>	147	193
SMF Me 207	<i>Palaeochiropteryx tupaiondon</i>	156	210
SMF Me 1032	<i>Palaeochiropteryx tupaiondon</i>	167	231
HLMD Me 32/29	<i>Palaeochiropteryx spiegelii</i>	147	193
SMF Me 1008	<i>Palaeochiropteryx spiegelii</i>	163	199
SMF Me 1469	<i>Hassianycteris messelensis</i>	164	242
SMF Me 492	<i>Hassianycteris messelensis</i>	184	232
HLMD 7539	<i>Hassianycteris magna</i>	185	246
BE 4-119	<i>Tachypteron franzeni</i>	159	235
UMMZ 64938	<i>Choloepus hoffmanni</i>	114	111
UMMZ 64950	<i>Bradypus variegatus</i>	111	172
----- ⁴¹	<i>Tupaia glis</i>	93	72
----- ⁴¹	<i>Ptilocercus lowii</i>	107	79
FMNH 56530	<i>Cynocephalus volans</i>	115	94

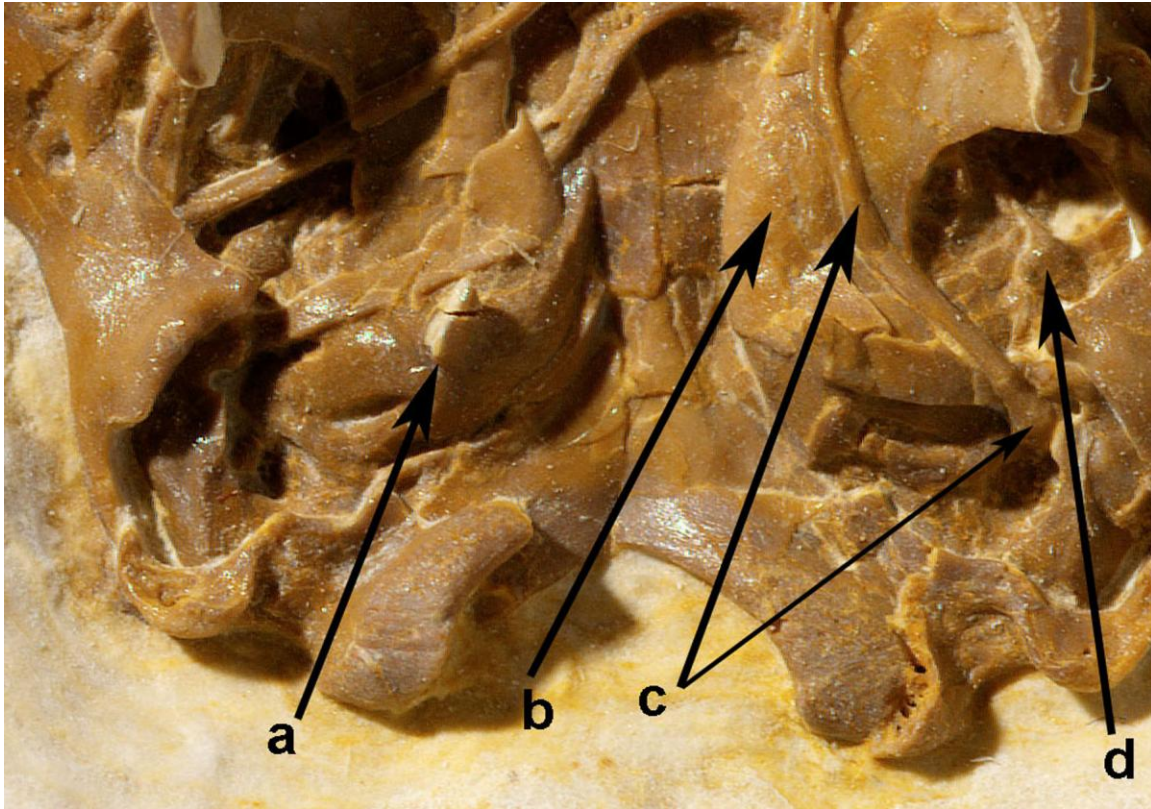
UMMZ 167069	<i>Glaucomys volans</i>	109	82
UMMZ 176224	<i>Sciurus niger</i>	96	71
UMMZ 56967	<i>Eutamias quadrivittatus</i>	99	71
UMMZ 67354	<i>Cynomys ludovicianus</i>	91	79
UMMZ 162638	<i>Spermophilus columbianus</i>	90	69
UMMZ 157292	<i>Lynx rufus</i>	93	85
UM R1605	<i>Procyon lotor</i>	100	84

2. Supplementary Figures

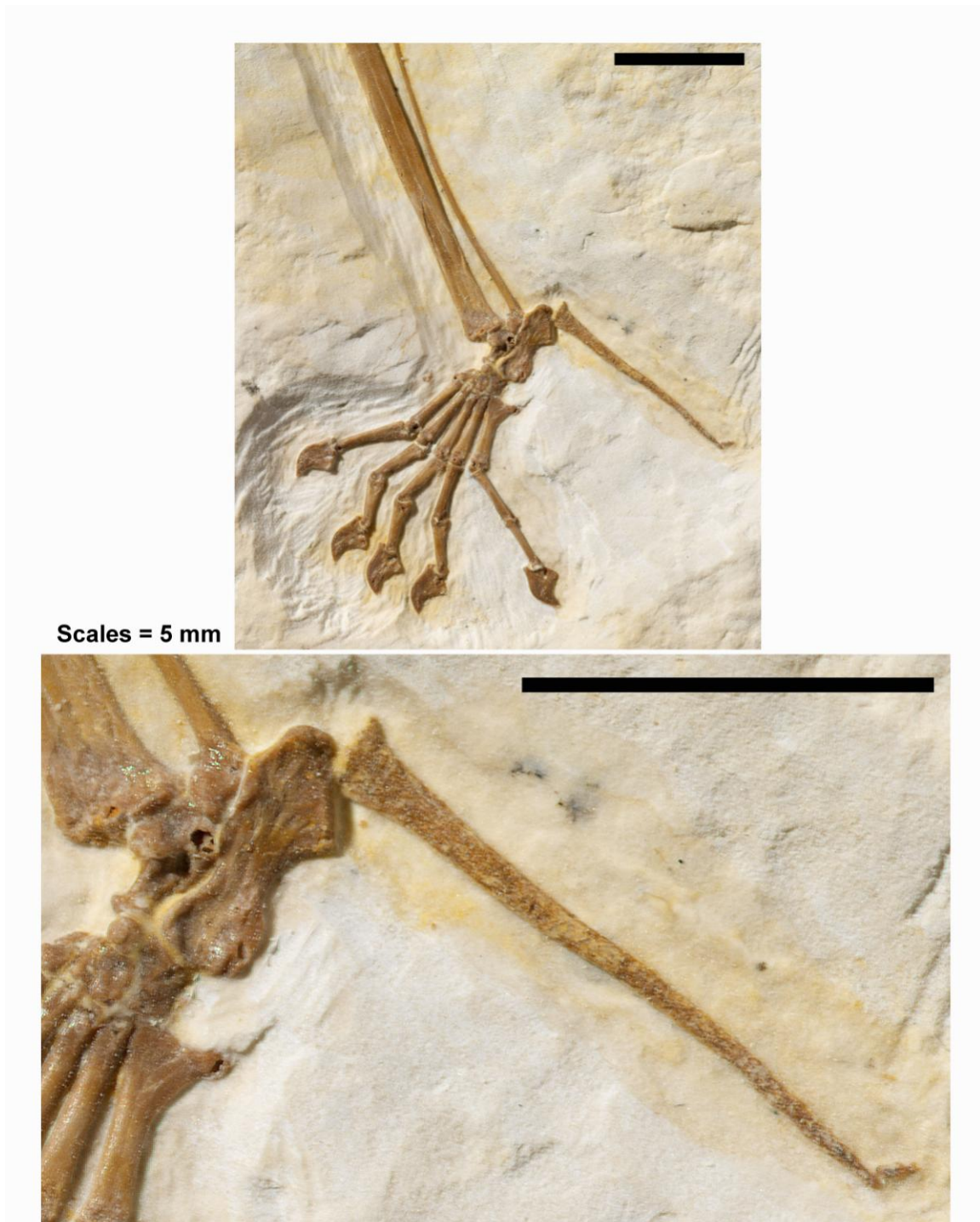


Supplementary Figure 1. Dentition of *Onychonycteris finneyi* (ROM 55351A, holotype skull, ventral view). Lower and upper jaws are in tight occlusion. Dental features that are evident include: primitive chiropteran dental formula of 2.1.3.3/3.1.3.3; tribosphenic dentition with dilambdodont upper molars; I1 smaller than I2 with I2 being nearly caniniform; upper canines dagger-like and bilaterally compressed with weak lingual cingulum, slightly stronger posterior cingulum and no labial cingulum; P2 single-rooted, pointed, simple; P3-4 triple-rooted, non-molariform; upper molars dilambdodont with parastylar hook, tall and acute cusps, sharply defined ectoloph crests, continuous labial cingulum (ectoflexus does not extend to cingulum), and no mesostyles; M1-2 paracone and metacone of equal height; M3 labial margin angled lingually but with both paracone and metacone present; lower incisors small and bicuspid; lower premolars with primitive

size pattern of $p4 > p2 > p3$; $p4$ non-molariform; lower molars with strong labial cingulids and tall and acute cusps. Extant small mammals with tribosphenic dentitions and dilambdodont upper molars are almost exclusively insectivorous⁴² suggesting that *Onychonycteris* was insectivorous like other known Eocene bats⁹.

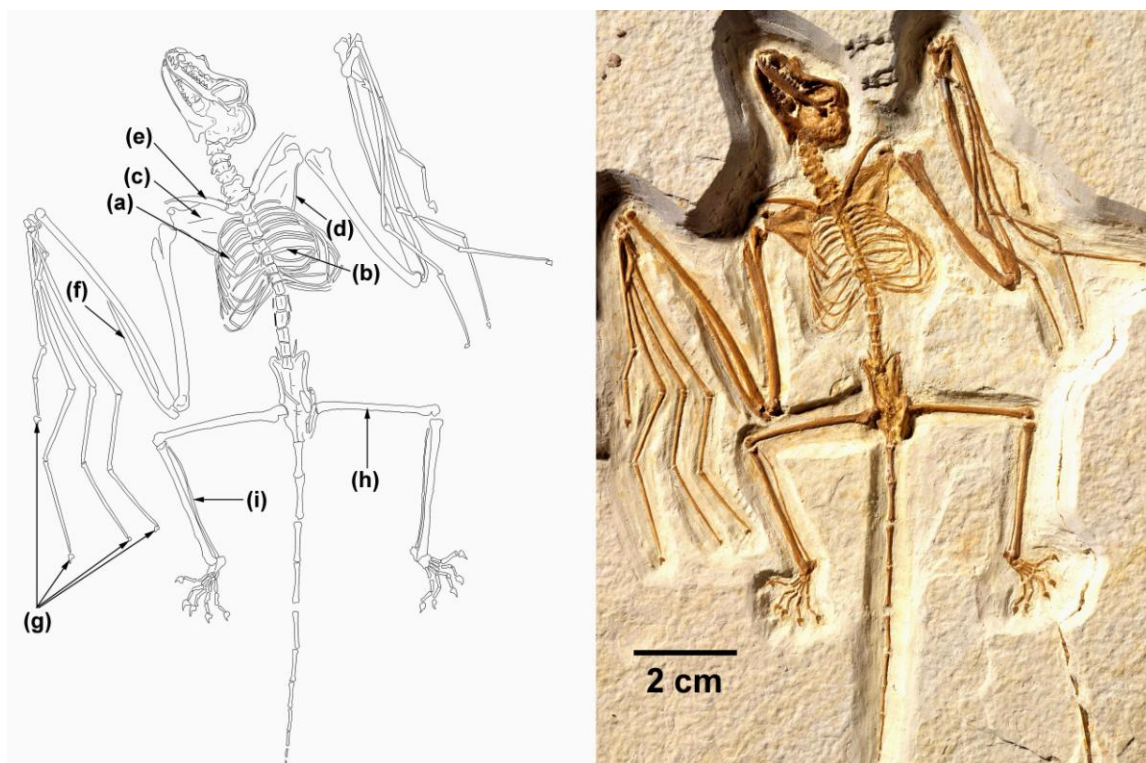


Supplementary Figure 2. Basicranium of *Onychonycteris finneyi* (ROM 55351A, Holotype). Lettering corresponds to: a) promontorial process; b) ectotympanic; c) stylohyal (smaller arrow indicates rounded but unexpanded cranial tip); d) small orbicular apophysis of malleus. Note also that the cochlea is relatively small (see Fig. 2) and cryptocochlear.



Supplementary Figure 3. Close-up view of foot and calcar of *Onychonycteris finneyi* (ROM 55351A, holotype). Note that the surface texture of the calcar along its entire length is irregular and porous, unlike the smooth surfaces of the bones of the rest of the

skeleton. This texture suggests that the calcar was cartilaginous rather than calcified in *Onychonycteris*. Many extant bat families (megadermatids, rhinolophids, hipposiderids, most phyllostomids, mystacinids, myzopodids, and thyropterids) are characterized by presence of uncalcified calcars¹⁸. Lack of calcification of the calcar may explain why the paratype of *Onychonycteris* (Supplementary Fig. 4) does not include a fossilized calcar. This also may be the case for other Eocene bats such as *Icaronycteris* and *Archaeonycteris* where the absence of a calcar simply may be the result of poor preservation.



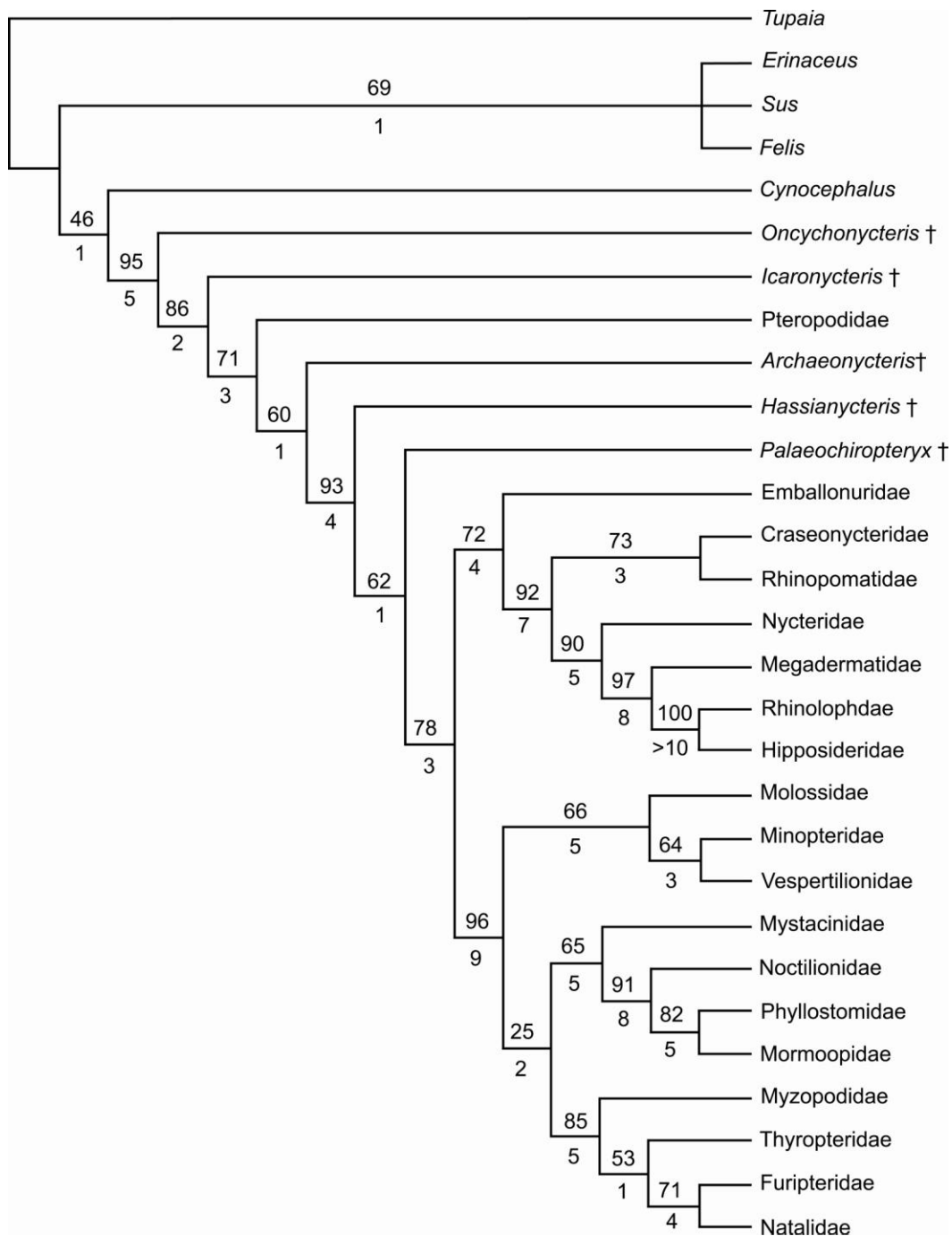
Supplementary Figure 4. Skeleton of *Onychonycteris finneyi* (ROM 55055, paratype) in ventral view. Morphological features include (letters correspond to labeled points on outline drawing) – **Vertebrae, sternum, and ribs:** no fusion of vertebrae or anterior ribs to vertebrae; first rib width similar to other ribs (a); manubrium extends laterally to the level of clavicular joint; no fusion of first costal cartilage to manubrium or first rib; second rib articulates with sternum via costal cartilage at the manubrium–mesosternum joint, 6 costal cartilages articulate with mesosternum posterior to this joint; ribs lack anterior or posterior laminae (b); anterior face of manubrium small and poorly defined; length of the manubrium posterior to lateral processes is less than twice transverse width; mesosternum narrow, mean width less than half the distance between the clavicles at sternoclavicular joint; xiphisternum lacks median keel. **Scapula and clavicles:** infrapinous fossa of scapula relatively narrow and divided into two facets (c); lateral facet does not extend into infraglenoid region; thick lip present along axillary border of

scapula (d) ; anteromedial edge of scapula lacks projections or flanges; coracoid process stout and curves ventrolaterally; clavicle not in contact with coracoid or acromion process

(e). **Forelimb:** shaft of radius gently arched; ulna fused to radius distal to the midpoint

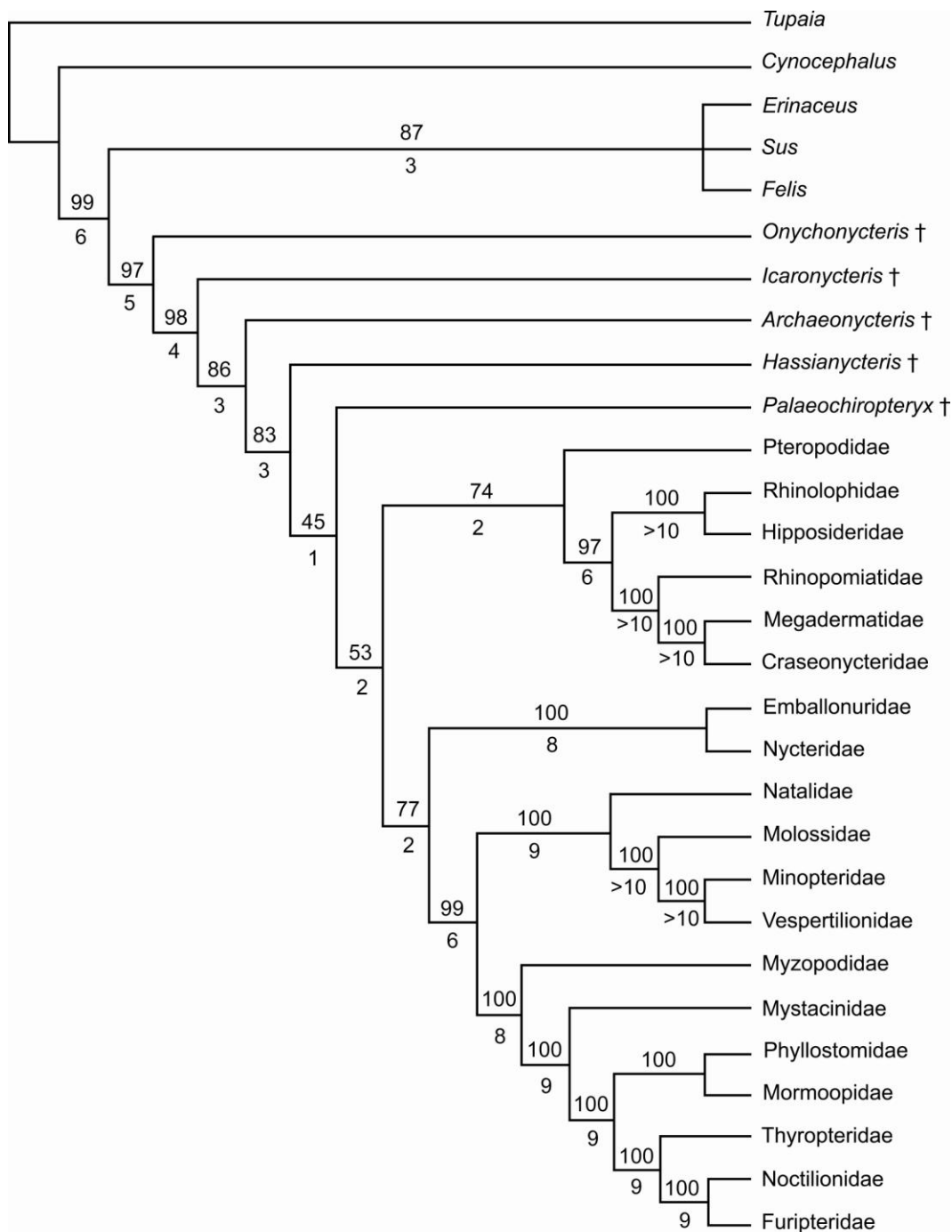
(f); metacarpals and proximal phalanges elongate; metacarpal formula (shortest to longest) I:II:III:IV:V; second phalanx longer than first phalanx in digits II-IV; first phalanx longer than second in digits I and V; claws present on all hand digits (g).

Hindlimb: shaft of femur straight (h); femoral head slightly offset, lacking a distinct neck; fibula complete and well-developed (i); phalangeal formula 2-3-3-3-3; each digit terminates in well-developed claw; first phalanx of digit I longer than first phalanx of digits II-V; overall length of first digit shorter than other digits; calcar absent but known to exist as an unossified element in the holotype (ROM 55351A) of *O. finneyi* (see Supplementary Fig. 3).



Supplementary Figure 5. Phylogenetic tree of bats based on unconstrained parsimony analysis of morphological data. Numbers above branches are bootstrap values, below branches are Bremer values. Note that *Onychonycteris* occupies the basal branch within

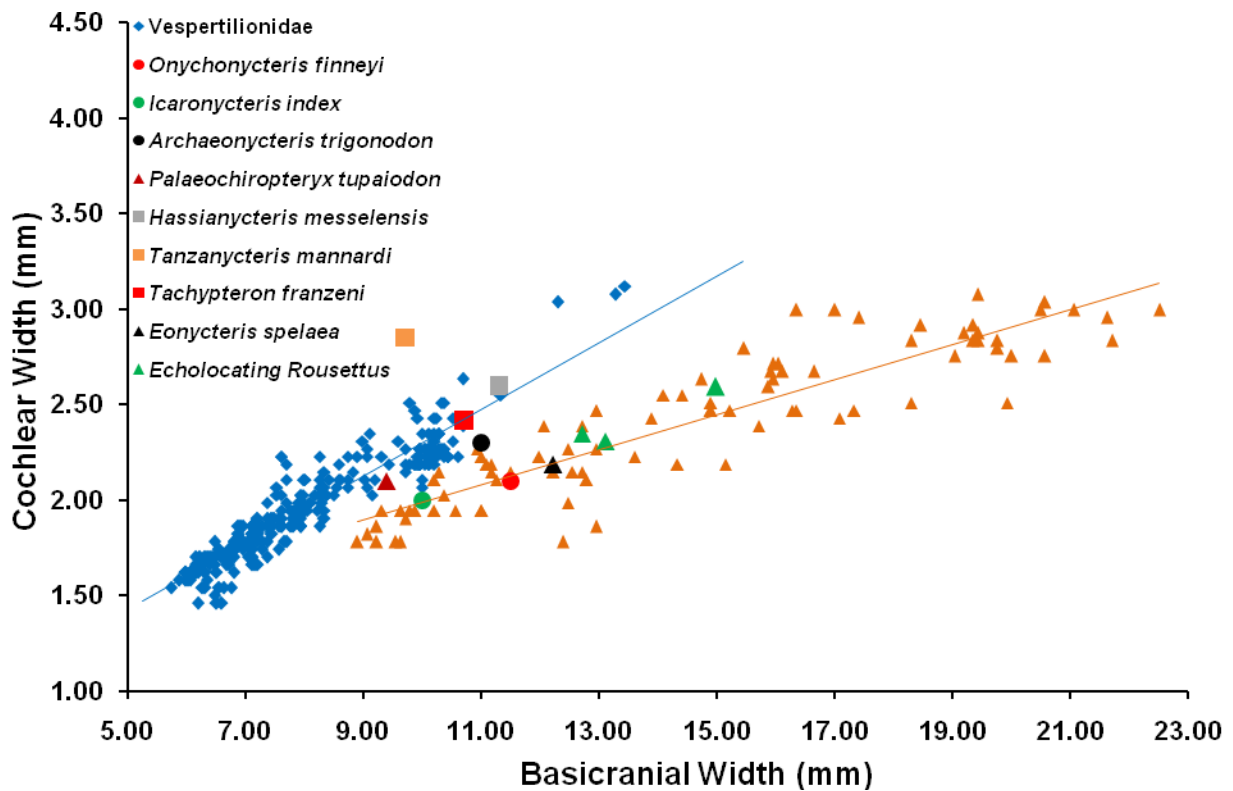
Chiroptera. Extinct Eocene taxa (indicated with a dagger) occupy most but not all of the basal branches; Pteropodidae (= Megachiroptera) nests among these lineages, well outside the smallest clade comprising the other extant families.



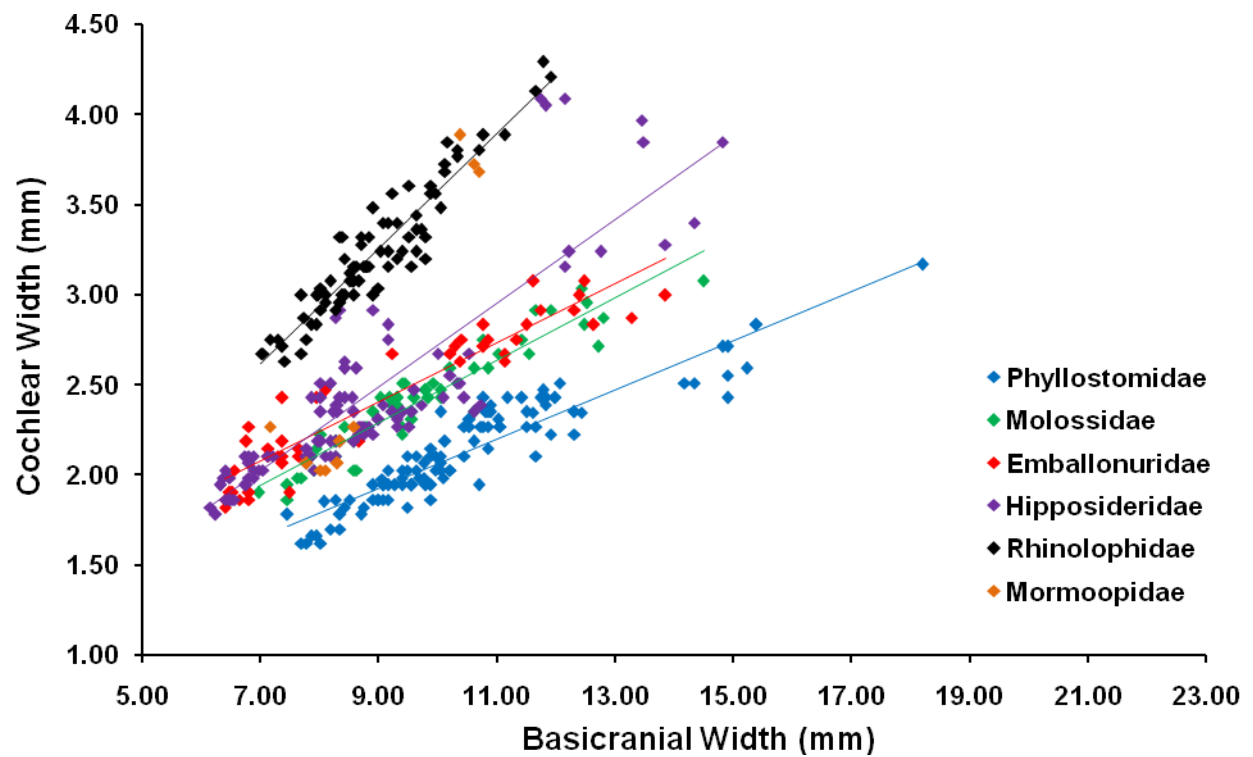
Supplementary Figure 6. Phylogenetic tree of bats based on a constrained parsimony analysis (molecular backbone tree). In this analysis, relationships of fossil taxa (indicated with a dagger) were determined based on a parsimony analysis of the same morphological data employed to recover the tree presented in Supplementary Fig. 5, but

in this case relationships among extant lineages were constrained using a backbone scaffold tree of family relationships derived from molecular studies (see Online Methods). A reduced version of this tree, in which subsets of families were grouped under their currently accepted Superfamily names, is presented in Fig. 4. Numbers above branches are bootstrap values, below branches are Bremer values. Based on results of this analysis, *Onychonycteris* occupies the most basal branch within Chiroptera, and a series of Eocene taxa are consecutive sister taxa to an extant chiropteran crown clade.

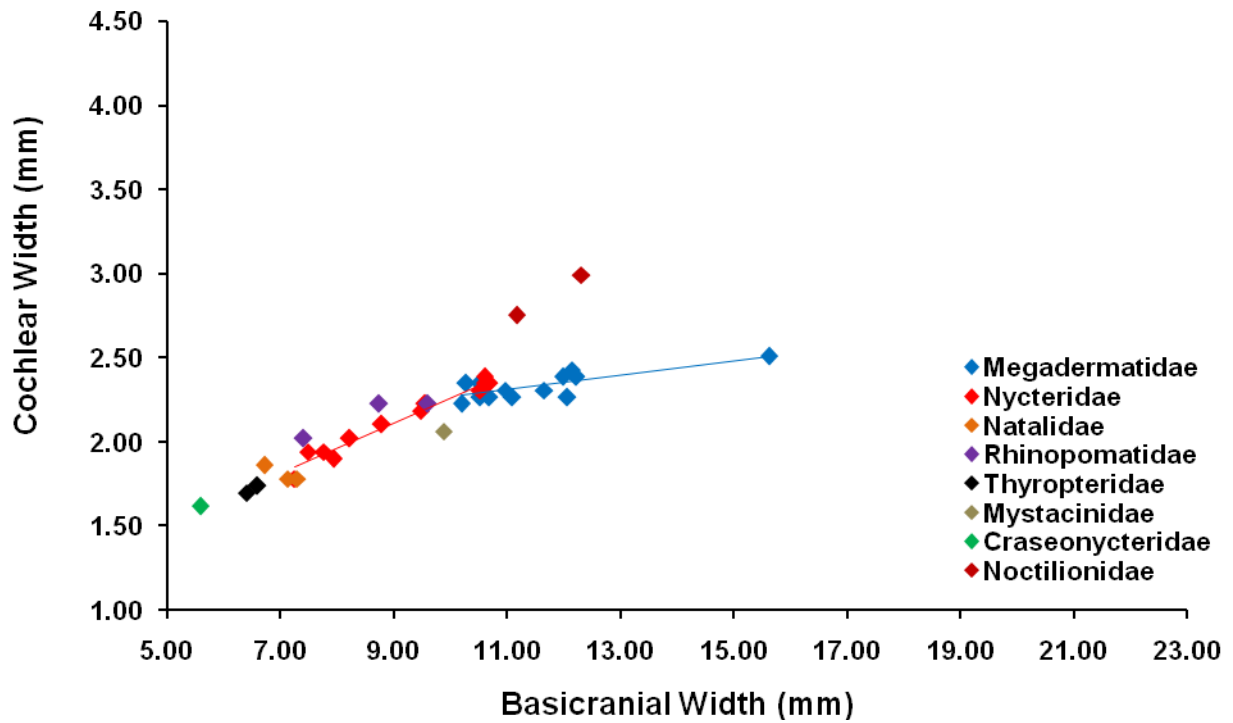
Unambiguous synapomorphies diagnosing the smallest clade including *Icaronycteris* + the chiropteran crown clade (and thus not seen in *Onychonycteris*) consist of the following features: enlarged orbicular apophysis on the malleus; stylohyal element with an expanded, paddle-like cranial tip; enlarged cochlea; ribs with posterior laminae present; claws absent on forelimb digits III, IV, and V. Ambiguous apomorphies which diagnose this clade under some but not all optimizations include: hard palate extends posteriorly into interorbital region; pars cochlearis of petrosal loosely attached to basisphenoid via ligaments and/or thin splints of bone; cochlea phanerocochlear; posteriorly directed ventral accessory processes present on centra of cervical vertebrae 2 and 3; mesosternum articulates with five or fewer costal cartilages posterior to second rib; suprascapular process present; epitrochlea broad, width greater than or equal to 40% of width of the articular facets of humerus.



Supplementary Figure 7. Basicranium vs. cochlear width in Pteropodidae, Vespertilionidae, and Eocene bats. Vespertilionids use sophisticated laryngeal echolocation to detect, track, and capture aerial prey, while pteropodids are not capable of laryngeal echolocation^{9,10,23}. Some Pteropodidae (e.g., *Rousettus aegyptiacus*, *R. amplexicaudatus*, *R. leschenaulti*, *Eonycteris spelaea*) may use crude forms of echolocation involving tongue clicks or wing slaps to detect major obstacles such as walls (⁹ and references cited therein), but their abilities do not approach those of bats that use laryngeal echolocation, and their cochleae are not noticeably enlarged.

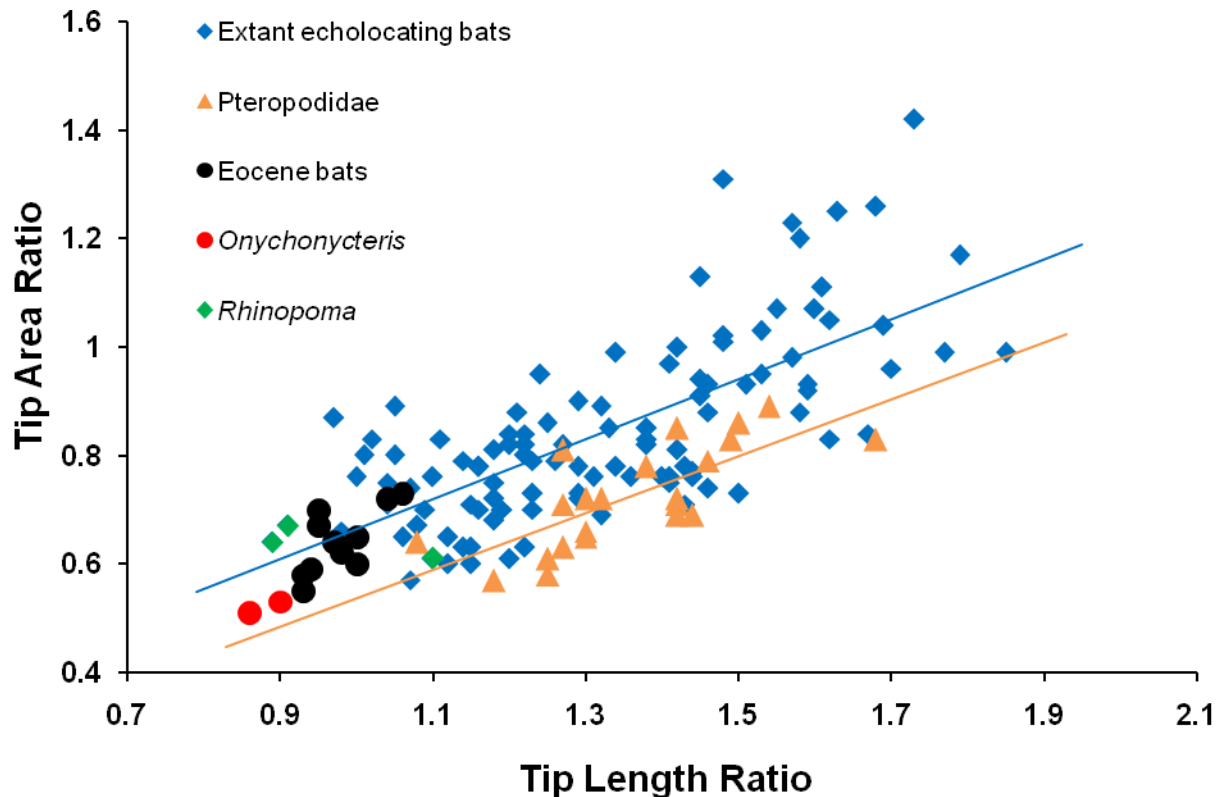


Supplementary Figure 8. Basicranium vs. cochlear width in Phyllostomidae, Molossidae, Emballonuridae, Hipposideridae, Rhinolophidae, and Mormoopidae. All of these taxa use laryngeal echolocation^{9,10,23}.



Supplementary Figure 9. Basicranium vs. cochlear width in Megadermatidae, Nycteridae, Natalidae, Rhinopomatidae, Thyropteridae, Mystacinidae, Craseonycteridae, and Noctilionidae. All of these taxa use laryngeal echolocation

9,10,23



Supplementary Figure 10. Distal wing form in *Onychonycteris* compared with other extinct and extant bats (data for extant taxa and other Eocene forms taken from ¹⁰⁻¹²; see ¹⁰ for measurement methods). Tip Length Ratio = Length of Hand Wing/Length of Arm Wing. Tip Area Ratio = Area of Hand Wing/Area of Arm Wing. Note that *Onychonycteris* exhibits the lowest known values for both Tip Length and Tip Area Ratios (ROM 55351A (Holotype), Tip Length Ratio (TLR) = 0.77, Tip Area Ratio (TAR) = 0.51; ROM 55055 (paratype), TLR = 0.80, TAR = 0.53). Among extant bats, the condition seen in *Onychonycteris* most closely matches that of *Rhinopoma*, a taxon known to use an unusual gliding-fluttering flight style^{10, 12, 28}. Most other echolocating bats not glide, although many members of Pteropodidae do employ gliding as part of their

flight repertoire¹⁰. Other Eocene bats include *Icaronycteris*, *Archaeonycteris*, *Palaeochiropteryx*, and *Hassianycteris*.

3. Supplementary References

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