

Icaronycteris index (holotype; PU 18150) from the Green River Formation, Wyoming.

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ABSTRACT

The Eocene fossil record of bats (Chiroptera) includes four genera known from relatively complete skeletons: *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. Phylogenetic relationships of these taxa to each other and to extant lineages of bats were investigated in a parsimony analysis of 195 morphological characters, 12 rDNA restriction site characters, and one character based on the number of R-1 tandem repeats in the mtDNA d-loop region. Results indicate that *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* represent a series of consecutive sister-taxa to extant microchiropteran bats. This conclusion stands in contrast to previous suggestions that these fossil forms represent either a primitive grade ancestral to both Megachiroptera and Microchiroptera (e.g., Eochiroptera) or a separate clade within Microchiroptera (e.g., Palaeochiropterygoidea). A new higher-level classification is proposed to better reflect hypothesized relationships among Eocene fossil bats and extant taxa. Critical features of this classification include restriction of Microchiroptera to the smallest clade that includes all extant bats that use sophisticated echolocation (Emballonuridae + Yinochiroptera + Yangochiroptera), and formal recognition of two more inclusive clades that encompass Microchiroptera plus the four fossil genera.

Comparisons of results of separate phylogenetic analyses including and subsequently excluding the fossil taxa indicate that inclusion of the fossils changes the results in two ways: (1) altering perceived relationships among extant forms at a few poorly supported nodes; and (2) reducing perceived support for some nodes near the base of the tree. Inclusion of the fossils affects some character polarities (hence slightly changing tree topology), and also changes the levels at which transformations appear to apply (hence altering perceived support for some clades). Results of an additional phylogenetic analysis in which soft-tissue and molecular characters were excluded from consideration indicate that these characters are critical for determination of relationships among extant lineages.

Our phylogeny provides a basis for evaluating previous hypotheses on the evolution of flight, echolocation, and foraging strategies. We propose that flight evolved before echolocation, and that the first bats used vision for orientation in their arboreal/aerial environment. The evolution of flight was followed by the origin of low-duty-cycle laryngeal echolocation in early members of the microchiropteran lineage. This system was most likely simple at first, permitting orientation

and obstacle detection but not detection or tracking of airborne prey. Owing to the mechanical coupling of ventilation and flight, the energy costs of echolocation to flying bats were relatively low. In contrast, the benefits of aerial insectivory were substantial, and a more sophisticated low-duty-cycle echolocation system capable of detecting, tracking, and assessing airborne prey subsequently evolved rapidly. The need for an increasingly derived auditory system, together with limits on body size imposed by the mechanics of flight, echolocation, and prey capture, may have resulted in reduction and simplification of the visual system as echolocation became increasingly important.

Our analysis confirms previous suggestions that *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* used echolocation. Foraging strategies of these forms were reconstructed based on postcranial osteology and wing form, cochlear size, and stomach contents. In the context of our phylogeny, we suggest that foraging behavior in the microchiropteran lineage evolved in a series of steps: (1) gleaned food objects during short flights from a perch using vision for orientation and obstacle detection; prey detection by passive means, including vision and/or listening for prey-generated sounds (no known examples in fossil record); (2) gleaned stationary prey from a perch using echolocation and vision for orientation and obstacle detection; prey detection by passive means (*Icaronycteris*, *Archaeonycteris*); (3) perch hunting for both stationary and flying prey using echolocation and vision for orientation and obstacle detection; prey detection and tracking using echolocation for flying prey and passive means for stationary prey (no known example, although *Icaronycteris* and/or *Archaeonycteris* may have done this at times); (4) combined perch hunting and continuous aerial hawking using echolocation and vision for orientation and obstacle detection; prey detection and tracking using echolocation for flying prey and passive means for stationary prey; calcar-supported uropatagium used for prey capture (common ancestor of *Hassianycteris* and *Palaeochiropteryx*; retained in *Palaeochiropteryx*); (5) exclusive reliance on continuous aerial hawking using echolocation and vision for orientation and obstacle detection; prey detection and tracking using echolocation (*Hassianycteris*; common ancestor of Microchiroptera). The transition to using echolocation to detect and track prey would have been difficult in cluttered environments owing to interference produced by multiple returning echoes. We therefore propose that this transition occurred in bats that foraged in forest gaps and along the edges of lakes and rivers

in situations where potential perch sites were adjacent to relatively clutter-free open spaces. Aerial hawking using echolocation to detect, track, and evaluate prey was apparently the primitive foraging strategy for Microchiroptera. This implies that gleaning, passive prey detection, and perch hunting among extant microchiropterans are secondarily derived specializations rather than retentions of primitive habits. Each of these habits has apparently evolved multiple times.

Only extensive phylogenetic analysis, based on as many suites of characters as possible, and carried out in conjunction with adaptational and aerodynamic studies, can form the basis for reconstruction of evolutionary change.

Padian (1987: 19)

The behavior of fossil animals and the evolution of flight will probably always be a subject of contention, and although we may never know for certain if we have found the right answers, we can always distinguish the possible from the impossible, the probable from the improbable.

Norberg (1990: 268)

INTRODUCTION

Bats first appear in the fossil record in Early Eocene deposits of North America, Europe, Africa, and Australia (table 1). The diversity of Eocene bats is remarkable—24 genera are currently recognized, and new species are described almost every year. Of the eight bat genera that make their first appearance in the Early Eocene, almost half are known from spectacular, nearly complete skeletons: *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. Much of what is known (or hypothesized) about the early evolution of bats is based on studies of these taxa (e.g., Jepsen, 1966, 1970; Russell and Sigé, 1970; Richter and Storch, 1980; Novacek 1985a, 1987; Habersetzer and Storch, 1987, 1988, 1989; Habersetzer et al., 1989, 1992, 1994; Norberg, 1989; Storch, 1989).

Icaronycteris was described by Jepsen (1966) on the basis of a beautifully preserved skeleton from the Early Eocene Green River Formation of Fossil Basin, Wyoming (see Frontispiece). A small bat with a long tail, *Icaronycteris* had a wingspan of approximately 30 cm and probably weighed 10–16 g (Habersetzer and Storch, 1987; Norberg, 1989). The holotype was collected from beds that are Middle Wasatchian in age, approximately 53 Ma (Woodburne, 1987; Woodburne

The evolution of continuous aerial hawking may have been the “key innovation” responsible for the burst of diversification in microchiropteran bats that occurred during the Eocene. Fossils referable to six major extant lineages are known from Middle–Late Eocene deposits, and reconstruction of ghost lineages leads to the conclusion that at least seven more extant lineages were minimally present by the end of the Eocene.

and Swisher, 1995). At least three additional skeletons of *Icaronycteris* were subsequently discovered in the same deposits (Novacek, 1985a, 1987; Habersetzer and Storch, 1987; see appendix 1). Isolated teeth from Clarkforkian deposits in North America were referred to cf. *Icaronycteris* sp. by Gingerich (1987), thus potentially extending the range of the genus to the Late Paleocene (fig. 1). Other fragmentary material suggests that *Icaronycteris* may have persisted in North America until the Gardenerbuttian (McKenna and Bell, 1997), an early Bridgerian interval that ended approximately 50 Ma (Woodburne, 1987; Woodburne and Swisher, 1995). Only one species, *Icaronycteris index* Jepsen, 1966, is currently recognized in North America. However, the geographic range of *Icaronycteris* may have extended beyond North America to Europe. Russell et al. (1973) recognized a new species (*Icaronycteris? menui*) based on a large collection of jaw fragments and isolated teeth from Early Eocene (fig. 1; MP¹ 8–9) deposits in

¹ Mammal Paleogene (MP) reference levels are biostratigraphic intervals used to subdivide the Paleogene of Europe. These units, which are of unspecified duration, are based on terrestrial mammalian faunas. The MP system is based on the assumption that the fossil record

France. However, the affinities of this material remain questionable because of the fragmentary nature of available specimens and lack of any diagnostic apomorphies shared with the North American form.

Palaeochiropteryx, *Archaeonycteris*, and *Hassianycteris* are known principally from the famous Early/Middle Eocene "Grube Messel" deposits (MP 11) near Darmstadt, Germany. Hundreds of complete and partial skeletons of bats have been found at Messel, many preserved with stomach contents indicating that they were insectivores that had been foraging successfully just prior to death (Smith et al., 1979; Richter and Storch, 1980; Richter, 1987; Habersetzer et al., 1992, 1994). This unusual concentration of fossil bats that show no evidence for cause of death may have resulted from release of poisonous gas that overcame bats foraging over the surface of Lake Messel (Habersetzer and Storch, 1988; Habersetzer et al., 1992). Another possibility is that the bats died as a result of poisoning by toxic alkaloids from a blue-green algal bloom (see Pybus et al. [1986] for a modern example).

Palaeochiropteryx is by far the most common bat at Messel, accounting for almost 75% of all bat finds (Habersetzer and Storch, 1989; Habersetzer et al., 1992). More than 50 skeletons of *Palaeochiropteryx* are known from Messel, and two species are currently

recognized: *Palaeochiropteryx tupaiodon* Revilliod, 1917 (fig. 2) and *Palaeochiropteryx spiegelii* Revilliod, 1917 (Smith and Storch, 1981; Habersetzer and Storch, 1987). *P. tupaiodon* was the smaller of the two species, probably weighing 7–10 g and having an estimated wingspan of 24–28 cm (Habersetzer and Storch, 1987; Norberg, 1989). In contrast, *P. spiegelii* had an estimated wingspan of 26–30 cm and probably weighed 10–18 g (Habersetzer and Storch, 1987; Norberg, 1989). In addition to the Messel material, isolated fragments referable to *Palaeochiropteryx* have also been reported from Sparnacian, Cuisian, Lutetian, and Bartonian (MP 10, 11–13, 16) deposits from elsewhere in Europe (Russell et al., 1973, 1982; Savage and Russell, 1983).

Archaeonycteris is known from at least six skeletons from Messel, and two species are currently recognized based on this material: *Archaeonycteris trigonodon* Revilliod, 1917b (fig. 3) and *A. pollex* Storch and Habersetzer, 1988 (Russell and Sigé, 1970; Smith and Storch, 1981; Habersetzer and Storch, 1987; Storch and Habersetzer, 1988). *A. trigonodon* probably had a wingspan of 32–37 cm and may have weighed 17–27 g (Habersetzer and Storch, 1987; Norberg, 1989). *A. pollex* was slightly larger, with an estimated body weight of 30–35 g (Storch and Habersetzer, 1988). In addition to the Messel material, fragmentary specimens referable to *Archaeonycteris* have been reported from Sparnacian, Cuisian, and possibly Bartonian deposits in France (MP 8–13, 16; Russell et al., 1973, 1982; Godinot, 1981; Savage and Russell, 1983; Schmidt-Kittler, 1987). This material includes at least one additional species, *Archaeonycteris brailloni* Russell, Louis, and Savage, 1973 (MP 8–9; Schmidt-Kittler, 1987). Another species, *Archaeonycteris revilliodi* Russell and Sigé, 1970, is based on a partial dentition from Messel. Always considered somewhat problematic, this form was transferred to Hassianycteridae as *Hassianycteris? revilliodi* by Habersetzer and Storch (1987). Smith and Russell (1992) subsequently reported discovery of a skull of *revilliodi* and confirmed that this species should be placed in *Hassianycteris*.

Hassianycteris is known from at least 20 skeletons from Messel. Three species are

consists of continuously evolving lineages; therefore, separation between ancestor and descendant species (and the temporal range of each species) is completely arbitrary. In an effort to prevent this subjective element from confounding biostratigraphy, the boundaries of the MP units were not defined by the first and last appearance of taxa; accordingly, they are not true biostratigraphic zones (Schmidt-Kittler, 1987). Each MP level has a reference locality whose fauna functions as the type for the reference level (Schmidt-Kittler, 1987). The method used to order MP levels not correlated to marine stages is not clear. It appears to be based on faunal similarity and the evolutionary stage of the lineages within the respective faunas (Russell et al., 1982; Schmidt-Kittler, 1987). Ordering of the MP levels by radiometric ages, magnetostratigraphy, and the superposition of strata has not been possible (Schmidt-Kittler, 1987). Although the use of faunal evolutionary stage in developing the sequence of MP levels is subjective and of questionable validity, it is currently the only option for placing European fossil mammals in geologic time.

currently recognized based on this material: *Hassianycteris messelensis* Smith and Storch, 1981; *Hassianycteris magna* Smith and Storch, 1981; and *Hassianycteris revilliodi* Russell and Sigé, 1970 (Smith and Storch, 1981; Habersetzer and Storch, 1988; Smith and Russell, 1992). Wingspans and weights have been estimated for only those species known from relatively complete skeletons (i.e., *H. messelensis* and *H. magna*). *H. messelensis* probably had a wingspan of 35–40 cm and weighed 25–45 g (Habersetzer and Storch, 1987; Norberg, 1989). *H. magna* had a wingspan of 45–50 cm and may have weighed 65 g, making it the largest known Eocene bat (Habersetzer and Storch, 1987; Norberg, 1989). A fourth species, *Hassianycteris joeli* Smith and Russell, 1992, is known from a partial dentary with teeth from upper Ypresian (Early Eocene) deposits in Belgium (Smith and Russell, 1992).

RELATIONSHIPS AND CLASSIFICATION OF EOCENE BATS: A HISTORICAL OVERVIEW

Phylogenetic relationships among *Icaronycteris*, *Palaeochiropteryx*, *Archaeonycteris*, and *Hassianycteris* have been the subject of considerable debate, as have their relationships to extant lineages. It has long been thought that many Eocene fossils represent early members of extant microchiropteran families, but *Icaronycteris*, *Palaeochiropteryx*, *Archaeonycteris*, and *Hassianycteris* (often referred to as the “archaic” Eocene bats) have remained enigmatic. Most workers have regarded some or all of these forms as representatives of an early grade of chiropteran evolution, but opinions have differed concerning their relationships to each other, other Eocene taxa, Megachiroptera, Microchiroptera, and to extant microchiropteran superfamilies. This uncertainty has been reflected in classifications, which have varied considerably over the last few decades. Because ideas concerning relationships of *Icaronycteris*, *Palaeochiropteryx*, *Archaeonycteris*, and *Hassianycteris* developed in the context of a rich body of literature on early Tertiary bats, we review here (in chronological order) the history of classification and phylogenetic hypotheses regarding all Eo-

cene chiropteran taxa, not just the four genera examined in the present study. The taxonomy and spelling of names are those of the original author(s) of each study. Question marks associated with taxonomic names to indicate uncertainty (e.g., *Icaronycteris? menui*) also reflect the usage of the original author(s).

Twenty-four genera of bats are now recognized from the Eocene, although some were originally described based on material from younger deposits (table 1). Several early Tertiary bat fossils were reported in the literature prior to 1875, but most were isolated teeth or fragments of jaws referred to either Chiroptera, *Rhinolophus*, or *Vespertilio*, the latter being a waste-basket taxon that once included most bats. Summaries of the history of fossil bat discoveries prior to 1875 were provided by Revilliod (1922) and Legendre and Sigé (1983).

Most modern bat classifications are based largely upon that of Dobson (1875: 345), who was the first to provide a comprehensive classification of extant bats “arranged according to their natural affinities.” Dobson (1875) briefly considered the origins of Chiroptera, although he did not explicitly discuss any of the fossil material known at the time. Accompanying Dobson’s (1875) account was a figure “illustrating the affinities of the families and genera of Chiroptera, and probable lines of descent from ancestral forms . . .” (fig. 5). In this diagram, Dobson (1875) used *Palaeochiroptera* as a name for the group of largely unknown fossil bats that he presumed were ancestral to all extant bat lineages.

Schlosser (1887) named *Pseudorhinolophus* and *Vespertiliavus* based on material from the Late Eocene to Early Oligocene Quercy phosphorite deposits in France (currently referred to MP 16–23; Crochet et al., 1981; Sigé and Legendre, 1983; Schmidt-Kittler, 1987). Drawing on extensive comparisons with extant genera, Schlosser (1887) suggested a close relationship between *Pseudorhinolophus* and *Rhinolophus* and noted several points of similarity between *Vespertiliavus*, species of *Vespertilio* (many now placed in other genera and even other families; see below), and *Taphozous*. He subsequently concluded that *Pseudorhinolophus* should be grouped with rhinolophids and

Ma.	EPOCH		AGE	N.A. Land Mammal Age	EU. Land Mammal Age ^a	EU. Land Mammal Age ^b	MP LEVEL	Ma.
30	OLIGOCENE	Early	Rupelian	Whitneyan	Suevium	Early Oligocene	23 ^c	30
				Orellan			22 ^c	
35		Late	Priabonian	Chadronian	Headonium	Headonian	21	35
							20 ^c	
40		Middle	Bartonian	Duchesnean	Rhenanium	Robiacian	19 ^c	40
							18 ^c	
45	EOCENE		Lutetian	Uintan		Lutetian	17 ^c	45
50		Early	Ypresian	Bridgerian		Cuisian	15	50
55	PALEOCENE	Late	Thanetian	Wasatchian	Neustrium	Sparnacian	13	55
60			Selandian	Clarkforkian	Cernaysium	Cernaysian	11 ^c	60
				Tiffanian			8/9 ^c	
							7	
							6 ^c	

Fig. 1. Chart showing geologic time scale, standard geologic ages based on marine strata, and the correlation of land mammal ages and levels. Data compiled from Fahlbusch (1976), Russell et al. (1982), Savage and Russell (1983), Berggren et al. (1995), Woodburne and Swisher (1995), and McKenna and Bell (1997). Correlations of MP levels to marine strata of known age are based on the following: MP 7 (Hooker, 1991; Woodburne and Swisher, 1995); MP 10, 13, 14, and 15 (Russell et al., 1982; Aubry, 1983); and MP 21 (Hooker, 1992). Abbreviations: EU., European; Ma., melleannus, millions of years before present; N.A., North American. For a definition of MP levels, see footnote 1 on page 5.

^aAges according to Fahlbusch (1976).

^bAges according to Savage and Russell (1983).

^cThese MP reference levels are not correlated to marine strata; instead, they are placed in an approximate chronological order (based on Russell et al. [1982] and Schmidt-Kittler [1987]) between MP levels that can be correlated to marine strata.

Vespertiliavus with vespertilionids. Schlosser (1887) also described fragmentary material that he referred to *Rhinolophus* sp. and to a later Tertiary species of *Rhinolophus* described by Filhol (1872). Schlosser (1887) also discussed an isolated humerus that he suggested was similar to that of rhinolophids.

Weithofer (1887) discussed new material of *Pseudorhinolophus* and suggested modifications of Schlosser's (1887) description and allocation of this taxon. Based on comparisons with extant material, Weithofer

(1887) concluded that *Pseudorhinolophus* was more closely related to *Phyllorhina* (= *Hipposideros*) than to *Rhinolophus*. He referred the isolated humerus described by Schlosser (1887) to "*Taphozous*?" noting that it was clearly different from the typical rhinolophid form. Weithofer (1887) also described several new taxa based on craniodental material from the Quercy deposits, including *Alastor* (which he associated with *Pseudorhinolophus* and *Phyllorhina*), *Necromantis* (which he concluded was related to

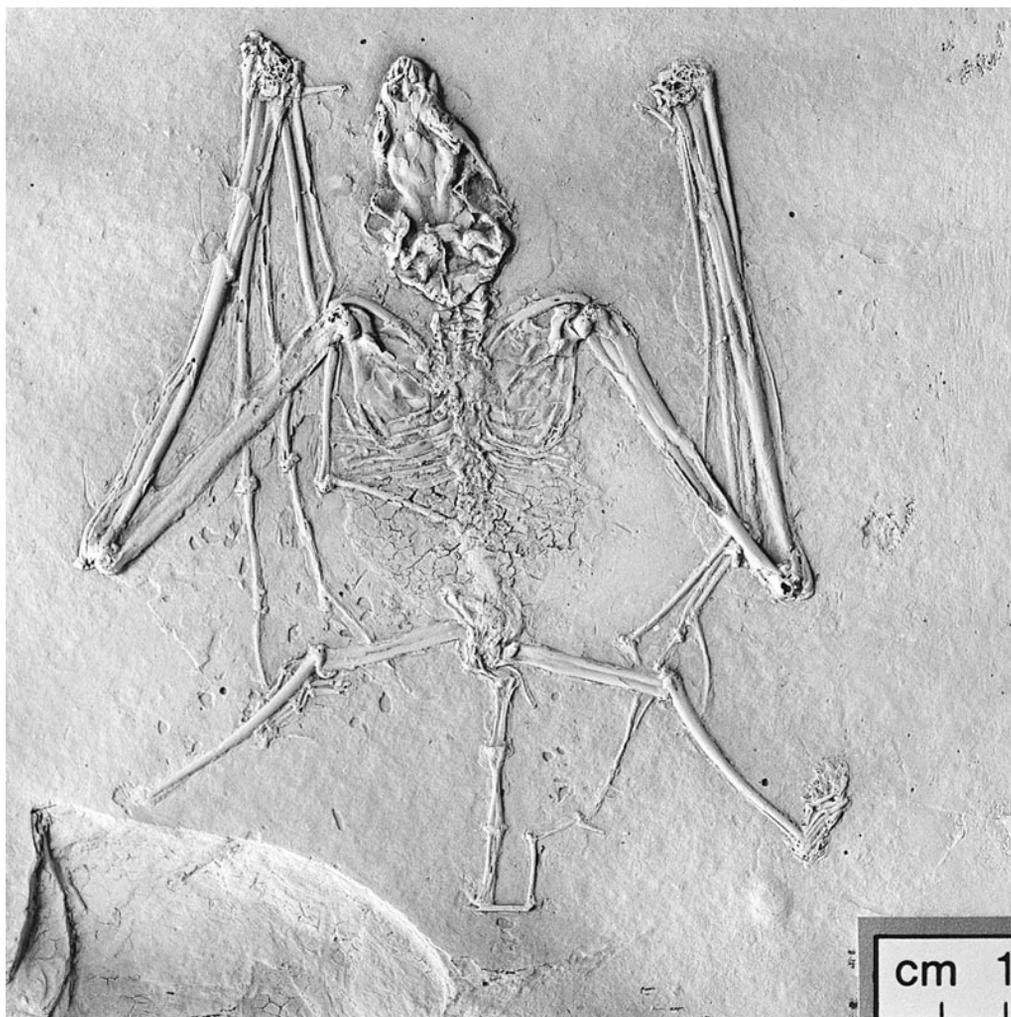


Fig. 2. *Palaeochiropteryx tupaiodon* (SMF ME 10) from Messel, Germany. From Habersetzer and Storch (1987: fig. 2). Photo by E. Pantak (Senckenbergmuseum).

Phyllostomidae), and a fossil species referred to “*Rhinolophus*(?).” Recent collections have suggested that *Necromantis* is restricted to the MP 17 fauna (Sigé and Legendre, 1983; Schmidt-Kittler, 1987).

Winge (1892 [translated into English in Winge, 1941]) discussed the status of *Pseudorhinolophus* and *Alastor*, noting that although some authors had treated these as genera separate from *Phyllorhina* (= *Hipposideros*), few had noted any significant differences. He concluded that *Palaeophyllophora* clearly belonged to the same group as *Pseudorhinolophus*, although *Palaeophyllo-*

phora is somewhat more specialized. Winge (1892) also discussed an undescribed, almost complete skull of *Vespertiliavus* from the collections at Copenhagen. Several features of this specimen led him to conclude that *Vespertiliavus* is a relatively specialized member of Emballonuridae, closely related to *Taphozous*. He noted that this conclusion was not surprising given the taxonomic history of species previously compared with *Vespertiliavus*. Citing Schlossers (1887) original description of *Vespertiliavus*, Winge (1892) observed that the “vespertilionid” that Schlosser thought was most similar to

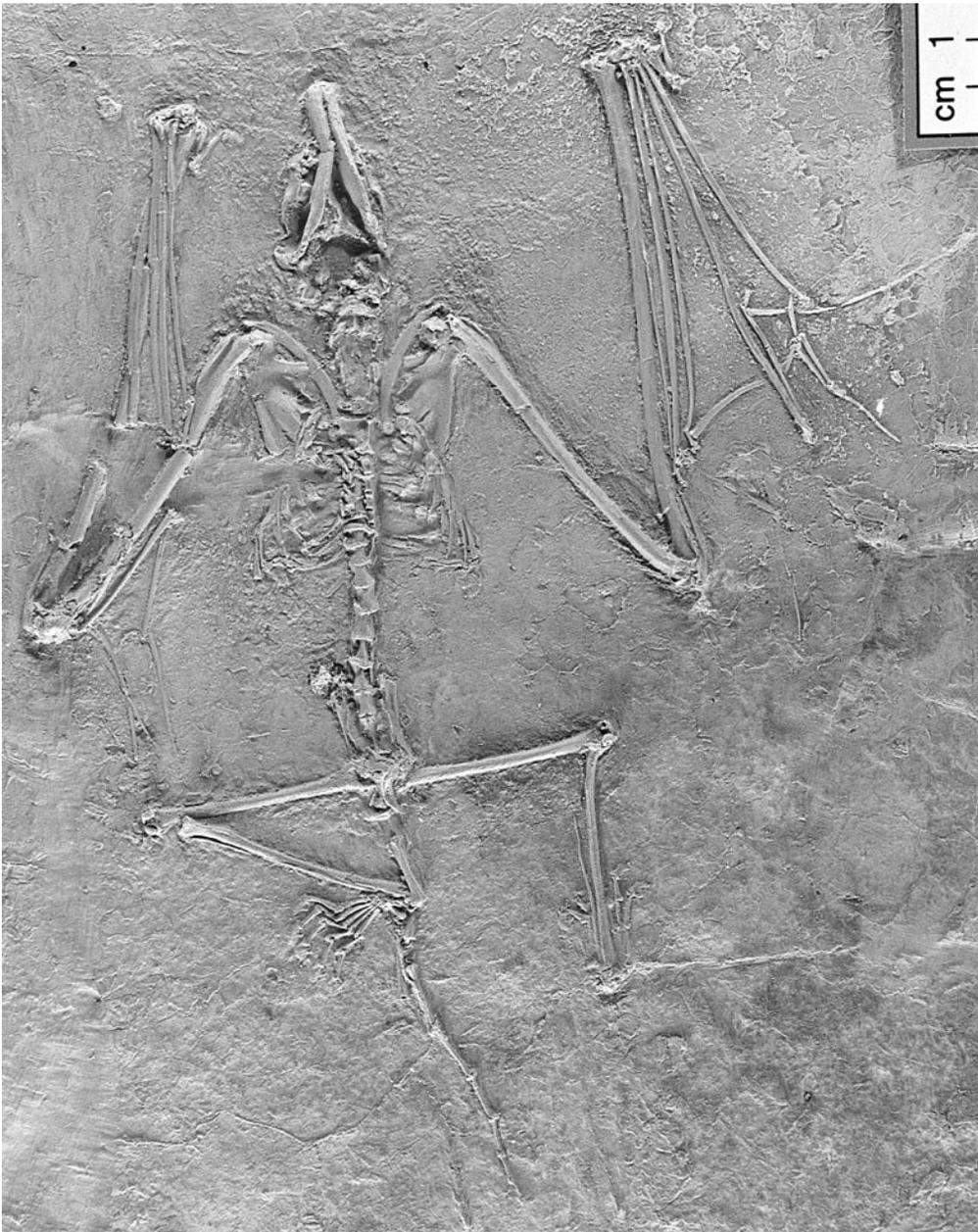


Fig. 3. *Archaeonycteris trigonodon* (SMF 80/1379) from Messel, Germany. From Habersetzer and Storch (1987: fig. 3). Photo by E. Pantak (Senckenbergmuseum).

Vespertiliavus—*Vespertilio alecto*—was considered by Dobson (1878) to be conspecific with *Emballonura monticola*. Winge further noted that the isolated humerus referred to “*Taphozous(?)*” by Weithofer

(1887) undoubtedly also represents *Vespertiliavus*.

Meschinelli (1903) described *Archaeopteropus* based on a skeleton with a poorly preserved skull from late Oligocene deposits



Fig. 4. *Hassianycteris messelensis* (SMF ME 1414a) from Messel, Germany. From Habersetzer and Storch (1987: fig. 5). Photo by E. Pantak (Senckenbergmuseum).

TABLE 1

Temporal and Geographic Distribution of Genera of Fossil Bats Known from Eocene Deposits^aFirst occurrence in Early Eocene^b:

- Ageina* Russell, Louis, and Savage, 1973
Early Eocene, Europe and North America
- Archaeonycteris* Revilliod, 1917b
Early Eocene–Middle Eocene, Europe
- Australonycteris* Hand, Novacek, Godthelp, and Archer, 1994
Early Eocene, Australia
- Dizzya* Sigé, 1991a
Early Eocene, Africa
- Eppsinonycteris* Hooker, 1996
Early Eocene, Europe
- Hassianycteris* Smith and Storch, 1981
?Early Eocene, Middle Eocene, Europe
- Honrovits* Beard, Sigé, and Krishtalka, 1992
Early Eocene, North America
- Icaronycteris* Jepsen, 1966
?Late Paleocene, Early Eocene, ?Middle Eocene, North America; ?Early Eocene, Europe
- Palaeochiropteryx* Revilliod, 1917b
Early Eocene–Middle Eocene, Europe

First occurrence in Middle Eocene:

- Cecilionycteris* Heller, 1935
Middle Eocene, Europe
- Hipposideros* Gray, 1831^c
Middle Eocene–Early Pliocene, Europe; Early Miocene–Recent, Africa; ?Pleistocene–Recent, Madagascar; Middle Pleistocene–Recent, Asia; Late Pleistocene–Recent, East Indies; Recent, Australia and New Guinea
- Matthesia* Sigé and Russell, 1980
Middle Eocene, Europe
- Palaeophyllophora* Revilliod, 1917b
Middle Eocene–Early Miocene, Europe
- Rhinolophus* Lacépède, 1799
Middle Eocene–Recent, Europe; Middle Miocene–Recent, Africa; Early Pleistocene–Recent, Asia; Late Pleistocene–Recent, East Indies; Late Pleistocene–Recent, Australia and New Guinea
- Stehlinia* Revilliod, 1919^d
Middle Eocene–Late Oligocene, Europe
- Vespertiliavus* Schlosser, 1887
Middle Eocene–Middle Oligocene, Europe
- Wallia* Storer, 1984^e
Middle Eocene, North America

First occurrence in Late Eocene:

- Chadronycteris* Ostrander, 1983
Late Eocene, North America
- Cuvierimops* Legendre and Sigé, 1983
Late Eocene–Early Oligocene, Europe
- Necromantis* Weithofer, 1887^f
Late Eocene, Europe
- Paraphyllophora* Revilliod, 1922
Late Eocene and/or Early Oligocene, Middle Miocene, Europe
- Philisis* Sigé, 1985
Late Eocene, Africa
- Vampyravus* Schlosser, 1910^g
Late Eocene, Africa
- Vaylatsia* Sigé, 1990^h
Late Eocene–?Early Miocene, Europe

in Italy. Although not explicit with regards to classification, Meschinelli (1903) clearly regarded *Archaeopteropus* as an early megachiropteran. Although *Archaeopteropus* does not appear in Eocene or even early Oligocene deposits, this taxon (still known only from a single specimen that was destroyed in World War II) has frequently been classified with Eocene bats and has had an important impact on discussions of the early diversification of Chiroptera (see below).

In the course of a preliminary description of an early Tertiary fauna from the Jebel El Qatrani Formation in Egypt, Schlosser (1910) recognized the existence of a large bat based on a single humerus. He noted similarities between this specimen and *Vampyrus* and *Stenoderma*, and he named the new form *Vampyravus*. The next year, Schlosser (1911) published a more detailed account of the mammals from Fayum (including the Jebel El Qatrani Formation), and described *Provampyrus* based on an isolated humerus.

Based on comparisons with extant pteropods and phyllostomids of similar size, Schlosser (1911) suggested that *Provampyrus* should be referred to Phyllostomidae. Later authors noted that *Provampyrus* and *Vampyravus* appear to have been based on the same specimen (e.g., Sigé, 1985; see below).

Leche (1911) compared a relatively well-preserved skull of *Pseudorhinolophus* with extant specimens of *Phyllorhina* (= *Hipposideros*) and *Rhinolophus*, and concluded that *Pseudorhinolophus* should be considered congeneric with *Phyllorhina*. He also concurred with Winge's (1892) conclusion that *Vespertiliavus* is an early member of Emballonuridae, probably a close relative of *Taphozous*.

Andersen (1912) considered the status of *Archaeopteropus* in his monograph on Megachiroptera. He noted that Meschinelli (1903) had confused the third and fifth digits of the wing; however, upon making this correction, Andersen (1912: xxxix) found that

←

^a Unless otherwise noted, age ranges are from McKenna and Bell (1997); see Russell et al. (1982) and Savage and Russell (1983) for summaries of species associated with many different formations, ages, and faunas in the Paleogene. Isolated teeth of uncertain affinities have been referred to Chiroptera based on material from Early and Middle Eocene deposits in France ("Eochiroptera incertae sedis, Fam. gen. et sp. indét.," Crochet et al., 1988: 422; "Eochiroptera, fam., gen., et sp. indet. 1 and 2," Marandat, 1991: 90; cf. *Vesperiliavus*, cf. *Necromantis*, Marandat et al., 1993), latest Early Eocene deposits of the Kuldana Formation in Pakistan ("Chiroptera indet. A and B"; Russell and Gingerich, 1981: 284, 286), and Middle Eocene Bridger Formation deposits in North America ("Chiroptera, Family uncertain, Undescribed genus and species"; McKenna et al., 1962: 27). An isolated tooth from Late Eocene deposits in Thailand was referred to Megachiroptera by Ducrocq et al. (1993).

^b *Wyonycteris* Gingerich, 1987, which was described as an Early Eocene palaeochiropterygid bat, is omitted from this list based on arguments developed by Hand et al. (1994). *Wyonycteris* is based on fragmentary dental remains that exhibit several features common to but not uniquely diagnostic of bats (Gingerich, 1987; Hand et al., 1994). Hand et al. (1994) noted the *Wyonycteris* seems to lack some putative dental synapomorphies of early bats, and concluded that no convincing evidence supports assignment of this form to chiroptera. Similarly, *Paradoxonycteris* Revilliod, 1919 from the Late Eocene of Europe is omitted based on arguments presented by Russell and Sigé (1970) and Sigé (1976). As with *Wyonycteris*, in the absence of more complete material there seems little reason to refer *Paradoxonycteris* to Chiroptera. *Zanycteris* Matthew, 1917 from the Wasatchian of Colorado is omitted because it is now thought to be a microdontid primate (Simpson, 1945; Romer, 1966; Savage and Russell, 1983; Carroll, 1988).

^c Includes *Pseudorhinolophus* Schlosser, 1887 and *Alastor* Weithofer, 1887. The range for *Hipposideros* (subgenus *Pseudorhinolophus*) is Middle Eocene–Middle Miocene, Europe (Hand and Kirsch, 1988).

^d Includes *Nycterobius* Revilliod, 1922, *Paleonycteris* Revilliod, 1922, and *Revilliodia* Simpson, 1945. See Handley (1955) for a discussion of the taxonomic history of *Stehlinia* and other names associated with Revilliod's 1919 and 1922 publications. Sigé (1974) provided a thorough revision of the genus and confirmed the synonymies.

^e Originally described as a proscalopid insectivoran, but transferred to Molossidae by Legendre (1985).

^f Includes *Necromanter* Lydekker, 1888 and *Necronycteris* Palmer, 1903.

^g Includes *Provampyrus* Schlosser, 1911, which is apparently an objective junior synonym of *Vampyravus* (Sigé, 1985). *Vampyravus* may be a senior synonym of *Philisis*, but this cannot be determined based on available material; see discussion in Sigé (1985).

^h Age range following Hand and Kirsch (1998).

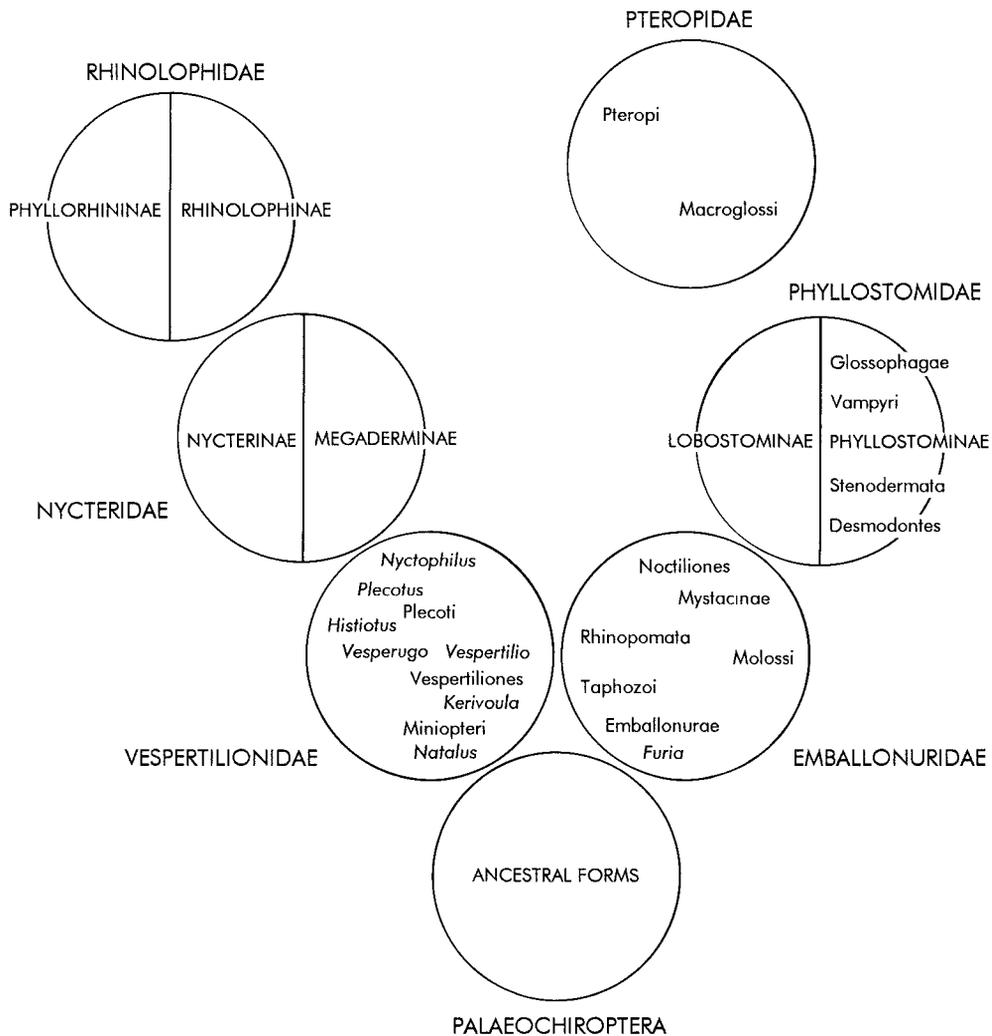


Fig. 5. Dobson's (1875) view of bat relationships (redrawn from Dobson, 1875: unnumbered foldout facing p. 350). The original caption for this figure read "Diagram illustrating the affinities of the families and genera of Chiroptera, and probable lines of descent from ancestral forms (Palaeochiroptera). The families are indicated by circles, the subfamilies by semicircles, and the relative position of both indicates their affinity. In the same manner, the affinity of the generic groups to each other, and to groups of other families, is indicated (as far as possible) by the relative position of the names of these groups in each circle . . . The position of the circle representing the Pteropidae is not intended (as in other cases) to indicate their descent from the Phyllostomidae, but to show their position with regard to the whole suborder Microchiroptera." We have retained Dobson's (1875) spellings of group names, many of which are no longer in common usage.

"the hand of *Archaeopteropus* was a genuine Megachiropteran hand."

Matthew (1917) described *Zanycteris* based on a partial maxilla from the Wasatch Formation in Colorado. Although Matthew (1917) considered *Zanycteris* to be a phyl-

lostomid, its affinities were questioned by subsequent authors (e.g. Winge, 1941), and it was later recognized as a picrodontid primate (Simpson, 1945; Romer, 1966; Savage and Russell, 1983; Carroll, 1988).

Revilliod (1917b) described *Palaeochi-*

ropteryx and *Archaeonycteris* based on craniodental and skeletal material from Messel (MP 11; Schmidt-Kittler, 1987). He compared these forms with other Eocene and Recent taxa, and proposed that *Palaeochiropteryx* and *Archaeonycteris* be placed in their own families, Palaeochiropterygidae and Archaeonycteridae. These family-group names have formed the basis for most subsequent classifications of archaic Eocene fossil bats.

Revilliod (1917a, 1920, 1922) published a three-part monograph on fossil bats of the Tertiary. A source of some confusion has been the fact that he published a preliminary note summarizing the entire monograph in 1919, one year before part II was published and three years before part III was published. This summary paper (Revilliod, 1919) included the first references to many named taxa described in later parts of the monograph, but did not include the descriptions required to make all of these names available. Handley (1955) resolved the taxonomic problems introduced by this work by noting that many names published in Revilliod (1919) were nomina nuda, but that descriptions provided by Revilliod (1920, 1922) subsequently made these names available from the later dates. Most of the conclusions described in Revilliod's (1919) "Note préliminaire" were discussed in greater depth in Revilliod (1922; see below). However, there are some minor differences between the 1919 and 1922 accounts. Revilliod (1919) suggested that *Paleonycteris* might represent a distinct family "des . . . Paleonyctérides," but by 1922 he had apparently decided against formally naming a separate family for this genus. Considering the origin of bats, Revilliod (1919) noted that *Archaeonycteris* exhibited the most primitive dentition, one from which all other chiropteran dentitions could be derived.

In part II of his monograph, Revilliod (1920) discussed fossil specimens of *Rhinolophus*, described two new species in this genus from Eocene deposits in France, and similarly discussed and named two new species of *Necromantis*. Based on extensive comparisons with extant forms, he placed *Necromantis* in "Mégadermidés" (= Megadermatidae). Revilliod (1920) also redescribed *Vespertiliavus* and described three new spe-

cies in this genus. Based on comparisons with extant forms, he concluded that *Vespertiliavus* is a relatively primitive emballonurid that is either closely related to *Taphozous* or ancestral to the family as a whole.

Finally, in part III of his monograph, Revilliod (1922) described *Paleonycteris* based on several dentary fragments with teeth from deposits at Quercy (MP 17–19; Crochet et al., 1981; Sigé and Legendre, 1983; Schmidt-Kittler, 1987) and Egerkingen (MP 14; Schmidt-Kittler, 1987), and described *Paradoxonycteris* based on a maxillary fragment with teeth from Mormont (MP 17–19; Sigé and Legendre, 1983; Schmidt-Kittler, 1987). Revilliod (1922) concluded that *Paleonycteris* was related either to vespertilionids (broadly defined to include natalids) or phyllostomids (defined as including mormoopids), and that *Paradoxonycteris* resembled emballonurids and primitive phyllostomids. Apparently because of the fragmentary nature of the available material, he declined to refer either genus to a particular family, although he placed both in Microchiroptera. Revilliod (1922) also described several taxa that he had mentioned but not described in his 1919 publication (see above and Handley, 1955). Initial descriptions were provided for *Palaeophyllophora* and *Paraphyllophora* (MP 18–19; Crochet et al., 1981; Schmidt-Kittler, 1987), and a revised description was presented for *Pseudorhinolophus* (including *Alastor*). Revilliod (1922) referred all of these genera (as well as the Eocene representatives of *Rhinolophus*) to Rhinolophidae sensu lato. He placed another new form, *Nycterobius* Revilliod, 1922 from Quercy Sainte Neboule (MP 18; Schmidt-Kittler, 1987), in "Vespertilionides" and noted a close resemblance to *Myotis*.

Revilliod (1922) additionally reviewed all of the other Tertiary bats considered in his earlier works (i.e., parts I and II of his monograph; Revilliod, 1917a, 1920) and presented final conclusions regarding each taxon. He referred *Archaeopteropos* to Megachiroptera, placed *Necromantis* in Megadermatidae, referred *Zanycteris* and *Provampyrus* to Phyllostomidae, and retained *Palaeochiropteryx* and *Archaeonycteris* in their own families within Microchiroptera. With respect to *Palaeochiropteryx*, he noted that "Ce genre re-

présente une famille éteinte isolée que l'on ne peut rattacher à aucune famille récente." *Archaeonycteris* was noted to "représentant d'une famille éteinte très primitive" (Revilliod, 1922: 177).

Heller (1935) described *Cecilonycteris* based on a series of skeletons and craniodental fragments from the Middle Eocene "Grube Cecilie" deposits (MP 13; Franzen and Haubold, 1987) in Germany. He compared *Cecilonycteris* with specimens and descriptions of *Palaeochiropteryx*, *Palaeophyllophora*, *Paleonycteris*, *Paraphyllophora*, *Necromantis*, *Vespertiliavus*, and several extant taxa. Noting similarities with representatives from several different family-level groups, Heller (1935) declined to refer *Cecilonycteris* to any particular family, instead leaving it incertae sedis within Chiroptera.

Winge (1941) discussed Revilliod's (1917a, 1917b, 1920, 1922) papers on early Tertiary bats of Europe and reevaluated the morphological data reported for *Palaeochiropteryx* and *Archaeonycteris*. Winge (1941: 304) concluded that

... there is hardly anything to prevent us from regarding *Palaeochiropteryx* as belonging to the vespertilionids, as one of the primitive forms, most likely of the nataline group.

Winge (1941) found that *Archaeonycteris* was too poorly known to assess its affinities with other chiropteran taxa, but attributed *Archaeopterus* to Pteropodidae. He also commented on *Provampyrus*, noting that while the holotype humerus resembles that of phyllostomids, a similar form might be expected in primitive genera of other families such as Vespertilionidae and Rhinolophidae.

Simpson (1945) considered the affinities of Eocene bats in his influential classification of mammals. He (1945: 60) placed *Archaeonycteris* in Archaeonycteridae and *Palaeochiropteryx* in Palaeochiropterygidae, and referred both families to Microchiroptera, "Superfam. uncertain." *Cecilonycteris* was referred to ?Palaeochiropterygidae incertae sedis, and several Eocene fossil forms were placed in extant microchiropteran families and subfamilies: *Vespertiliavus* in Emballonuridae, *Necromantis* in Megadermatidae, Eocene *Rhinolophus* in Rhinolophidae, *Palaeophyllophora* and *Paraphyllophora* in their

own subfamily (Palaeophyllophorinae) within Hipposideridae, *Pseudorhinolophus* in Hipposiderinae, and *Stehlinia* and *Revilliodia* (a new name for *Nycterobius*) in Vespertilioninae. Simpson (1945) proposed a new subfamily (Archaeopteropodinae) for *Archaeopterus*, which he placed in Pteropodidae. *Paleonycteris* and *Paradoxonycteris* were referred to Chiroptera incertae sedis.

Savage (1951) described *Notonycteris*, a phyllostomid from the Miocene La Venta fauna of Colombia. In the course of his discussion, Savage (1951: 362) noted that *Provampyrus* "is clearly separable" from phyllostomids based on location of the capitulum of the humerus, which is in line with the shaft in *Provampyrus* but not in phyllostomids. He did not comment further on the affinities of *Provampyrus*, but observed that *Notonycteris* was the only Tertiary representative of Phyllostomidae.

Handley (1955) addressed the nomenclatural confusion resulting from Revilliod's (1919) publication, and discussed the status of *Nycterobius* Revilliod, 1922 and *Revilliodia* Simpson, 1945. He concluded that both are junior synonyms of *Stehlinia* Revilliod, 1919.

Friant (1963) revised the Tertiary rhinolophids, referring Eocene *Rhinolophus* to Rhinolophinae, and *Palaeophyllophora*, *Paraphyllophora*, and *Pseudorhinolophus* to Hipposiderinae. She also reviewed the higher-level classification of Microchiroptera, recognizing two families of Eocene bats, Archaeonycteridae and Palaeochiropterygidae (Friant, 1963). *Paleonycteris* and *Paradoxonycteris* were placed incertae sedis in Microchiroptera.

Romer (1966) summarized the classification of fossil bats and placed many Eocene and Oligocene fossils in extant families following the recommendations of previous authors. He placed *Vespertiliavus* in Emballonuridae, *Necromantis* in Megadermatidae, Eocene *Rhinolophus* in Rhinolophidae, *Palaeophyllophora*, *Paraphyllophora*, *Hipposideros*, and *Pseudorhinolophus* in Hipposideridae, *Provampyrus* and ?*Vampyravus* in Phyllostomidae, *Stehlinia* in Vespertilionidae, and *Archaeopterus* in Pteropodidae. He recognized two archaic families, Archaeonycteridae (including only *Archaeonycteris*) and

Palaeochiropterygidae (including *Palaeochiropteryx* and *Cecilionycteris*). Both of these families were left in "Superfamily uncertain" within Microchiroptera (Romer, 1966: 382). *Paradoxonycteris* was referred to Chiroptera incertae sedis (Romer, 1966).

Jepsen (1966) described *Icaronycteris* from a single, beautifully preserved skeleton from Fossil Basin in the Green River Formation of Wyoming. He placed this form in the new family Icaronycteridae within Microchiroptera. Jepsen discussed other putative bats from early Tertiary deposits in North America, but did not make any detailed comparisons with Eocene bats from Europe.

Sigé (1968) described the bats of an Early Miocene fauna from Bouzigue, France, including a new species of *Pseudorhinolophus*. He reviewed the contents and stratigraphic range of *Pseudorhinolophus* and presented a revised diagnosis of this taxon, which he considered to represent a subgenus of *Hipposideros*. He suggested several possibilities for relationships among *Pseudorhinolophus*, *Brachyhipposideros* (a subgenus known from Oligocene and Miocene deposits), and modern species of *Hipposideros*, but he reached no definitive conclusions other than that these forms are very closely related.

Jepsen (1970) published detailed stereophotographs of *Icaronycteris* in an essay concerning the evolution of bats and powered flight. However, the text of his publication contained little information on *Icaronycteris* that was not available in the original description (Jepsen, 1966), and no comparisons were drawn between *Icaronycteris* and Eocene bats from Europe. Concerning the relationships of *Icaronycteris* to other bats, Jepsen (1970: 40) noted only that "*Icaronycteris index* as a species may have been directly ancestral to all or to some living microbats or megabats or to none of our contemporary chiropts."

In a short paper on the classification of bats, Koopman and Jones (1970) recognized three families of Eocene bats: Icaronycteridae (including only *Icaronycteris*), Archaeonycteridae (*Archaeonycteris*), and Palaeochiropterygidae (*Palaeochiropteryx* and *Cecilionycteris*, the latter of which was placed incertae sedis). These families were listed

under the heading "Fossil Chiroptera of uncertain status" (Koopman and Jones, 1970: 28). *Paleuonycteris* and *Paradoxonycteris* were referred to Chiroptera incertae sedis, and several Eocene taxa were placed in modern families: *Vespertiliavus* in Emballonuridae, *Necromantis* in Megadermatidae, and *Stehlinia* in Vespertilionidae (Koopman and Jones, 1970). *Palaeophyllophora* and *Paraphyllophora* were placed in their own tribe Palaeophyllophorini in Hipposiderinae (Koopman and Jones, 1970). *Archaeopteropus* was placed in Archaeopteropodinae within Megachiroptera.

Slaughter (1970) discussed evolution of the chiropteran dentition, drawing conclusions about the affinities of many fossil taxa based on their dental morphology. Slaughter (1970: 59) observed that the dentition of *Icaronycteris* is "more like the ancestral condition than any other known chiropteran." He went on to note that *Cecilionycteris*, *Palaeochiropteryx*, and *Archaeonycteris* have slightly more derived dentitions, but did not associate them with any extant lineages. He observed that *Necromantis* is clearly a megadermatid, although somewhat less derived than extant members of the family. Slaughter placed *Pseudorhinolophus* on the lineage leading to modern *Hipposideros*, and recognized Palaeophyllophorinae as close relatives of hipposiderines. The "Eocene *Rhinolophus*" were placed at the base of the lineage leading to modern *Rhinolophus*, palaeophyllophorines, and hipposiderines (Slaughter, 1970: fig. 5), with *Nycteris* shown as the sister-group to this rhinolophid clade. He also recognized *Vespertiliavus* as the oldest member of Emballonuridae, noting that the prototypic dentition for the superfamily Emballonuroidea (which he defined as including noctilionids) would be like that of *Vespertiliavus* except for the form of the hypocone. Finally, Slaughter noted that *Stehlinia* appears to be intermediate between ancestral vespertilionids and the lineage leading to all vespertilionids except miniopterines and murinines.

Russell and Sigé (1970) were among the first to present detailed comparisons of the Messel bats with extant taxa. Their study concluded with an updated classification of the archaic Eocene bats and emended diag-

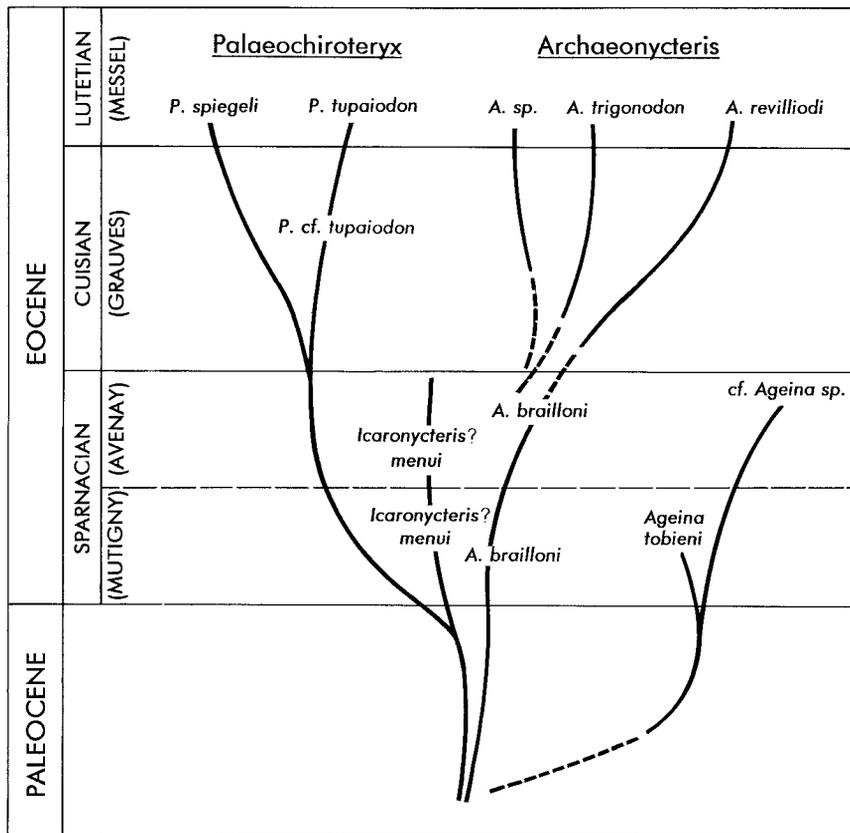


Fig. 6. Russell, Louis, and Savage's hypothesis of phylogeny and divergence times of Eocene bats (redrawn from Russell et al., 1973: fig. 11). The original caption for this figure read "Hypothetical relationships between the earliest European bats."

noses for each taxon. They placed the archaic Eocene genera in a new superfamily Palaeochiropterygoidea within Microchiroptera. Two families were recognized within this group: Palaeochiropterygidae and Icaronycteridae. Icaronycteridae was defined as including *Icaronycteris* and possibly *Archaeopterus*. In contrast, Palaeochiropterygidae was divided into two subfamilies, Palaeochiropteryginae (including *Palaeochiropteryx* and *Cecilonycteris*) and Archaeonycteridinae (containing only *Archaeonycteris*).

Sigé (1971) described an isolated forelimb from Stampien deposits in France (MP 21–24; Russell et al., 1982; Schmidt-Kittler, 1987) and referred it to *Tadarida* sp. Although this specimen may represent *Cuvierimops*, lack of associated dental material has

prevented a confirmed identification. Hand (1990) referred this specimen to Tadaridinae indet. (Tadaridinae was named by Legendre [1984] in a review of extant molossids).

Russell et al. (1973) described fragmentary dental remains from the Early Eocene of France (MP 8–9; Schmidt-Kittler, 1987) that they referred to new species of *Icaronycteris?* and *Archaeonycteris* as well as a new genus, *Ageina*. Based on dental morphology, they hypothesized that *Icaronycteris? menui* was closely related to *Palaeochiropteryx*. *Archaeonycteris* was recognized as a distinct yet related lineage, while *Ageina* was placed on a distant branch of uncertain affinities (fig. 6; Russell et al., 1973: fig. 11). Although classification was not explicitly discussed, they placed *Icaronycteris? menui* in Palaeochiropterygoidea: Icaronycteridae?,

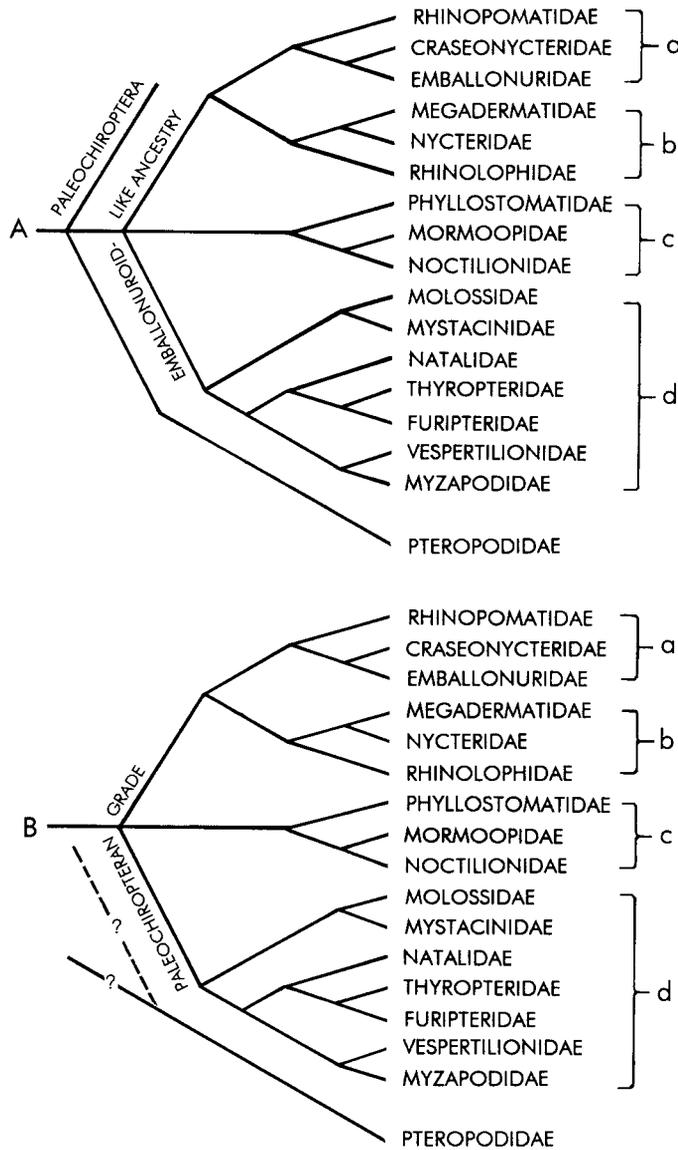


Fig. 7. Smith's hypotheses of bat relationships (redrawn from Smith, 1976: fig. 1). The original caption for this figure read "A, cladogram of the generally accepted view of chiropteran phylogeny with the Microchiroptera derived from a common emballonuridlike ancestry. B, an alternative proposal for chiropteran evolution with several microchiropteran lineages being derived, independently, from a world-wide paleochiropteran grade and the Megachiroptera (Pteropodidae) derived either separately from an insectivorous stock or from the paleochiropteran grade. a, Emballonuroidea; b, Rhinolophoidea; c, Phyllostomatoidea; d, Vespertilionoidea." Note that Smith (1976) used "Myzapodidae" instead of "Myzopodidae," and "Phyllostomatoidea" instead of "Phyllostomoidea" (= Noctilionoidea).

Archaeonycteris brailloni in Archaeonycterinae (family not specified), and *Ageina* in "Family uncertain" (Russell et al., 1973: 35).

Sigé (1974) reviewed the available mate-

rial of *Stehlinia* and compared it to other fossil and extant taxa. Based on his analysis, Sigé recognized *Nycterobius*, *Paleonycteris*, and *Revilliodia* as junior synonyms of *Steh-*

linia, and concluded that *Stehlinia* was best placed in the family Kerivoulidae within Vespertilionoidea. He compared *Stehlinia* with "les paléochiroptérygoïdés" but did not comment on contents or classification of this group.

Smith (1976) discussed Eocene fossil bats in a review of phylogenetic relationships and patterns of evolutionary radiation of extant bats (fig. 7). Apparently drawing on Dobson's (1875) concept, Smith (1976: 52–53) used the informal name "Paleochiroptera" to collectively refer to *Icaronycteris*, *Palaeochiropteryx*, *Archaeonycteris*, *Cecilionycteris*, and *Ageina*. He perceived this group as representing "a world-wide paleochiropteran grade in early to middle Eocene times . . . [that] was primitive and generalized in most respects." He suggested that extant Microchiroptera could be easily derived from the paleochiropteran grade, and that this divergence probably occurred in the Paleocene. He clearly did not think that any of the Eocene taxa listed above were ancestral to extant microchiropterans. Smith further suggested that *Archaeopteropus* was probably also derived from the paleochiropteran grade, although he questioned the megachiropteran affinities of this form. Smith (1976: 54) observed that "The distinctness and marked departure of megachiropteran dentition from that of the Microchiroptera, as well as from known Tertiary fossils, suggests to me that this group of bats had their origin much earlier in the paleochiropteran grade or perhaps . . . separately from an insectivorous ancestral stock."

Smith (1976) also discussed other Eocene fossils that he thought could be referred to extant families. These included *Vespertiliavus* (referred to Emballonuridae); *Palaeophyllophora*, *Paraphyllophora*, *Rhinolophus*, *Pseudorhinolophus*, and *Hipposideros* (Rhinolophidae); *Necromantis* and *Provampyrus* (Megadermatidae); and *Stehlinia* and *Nycterobius* (Vespertilionidae). The presence of modern families (and even genera) in Middle and Late Eocene deposits was interpreted as additional evidence for an early divergence of microchiropterans from the paleochiropteran stock (Smith, 1976).

Sigé (1977) discussed the fossil record of Eocene bats in a review of Paleogene mam-

malian faunas of Europe. He referred to the Messel bats as "chiroptères paléochiroptérygoïdés," including within this group Icaronycteridae and Palaeochiropterygidae. The latter family contained two subfamilies: Archaeonycteridinae and Palaeochiropteryginae. *Vespertiliavus* was referred to Emballonuridae, *Stehlinia* to Vespertilionoidea (Kerivoulidae), *Hipposideros* (*Pseudorhinolophus*) and *Palaeophyllophora* to Rhinolophoidea (Hipposideridae), and *Necromantis* to Megadermatidae. In the absence of contradictory evidence, Sigé suggested that palaeochiropterygines, emballonuroids, vespertilionoids, and rhinolophoids might have originated from unspecified endemic European groups. Based on its supposed "denture apparemment insectivore" (insectivorous dentition), Sigé (1977: 185) interpreted *Archaeopteropus* as a form intermediate between megachiropterans and icaronycterids.

In a review paper concerning the evolution of bat flight, Smith (1977) noted that one of the "five monophyletic superfamilies" of Microchiroptera was Palaeochiropterygoidea, which included Palaeochiropterygidae and Icaronycteridae. While Russell and Sigé (1970) had tentatively referred *Archaeopteropus* to Icaronycteridae, Smith (1977) noted that he had examined the only known specimen of *Archaeopteropus* and had found no justification for this arrangement. Accordingly, he restricted Icaronycteridae to only *Icaronycteris*. To our knowledge, Smith was the first to suggest that *Icaronycteris*, *Palaeochiropteryx*, *Archaeonycteris*, *Cecilionycteris*, and *Ageina* formed a clade (rather than a grade) distinct from other microchiropteran bats.

Barghoorn (1977) described two new skulls of *Vespertiliavus* from the Quercy Phosphorites in southern France. Based on a cladistic analysis of cranial characters in extant and fossil emballonurids and several outgroups, Barghoorn concluded that *Vespertiliavus* is the sister-group of a clade comprised of *Taphozous* and *Saccolaimus*.

Butler (1978) reviewed the evolutionary history of bats in Africa and provided a classification of fossil forms known from that continent. In this context, he placed *Vampyravus* in Microchiroptera incertae sedis, ex-

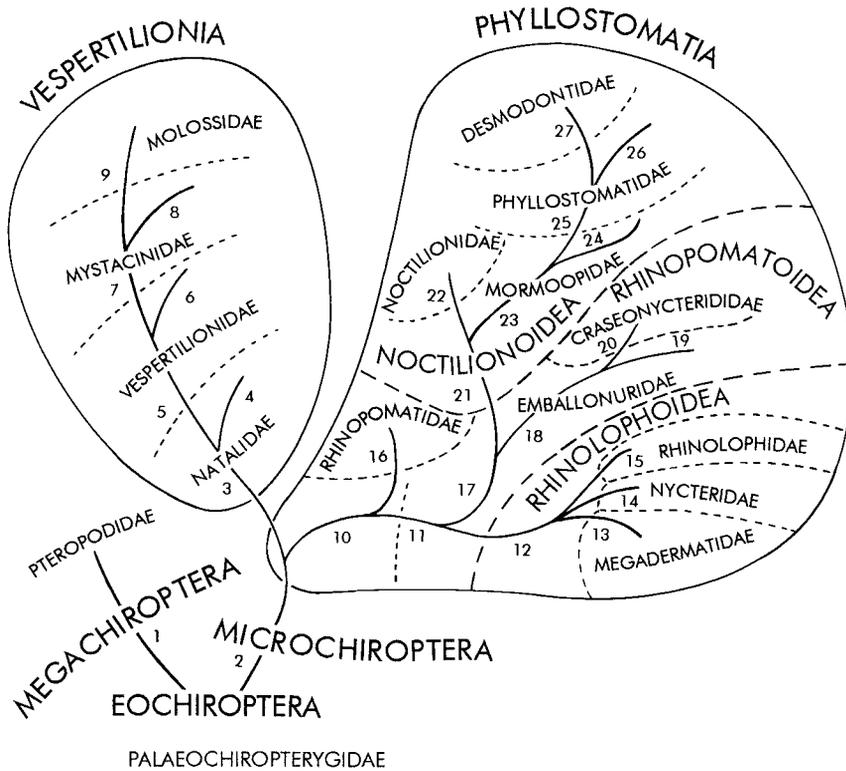


Fig. 8. Van Valen's (1979) hypothesis of bat relationships (redrawn from Van Valen, 1979: fig. 1). The original caption for this figure read "Phylogeny of the known families of bats . . . Infraorders, superfamilies, and families of the Microchiroptera are separated by solid, dashed, and dotted lines respectively." The numbers refer to taxa discussed in an appendix; we reproduce these here because they are informative with respect to Van Valen's unconventional concepts of group membership: 1, Megachiroptera, Pteropodidae; 2, Microchiroptera, undiscovered family; 3, Vespertilionia, Vespertilionoidea, Natalidae; 4, Recent Natalidae; 5, Vespertilionidae; 6, Recent Vespertilionidae; 7, Mystacinidae; 8, Recent Mystacinidae; 9, Molossidae; 10, Phyllostomatia, Rhinopomatoidea, undiscovered Family; 11, Emballonurid-rhinolophoid stem; 12, Rhinolophoidea; 13, Megadermatidae; 14, Nycteridae; 15, Rhinolophidae; 16, Rhinopomatidae; 17, Emballonurid-noctilionoid stem; 18, Emballonuridae (family should perhaps extend as far back as 11); 19, Recent Emballonuridae; 20, Craseonycteridae; 21, Noctilionoidea, perhaps early Mormoopidae; 22, Noctilionidae; 23, Mormoopidae; 24, Recent Mormoopidae; 25, Phyllostomatidae; 26, Recent Phyllostomatidae; 27, Desmodontidae. Spelling of group names follows those of the original author.

explicitly rejecting the conclusions of Schlosser (1911) and Smith (1976).

Van Valen (1979) published the first cladistic assessment of higher-level bat relationships (fig. 8). This study was based on diverse morphological characters, although specific methods of analysis were not described and a taxon-character matrix was not included. The focus of Van Valen's study was extant bats, but he also discussed some features of the better known fossil forms as reported in the literature. He proposed the new

suborder Eochiroptera for the archaic Eocene bats, within which he recognized one family (Palaeochiropterygidae). The latter group was described as "including Archaeonycter(id)idae and probably Icaronycter(id)idae and Archaeopteropodinae as subfamilies" (Van Valen, 1979: 109). Van Valen indicated that Eochiroptera was ancestral to all extant bats including Megachiroptera and Microchiroptera. He noted that extant megachiropterans were probably derived from persistent eochiropterans such as *Archaeopteropus*. The

criteria used to lump forms ancestral to different clades into one group (Eochiroptera) appears to have been perceived adaptive similarity and their shared retention of numerous primitive traits. Van Valen (1979: 109) acknowledged that many of the taxa in his classification were paraphyletic, which he noted “reflects the progressive evolution of grades of adaptation.”

Sigé and Russell (1980) provided detailed descriptions and comparisons of *Palaeochiropteryx tupaiodon* and *Cecilionycteris*, and described a new genus *Matthesia* based on dental material from Geiseltal, “Grube Cecilie” (MP 13; Franzen and Haubold, 1987). All of these forms were placed in Eochiroptera: Palaeochiropterygidae: Palaeochiropteryginae by Sigé and Russell (1980).

Smith and Storch (1981) described the new genus *Hassianycteris* from Messel (MP 12; Schmidt-Kittler, 1987). *Hassianycteris* was described as differing significantly from palaeochiropterygoids in possessing an advanced degree of dental reduction and other derived dental and osteological features. Smith and Storch (1981: 164) concluded that *Hassianycteris* “is more closely associated with the emballonuroid/rhinolophoid section of the Microchiroptera than to any other group.” As a result, they referred *Hassianycteris* to Microchiroptera incertae sedis rather than placing it in Palaeochiropterygoidea.

Following many earlier authors, Smith and Storch (1981) recommended removal of *Archaeopteropus* from Palaeochiropterygoidea and subsequent placement in Pteropodidae based on morphological evidence that *Archaeopteropus* is an early megachiropteran (for details of this argument, see Habersetzer and Storch, 1987). In doing so, Smith and Storch explicitly restricted Palaeochiropterygoidea to *Palaeochiropteryx*, *Archaeonycteris*, *Icaronycteris*, *Cecilionycteris*, *Ageina*, and *Matthesia*. They (1981: 163) noted the following concerning possible relationships of Palaeochiropterygoidea as thus defined:

While we would not now go so far as including these bats in the family Vespertilionidae Gray 1821, they may well share a close sister-group relationship with the superfamily Vespertilionoidea or they may be placed as the sister-group of a larger one including the Phyllostomatoidea and Vespertilionoidea.

Legendre and Sigé (1983) went back to one of the first fossil bats discussed in the scientific literature—Cuvier’s (1822) “Vespertilion de Montmartre”—and found that additional preparation of the original specimen (a partial skeleton) revealed features diagnostic of Molossidae. This form, which was variously referred to *Vespertilio parisiensis*, *Serotinoides antiquus*, “*Vespertilio*” *serotinoides*, and cf. *Tadarida* sp. by previous 19th-century authors, was named *Cuvierimops* by Legendre and Sigé (1983). It is currently thought to be Late Eocene (Priabonian) in age (MP 19; Russell et al., 1982; Schmidt-Kittler, 1987). Legendre and Sigé (1983) suggested that *Cuvierimops* was possibly ancestral to a large complex including all extant molossids with the exception of *Tadarida* and *Mormopterus*.

Sigé and Legendre (1983) reviewed the fossil record of bats in different depositional environments and regions in the Mediterranean basin. They referred *Icaronycteris*, *Palaeochiropteryx*, *Cecilionycteris*, *Matthesia*, *Archaeonycteris*, and *Ageina* to Eochiroptera. *Hassianycteris* was described as an early microchiropteran not clearly related to any of the extant superfamilies. Several additional Eocene forms were referred to extant families, including *Vespertiliavus*, *Hipposideros* (*Pseudorhinolophus*), *Palaeophyllophora*, *Necromantis*, *Rhinolophus*, *Stehlinia*, *Cuvierimops*, and cf. *Tadarida*. Although family affinities were not specified, these references were clearly intended to follow past classifications of these taxa.

Ostrander (1983) described *Chadronycteris* based on a maxillary fragment with teeth from what are now considered to be Late Eocene (Chadronian) deposits in Nebraska. Based on comparisons with *Stehlinia* (referred to Kerivoulidae by Sigé, 1974) and “Palaeochiropterygidae,” Ostrander referred *Chadronycteris* to Vespertilionoidea: Kerivoulidae.

Gupta (1984) discussed bat phylogeny and relationships of *Icaronycteris*. Apparently failing to draw any distinction between symplesiomorphy and synapomorphy, Gupta suggested that *Icaronycteris* may be a megachiropteran based on several shared primitive features (e.g., presence of a claw on the index finger). Gupta (1984: 42) also pro-

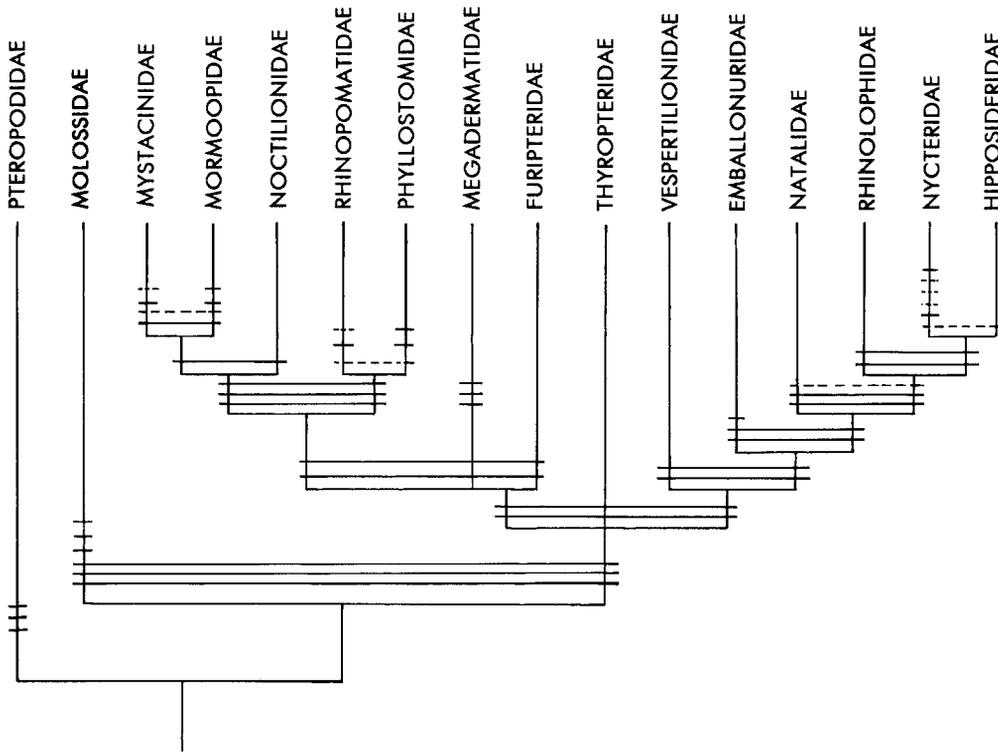


Fig. 9. Cladogram of interfamilial relationships inferred from auditory characters (redrawn from Novacek, 1980a: fig. 1). The original caption for this figure read "Wagner tree resulting from analysis of 18 auditory characters for Recent chiropteran families. Craseonycteridae and Myzopodidae are omitted. Horizontal bars bridging two or more branches are synapomorphies; short black bars are independently derived characters under this arrangement; striped bars represent character state reversals."

posed an unusual hypothesis concerning the origin of bats:

The close similarity in the structure of the patagium of Pterosaurs and of bats, and the presence of hair in both, can compel us to think that the bats might have evolved from the Pterosaurs with modifications of mammalian characters during 12 million years [of the] Paleocene, the period during which no fossils [of pterosaurs or bats] have so far been reported.

None of these ideas have been accepted by subsequent authors because all published data sets indicate that bats are therian mammals (e.g., Novacek, 1980a, 1986, 1990; Novacek and Wyss, 1986; Simmons, 1993a, 1994, 1995). Pterosaurs are almost universally regarded as archosaurian diapsid reptiles that are more closely related to crocodiles and birds than to mammals (e.g., Padian, 1984, 1987; Gauthier, 1986).

Hill and Smith (1984) provided a classi-

fication of all chiropteran genera in their book on the natural history of bats. They recognized three families in Palaeochiropterygoidea: Palaeochiropterygidae (including *Palaeochiropteryx*, *Cecilionycteris*, and *Matthesia*), Archaeonycteridae (including *Archaeonycteris* and *Ageina*), and Icaronycteridae (including only *Icaronycteris*). *Paradoxonycteris* and *Hassianonycteris* were left as "Family incertae sedis" within Microchiroptera (Hill and Smith, 1984: 221). Following Smith and Storch (1981), Hill and Smith (1984) suggested that Palaeochiropterygoidea appeared to have affinities with Vespertilionoidea, while *Hassianonycteris* might be associated with Emballonuroidea and Rhinolophoidea. Many Eocene and Oligocene fossils were referred to extant families by Hill and Smith (1984). They placed *Archaeopteropus* in its own subfamily Ar-

chaeopteropodinae within Pteropodidae, *Vespertiliavus* in Emballonurinae within Emballonuridae, *Necromantis* and *Provampyrus* in Megadermatidae, *Pseudorhinolophus* in Hipposiderinae within Hipposideridae, *Palaeophyllophora* and *Paraphyllophora* in Palaeophyllophorinae within Hipposideridae, and *Stehlinia* in Vespertilioninae within Vespertilionidae.

Legendre (1985) reviewed the fossil record of molossids and reevaluated the affinities of *Wallia*, a taxon originally described by Storer (1984) as a proscalopid insectivore from the Uintan (Middle Eocene) Swift Creek Local Fauna of Saskatchewan, Canada. Legendre concluded that *Wallia* probably represents the oldest known molossid, and he placed both *Wallia* and *Cuvierimops* in Tadaridinae, the subfamily to which all Tertiary fossil molossids have been referred (Hand, 1990).

Sigé (1985) focused on fossil bats from Late Eocene deposits of the Fayum area, Egypt, and redescribed and discussed the status of *Vampyravus* Schlosser, 1910 and *Provampyrus* Schlosser, 1911. He concluded that these two taxa are objective synonyms based on a single specimen, a well-preserved humerus. Sigé (1985) concluded that *Vampyravus* was too poorly known to be assigned to any family, but suggested that morphology of the holotype indicated affinities with either hipposiderids, natalids, or phyllostomids. Sigé also described a new taxon based on craniodental material, *Philisis*, which he placed in its own family, Philisidae. Based on comparisons with fossil and extant forms, Sigé placed Philisidae within Vespertilionoidea and suggested that it was more closely related to Vespertilionidae *sensu lato* than to Molossidae (fig. 12). Speculating that *Vampyravus* and *Philisis* might eventually be shown to be conspecific if more complete material were to be discovered, Sigé (1985) hypothesized that Vampyridae (which would replace Philisidae as the correct family name in this case) would prove to be more closely related to Natalidae than to Vespertilionidae or Molossidae. In each of Sigé's phylogenetic trees (fig. 12), Echioptera was shown as occupying the basal branch. It is not clear, however, whether this was meant to imply monophyly of Echioptera; com-

ments in the text suggest that Sigé included Echioptera to represent the basal stock of Chiroptera.

Horáček (1986) discussed relationships of *Stehlinia* and *Kerivoula* and concluded (contra Sigé, 1974) that these taxa were not closely related. Instead, Horáček suggested that *Stehlinia* might be related to Miniopterinae.

Mein and Tupinier (1986) briefly reviewed the early Tertiary record of bats in a short paper on the evolution of echolocation systems. They followed Van Valen (1979) in considering *Icaronycteris*, *Archaeonycteris*, and *Palaeochiropteryx* as representatives of Echioptera, while referring other fossil taxa to extant superfamilies or families. Mein and Tupinier listed *Vespertiliavus* in Emballonuridae, *Stehlinia* in Vespertilionoidea, and referred *Necromantis* and possibly *Provampyrus* to Megadermatidae.

Gingerich (1987) described *Wyonycteris* based on a partial dentary and isolated teeth from Late Paleocene (Clarkforkian) deposits of the Willwood Formation of Wyoming. He referred *Wyonycteris* to Palaeochiropterygidae on the basis of dental similarities, but subsequent authors (e.g., Habersetzer et al., 1994; Hand et al., 1994) have questioned the chiropteran affinities of this form (see footnotes to table 1). Gingerich also described teeth referred to cf. *Icaronycteris* from the Willwood Formation.

Habersetzer and Storch (1987) discussed in detail the classification and functional morphology of Paleogene bats, concentrating on the fossil bats from Messel. They argued against usage of Palaeochiropterygoidea and Echioptera, recognizing that each was probably paraphyletic even if *Archaeopteryx* was removed. Instead, they recognized and provided revised diagnoses for three families placed in Microchiroptera incertae sedis: Archaeonycterididae (including *Archaeonycteris* and *Icaronycteris*), Palaeochiropterygidae (*Palaeochiropteryx*), and a new family, Hassianycterididae (*Hassianycteris*, including "*Archaeonycteris*" *revilliodi* Russell and Sigé, 1970). The relationships of *Cecilonycteris*, *Ageina*, and *Matthesia* were not addressed.

Novacek (1987) focused on phylogenetic relationships of the best known Eocene taxa (*Icaronycteris* and *Palaeochiropteryx*) rather

than on issues of classification. Following a detailed review of a wide array of morphological features, Novacek (1987) concluded that both *Icaronycteris* and *Palaeochiropteryx* are more closely related to extant microchiropterans than to extant megachiropterans (fig. 14). He concluded that *Icaronycteris* and probably *Palaeochiropteryx* are outgroups of all Recent families of Microchiroptera, but could not rule out the possibility that one or both of these Eocene taxa might have special affinities within Microchiroptera (i.e., might be more closely related to one or more extant families than to others). Novacek (1987: 15–16) further concluded that

... the Palaeochiropterygoidea seems merely an artificial convention to group several early microchiropterans whose relationships with modern families of this suborder remain poorly known ... *Icaronycteris* and *Palaeochiropteryx* are more accurately designated as Microchiroptera incertae sedis. Moreover, there seems no justification for a formal designation of an "ancestral" group (e.g., Eochiroptera sensu Van Valen, 1979) to distinguish *Icaronycteris*, *Palaeochiropteryx*, and other Eocene bats from the Recent chiropteran suborders.

In a classification of fossil vertebrates, Carroll (1988) named a new superfamily for the archaic Eocene bats, Icaronycterioidea, which he placed within Microchiroptera. He included two families in Icaronycterioidea: Icaronycteridae (*Icaronycteris*) and Palaeochiropterygidae (*Archaeonycteris*, *Palaeochiropteryx*, *Cecilonycteris*, and *Matthesia*). In concept and contents, Icaronycterioidea is identical to Palaeochiropterygoidea as recognized by most previous authors. Carroll gave no justification for this apparently unnecessary name change, and no subsequent authors have used Icaronycterioidea. Carroll additionally provided a classification for other Eocene bats, placing *Vespertiliavus* in Emballonuridae, *Necromantis* in Megadermatidae, *Rhinolophus* in Rhinolophidae, *Hipposideros*, *Palaeophyllophora*, and *Paraphyllophora* in Hipposideridae, *?Vampyravus* in Phyllostomidae, and *Stehlinia* in Vespertilionidae. He also placed *Archaeopteropus* in Pteropodidae.

Robbins and Sarich (1988) used protein electrophoresis and immunological distance data to address relationships among extant Emballonuridae. They also considered morphological data presented by Barghoorn

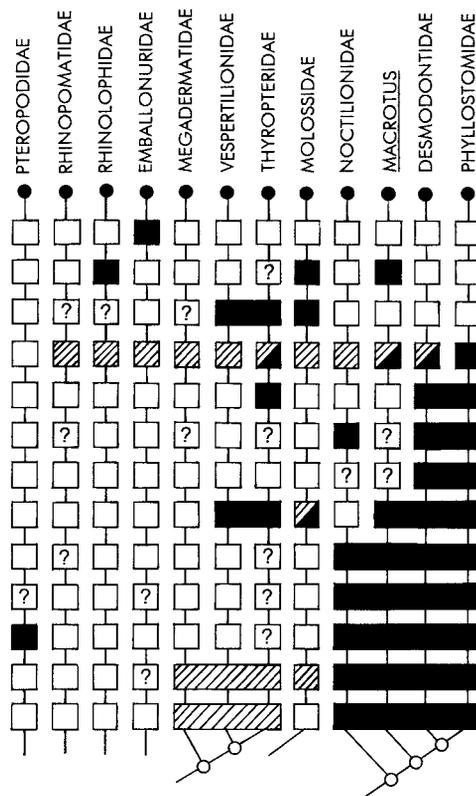


Fig. 10. Relationships of selected taxa inferred from features of fetal membrane structure and development (redrawn from Lockett, 1980a: fig. 5). The original caption for this figure read "Character state distribution of fetal membrane and reproductive features of Chiroptera ..."

(1977), and included a brief discussion of the affinities of *Vespertiliavus*. Robbins and Sarich concluded by assigning *Vespertiliavus* to a new tribe, Vespertiliavini, within the subfamily Taphozoinae.

Sigé (1988) described the fossil bats from the Marinesian (= Robiacian; MP 16) Le Bretou fauna from the Quercy Phosphorites in France. He referred *Vespertiliavus* to Emballonuridae, *Necromantis* to Megadermatidae, *Rhinolophus* to Rhinolophidae, *Hipposideros*, *Palaeophyllophora*, and *Paraphyllophora* to Hipposideridae, *?Vampyravus* to Phyllostomidae, and *Stehlinia* to Vespertilionidae. He also placed *Archaeopteropus* in Pteropodidae.

Storch and Habersetzer (1988) described a new species of *Archaeonycteris* (*A. pollex*) based on two skeletons from Messel, and compared this taxon with other Eocene bats.

They also reported the discovery of a new skull that confirmed Habersetzer and Storch's (1987) suggestion that "*Archaeonycteris revilliodi* should be referred to *Hassianycteris* rather than to *Archaeonycteris* or Archaeonycteridae.

Habersetzer and Storch (1989) discussed ecology and echolocation abilities of Eocene bats from Messel as inferred from wing and cochlear morphology. Based on comparisons with various extinct and extant bats, Habersetzer and Storch (1989: 214) noted that

Archaeonycteris trigonodon Revilliod 1917 (family Archaeonycteridae) is an archaic species. . . . *Palaeochiropteryx tupaiodon* Revilliod 1917, and *P. spiegelii* Revilliod 1917, (family Palaeochiropterygidae) are small specialized species. . . . *Hassianycteris messelensis* Smith and Storch 1981, *H. magna* Smith and Storch 1981, and *H. revilliodi* (Russell and Sigé 1970) (Family Hassianycteridae) are the most advanced species in dental and skeletal features.

Habersetzer and Storch (1989) argued against Van Valen's (1979) concept of Eochiroptera, which was originally defined as including all of the taxa mentioned in the excerpt above. They noted that Eochiroptera as conceived by Van Valen would be a group of primitive and unspecialized species that ultimately gave rise to both Megachiroptera and Microchiroptera. Noting that the Messel bat fauna includes ecologically diverse forms that are all "completely developed" microchiropterans, Habersetzer and Storch (1989: 231) suggested that Eochiroptera was a misleading concept, at least when applied to the Messel bats.

Sigé (1990) and Sudre et al. (1990) described new species of *Vespertiliavus* from Stampian (MP 25) and early Bartonian (MP 14) deposits of France, respectively. Both retained *Vespertiliavus* in Emballonuridae. Sigé additionally described a new species of *Hipposideros* (subgenus *Pseudorhinolophus*), a new species of *Stehlinia* (which he referred to Natalidae sensu Van Valen, 1979), and a new genus *Vaylatsia*. All four of the new taxa described by Sigé (1990) were based on fragmentary dentitions and isolated postcranial elements from the Quercy Phosphorites. *Vaylatsia* was referred to Hipposideridae based on dental and humeral characters, but Sigé (1990: 1132) noted that it

"probably represents the stem group of the genus *Rhinolophus*."

Sigé (1991a) later described the genus *Dizzya* from the Early Eocene of Chambi in northern Africa. Following broad comparisons with extant and extinct forms, he referred *Dizzya* to Vespertilionoidea: Philisidae. A specimen referred to Rhinolophoidea gen. and sp. indet. was also described, and Sigé went on to extensively discuss the biostratigraphic, biogeographic, and paleoecological implications of the bat fauna from the African Eocene. In a final note, Sigé discussed usage of the name Eochiroptera. Contra Habersetzer and Storch (1987, 1989) and Novacek (1987), he (1991a: 372) argued that this taxon "est préféré par logique, commodité, et efficacité à celui super-familial des Palaeochiropterygoidea inclus dans les Microchiroptera." Sigé (1991a: 373) argued that recognizing the "taxon-grade" Eochiroptera is a simple, operational approach to classifying organisms of uncertain affinities that share a large number of primitive characters. Expressing the unusual opinion that Microchiroptera must itself be considered paraphyletic ("l'unité sub-ordinale Microchiroptera, qui . . . doit être clairement perçue comme un rassemblement paraphylétique, mais se valeur empirique. . . ."; Sigé, 1991a: 373), he emphasized the empirical value of formally grouping taxa based on their perceived grade of evolution. He argued that such a classification system should perhaps be maintained for the chiropteran suborders (to indicate their adaptive level in the continuum of bat evolution), even if it becomes possible to diagnose strongly supported, monophyletic superfamilies including some of the archaic Eocene taxa.

Sigé (1991b) discussed morphology of the deciduous dentition of Eocene bats and presented a figure summarizing relationships and stratigraphic ranges (fig. 15). He indicated that five extant lineages (Megachiroptera, Phyllostomatoidea [= Noctilionoidea], Rhinolophoidea, Emballonurioidea, and Vespertilionoidea) and three extinct lineages (Hassianycteridae, Archaeonycteridae, and Palaeochiropterygidae) were in existence in the Eocene. He placed Archaeonycteridae and Hassianycteridae in Eochiroptera,

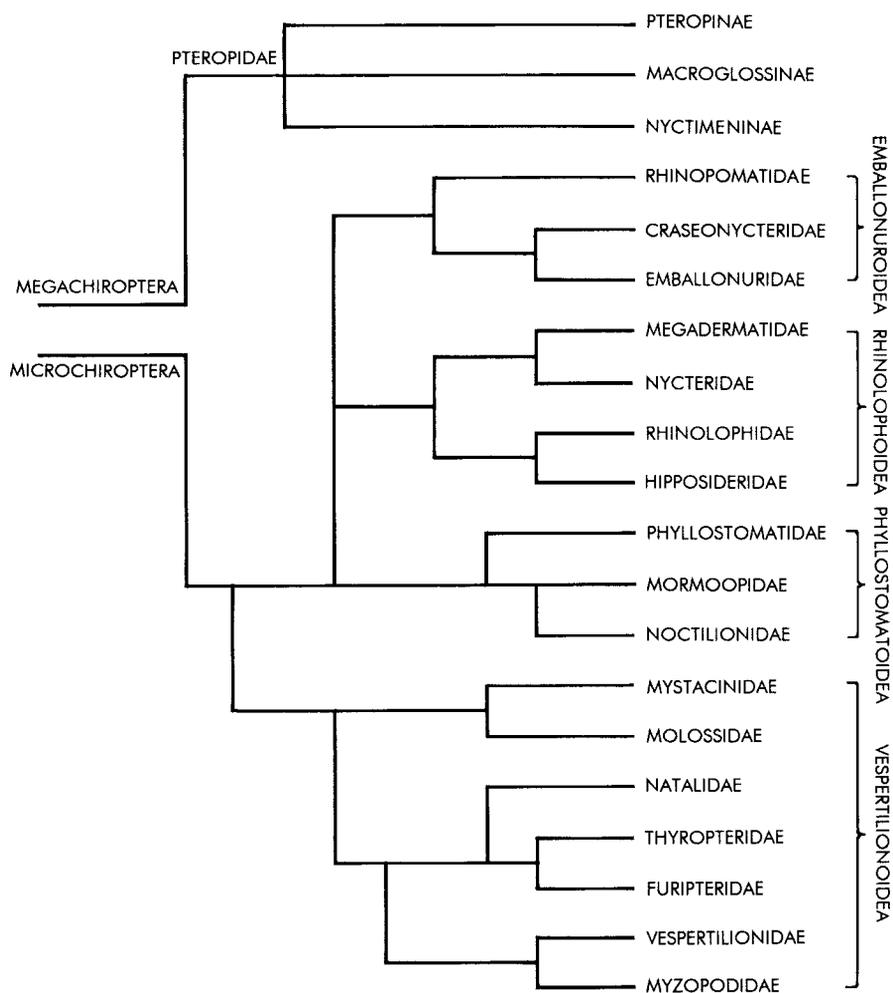


Fig. 11. Eisenberg's hypothesis of bat relationships (redrawn from Eisenberg, 1981: fig. 27). The original caption read "Diagram of the classification of the Chiroptera. Based in part on Smith 1976."

but excluded *Hassianycterididae* from this group.

Smith and Russell (1992) described a new species of *Hassianycteris* from Upper Ypresian deposits in Belgium. This discovery extended the age range of *Hassianycteris* (previously known only from Messel) into the Early Eocene. Because the basal Middle Eocene age generally supposed for Messel is an estimate, this temporal range extension may be more apparent than real.

Beard et al. (1992) described the fossil genus *Honrovits* from Early Eocene (Late Wasatchian) beds in North America. Based on

comparisons with extant taxa, they referred *Honrovits* to *Natalidae* sensu Van Valen, 1979 along with *Stehlinia*, *Chadronycteris*, *Chamtwaria* (an Early Miocene form from Africa described by Butler, 1984), and probably *Ageina*. In the course of comparisons with other Eocene forms, Beard et al. (1992) recognized *Archaeonycterididae* as including *Archaeonycteris* and *Icaronycteris*; *Palaeochiropterygidae* as including *Palaeochiropteryx*, *Cecilionycteris*, and *Matthesia*; and *Hassianycterididae* as including *Hassianycteris*. This usage essentially follows that of Habersetzer and Storch (1987, 1988), differ-

ing only in the explicit referral of *Cecilionycteris* and *Matthesia* to Palaeochiropterygidae.

Hand et al. (1994) described the first Eocene bat from Australia, which they named *Australonycteris* and placed in Microchiroptera, family indeterminate. Drawing comparisons with other Eocene bats, Hand et al. indicated that *Australonycteris* is most similar to Archaeonycteridae (defined as including *Archaeonycteris* and *?Icaronycteris*) in terms of overall dental morphology and lack of derived features characteristic of extant families. They suggested, however, that morphology of an isolated periotic indicated that *Australonycteris* might instead represent “a very early vespertilionoid with a plesiomorphic dentition—or that more than one species is represented” (i.e., that the periotic and dental fragments represent different species; Hand et al., 1994: 378). They went on to discuss the affinities of *Wyonycteris*, concluding that there is no convincing evidence that this taxon is closely related to bats.

Habersetzer et al. (1994) discussed paleoecology of the Messel bats (*Palaeochiropteryx*, *Archaeonycteris*, and *Hassianycteris*) based on morphology of the wing and cochlea as well as fossilized stomach contents. In their introduction, they reviewed the Eocene record of bats and noted that *Wyonycteris* should be removed from Palaeochiropterygidae and possibly from Chiroptera. Habersetzer et al. (1994) followed Habersetzer and Storch (1987) in abandoning both Palaeochiropterygoidea and Eochiroptera, instead recognizing three families of uncertain affinities (Palaeochiropterygidae, Archaeonycteridae, and Hassianycterididae). They noted that these families share some symplesiomorphic features, but differ markedly from one another in morphology and apparent grade of evolution. Like Habersetzer and Storch (1989), Habersetzer et al. (1994: 236) suggested that Archaeonycteridae retains a large number of primitive features, that Palaeochiropterygidae has a primitive dentition but more specialized wing skeleton, and that members of Hassianycterididae “are clearly more advanced than the preceding families and are of rather more modern appearance dentally and osteologically.”

Hooker (1996) described a new genus

Eppsinycteris based on a partial dentary from early Ypresian beds (MP 8/9) near London, England. This specimen had been previously identified as a geolabid insectivoran, but Hooker noted the presence of a buccal cingulum on the lower molars, which was identified by Hand et al. (1994) as a possible synapomorphy of Chiroptera. The presence of a buccal cingulum, combined with other characters thought to have a very limited distribution among insectivorous mammals, led Hooker to identify *Eppsinycteris* as a bat. Based on three other derived features common in emballonurids, he referred *Eppsinycteris* to Emballonuridae. This allocation extended the temporal range of Emballonuridae by 10 million years, back into the earliest Eocene.

McKenna and Bell (1997) summarized an enormous amount of information from the literature and provided a classification for all mammals at the genus level and above. Among bats, they referred *Aegina*, *Australonycteris*, *Provampyrus* (= *Vampyravus*), and *Chadronycteris* to Microchiroptera incertae sedis. *Archaeonycteris* and *Icaronycteris* were placed in Archaeonycteridae, while *Palaeochiropteryx*, *Matthesia*, and *Cecilionycteris* were referred to Palaeochiropterygidae. *Hassianycteris* was referred to Hassianycterididae. All three of the archaic families—Archaeonycteridae, Palaeochiropterygidae, and Hassianycterididae—were referred to Microchiroptera incertae sedis. Among the extant lineages, *Vespertiliavus* was referred to Emballonuridae: Taphozoinae: Vespertiliavini, *Necromantis* was referred to Megadermatidae, and *Vaylatsia* was placed incertae sedis in Rhinolophidae. In a major nomenclatural change based upon priority of stem generic names, McKenna and Bell recognized Hipposiderinae as a junior synonym of Rhinonycterinae. *Hipposideros* (including *Pseudorhinolophus*) was subsequently placed in Rhinolophidae: Rhinonycterinae: Rhinonycterini: Hipposiderina, and *Palaeophyllophora* and *Paraphyllophora* were placed in Rhinolophidae: Rhinonycterinae: Palaeophyllophorini. Philisidae, including *Dizyia* and *Philisis*, was placed in Vespertilionoidea by McKenna and Bell (1997), and *Honrovits* was referred to Natalidae. *Stehlinia* was placed in Vespertilionidae:

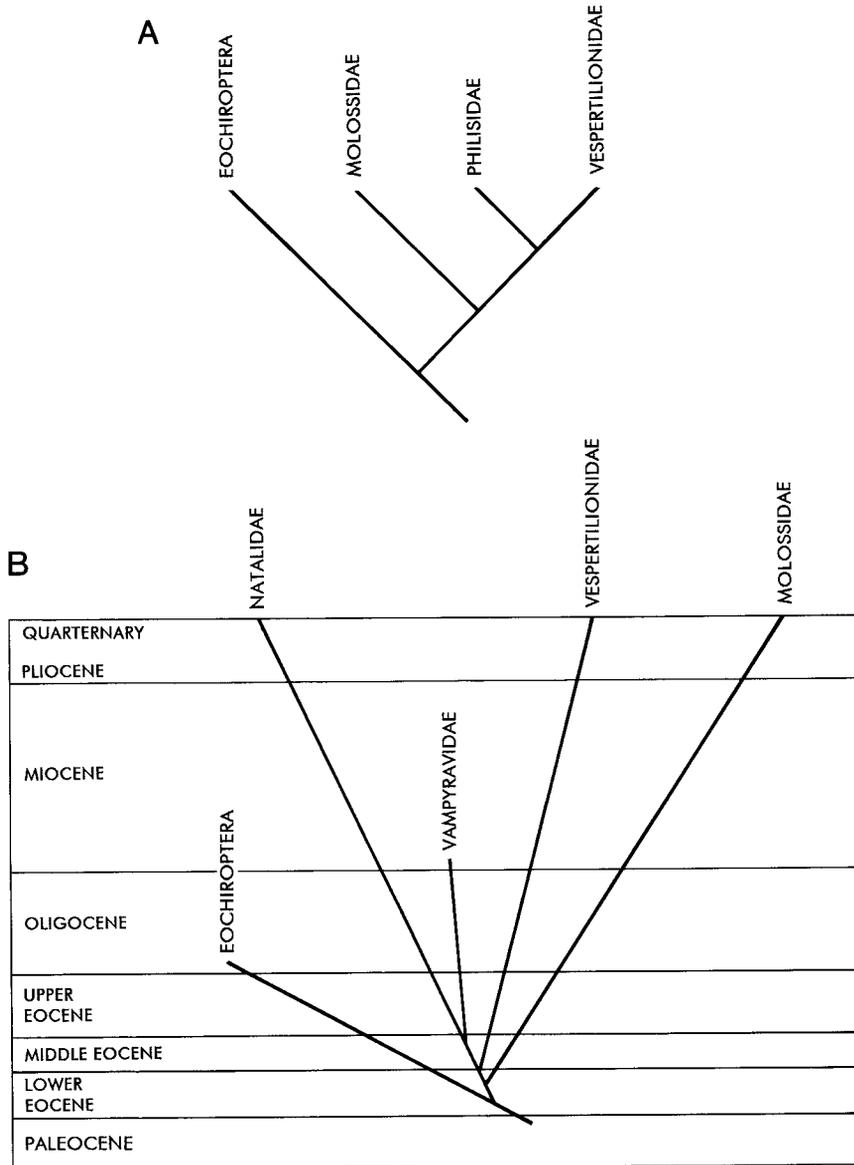


Fig. 12. Sigé's (1985) hypotheses of relationships of Philisidae and Vespertilionoidea (redrawn from Sigé, 1985: figs. 8, 9). The original caption for **A** read "Phylogénie présumée des Philisidae"; the caption for **B** read "Branchements majeurs présumés Vespertilionoidea et leur chronologie." See text for explanation of "Vampyravidae."

Vespertilioninae: Myotini. *Wallia* and *Cuvierimops* were referred to Molossidae: Molossinae, incertae sedis. Because Tomopeatinae was included in Molossidae, Molossinae sensu McKenna and Bell is equivalent to Molossidae sensu Legendre and others. Finally, McKenna and Bell referred *Archaeop-*

teropus to Megachiroptera: Pteropodidae: Archaeopteropodinae.

Hand and Kirsch (1998) examined relationships among extant and extinct Hipposideridae in a cladistic analysis of craniodental and postcranial osteological characters. Several species of *Rhinolophus* were included as

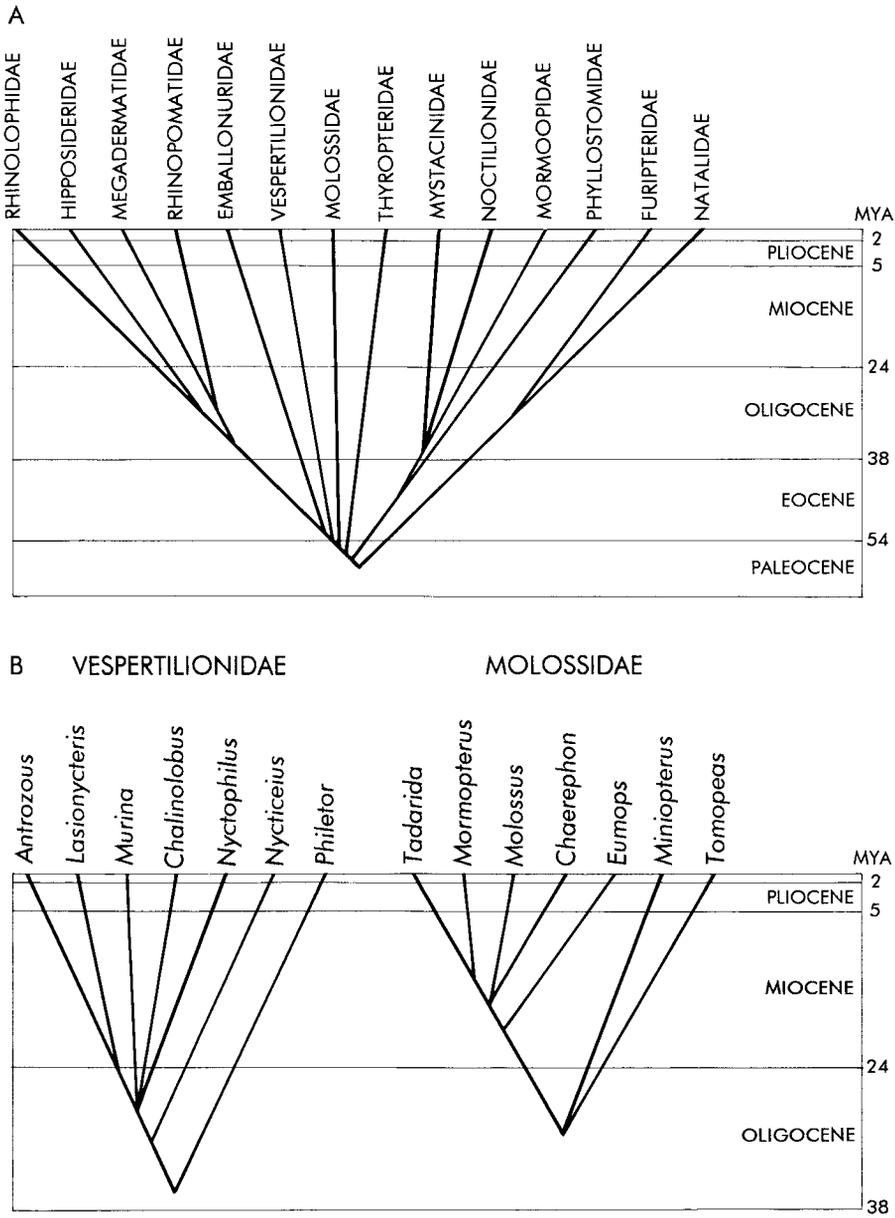


Fig. 13. Pierson's hypotheses of relationships and temporal patterns of divergence based on transferrin immunological distance data (redrawn from Pierson, 1986: figs. 31, 37). The original caption for **A** read "A proposed phylogeny for microchiropteran families, showing hypothesized times of divergence for major lineages . . . Calibration of immunological distances assumed Paleocene (55 MYA) origins for the current radiation." The caption for **B** read "vespertilionid relationships [were derived] using anti-*Anrozous* transferrin"; and the caption for **C** read "molossid relationships [were derived] using anti-*Tadarida* transferrin."

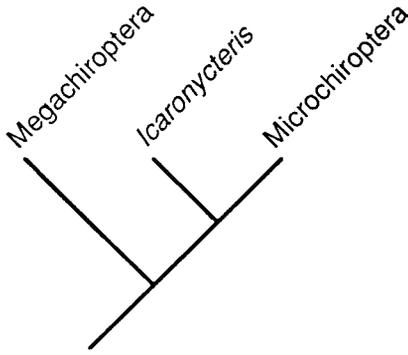


Fig. 14. Novacek's (1987) hypothesis of relationships of *Icaronycteris* to extant bats (redrawn from Novacek, 1987: fig. 10). The original caption read "Cladogram favoring a close relationship between *Icaronycteris* and recent Microchiroptera . . .," and went on to list morphological characters associated with each branch (omitted here). Novacek (1987) also concluded that *Palaeochiropterus* was more closely related to Microchiroptera than to Megachiroptera, but he did not include it in the figured phylogenetic tree.

outgroup taxa, and a variety of other microchiropterans were used to assess character polarity. Hand and Kirsch concluded that *Pseudorhinolophus* and *Palaeophyllophora* represent relatively derived hipposiderids, while *Vaylatsia* may be the plesiomorphic sister-group of extant rhinolophids (= rhinolophines).

RELATIONSHIPS AMONG EXTANT LINEAGES OF BATS

Relationships among extant bats have been a source of debate for as long as scientists have been classifying mammals. Excellent summaries of the early history of chiropteran classification can be found in Winge (1941) and Smith (1976, 1980). As noted by both authors, most recent bat classifications are ultimately based on that of Dobson (1875: 345), who purported to arrange the suborders, families, and genera of bats "according to their natural affinities" (see fig. 5). In the hundred years that followed, many major and minor changes to this classification scheme were suggested by such workers as Winge (1892), Miller (1907), Simpson (1945), Davis (1970), and Koopman and Jones (1970). In 1976, James Dale Smith, an early propo-

nent of cladistic methods, drew upon this rich history and presented a pair of cladograms (fig. 7) intended to summarize the then "generally accepted view" of bat phylogeny (Smith, 1976: 56). These trees differed only in the perceived origins of lineages from various ancestral stock(s); relationships among the extant families were the same in both trees. Although Smith (1976, 1980) stressed the importance of cladistic methods (i.e., distinguishing primitive from derived similarity), his phylogeny was apparently not based on an explicit character analysis, but rather on his perceptions of character polarities as informed by his own research on mormoopids (Smith, 1972) and the ideas of earlier workers (e.g., those listed above, as well as Hill, 1974).

Smith's (1976) trees (fig. 7) indicated monophyly of several higher-level taxa including four extant superfamilies: (1) Emballonuroidea, including Rhinopomatidae, Craseonycteridae, and Emballonuridae; (2) Rhinolophoidea, including Megadermatidae, Nycteridae, and Rhinolophidae (including Hipposiderinae); (3) Phyllostomatoidea (= Noctilionoidea), including Phyllostomatidae (= Phyllostomidae), Mormoopidae, and Noctilionidae; and (4) Vespertilionoidea, including Molossidae, Mystacinidae, Natalidae, Thyropteridae, Furipteridae, Vespertilionidae, and Myzopodidae. Monophyly of Vespertilionidae was apparently assumed. Two clades subsequently named as infraorders by Koopman (1985) also appeared in Smith's trees: Yinochiroptera (Emballonuroidea + Rhinolophoidea) and Yangochiroptera (Noctilionoidea + Vespertilionoidea).

Mein and Tupinier (1977) discussed the dental formula of *Miniopterus*, a genus usually placed in its own subfamily (Miniopterinae) in Vespertilionidae. Based on their analysis, they suggested that this group be removed from Vespertilionidae to its own family, Miniopteridae.

Van Valen (1979) presented a significantly different hypothesis of bat relationships (fig. 8) based on a cladistic analysis of morphological traits, including many features described for the first time in studies published in the 1970s (e.g., Henson, 1970; Strickler, 1978). Although Van Valen published lists of derived characters supporting each clade in

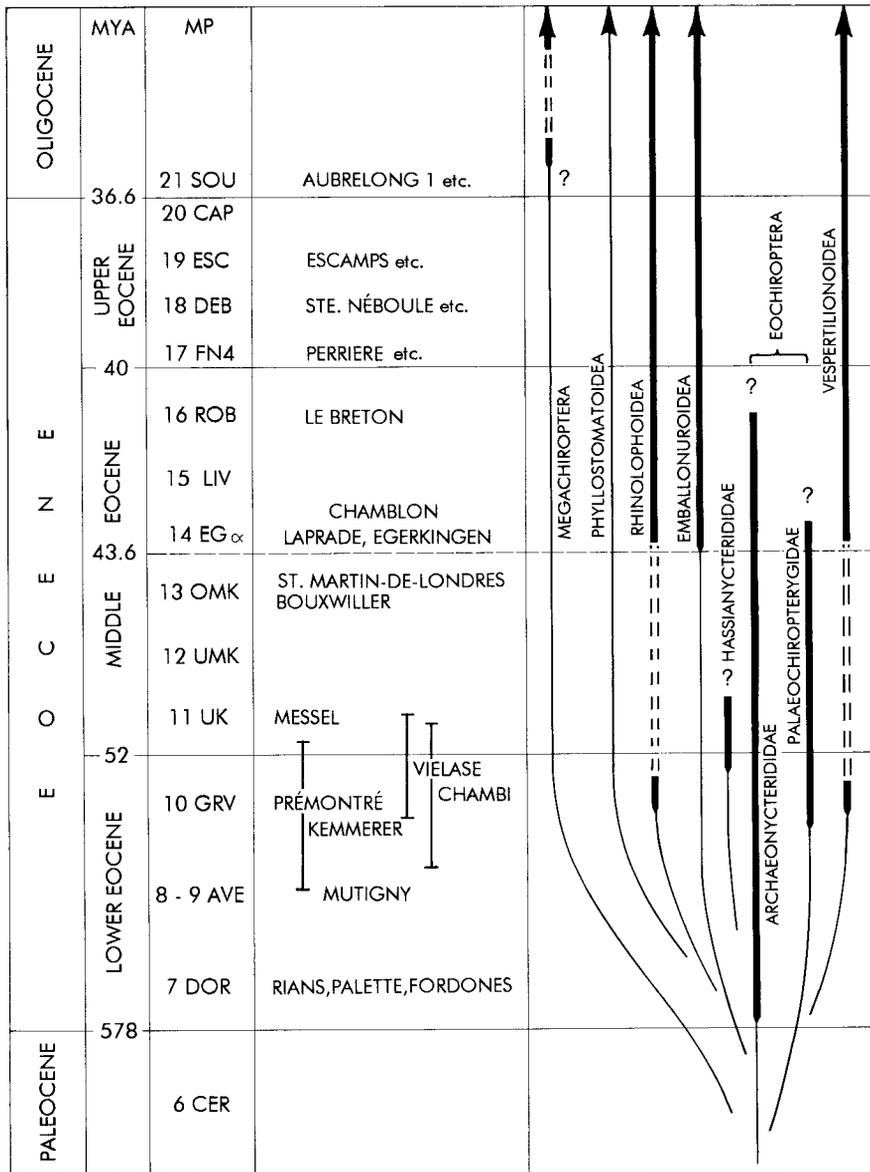


Fig. 15. Sigé's (1991b) summary of biostratigraphic data for Eocene bats (redrawn from Sigé, 1991b: fig. 5). The original caption read "Biostratigraphic position of the main Early Paleogene bat localities and temporal distribution of major bat groups. The geological frame is that of Berggren et al. 1985 and the mammalian biostratigraphy MP that of Mainz 1987 (Schmidt-Kittler, 1987). Bold lines: fossil evidence; double dotted lines: unevicenced existence; thin lines: presumed existence."

his tree, he did not discuss the methods used to identify these traits as derived. Van Valen's tree indicated monophyly of three of the four superfamilies (Rhinolophoidea, Noctilionoidea, and Vespertilionoidea); Emballon-

uroidea, Yinochiroptera, and Yangochiroptera did not appear as monophyletic groups. Although Miniopterinae was retained in Vespertilionidae, Kerivoulinae was removed from the latter family and placed in Natalidae

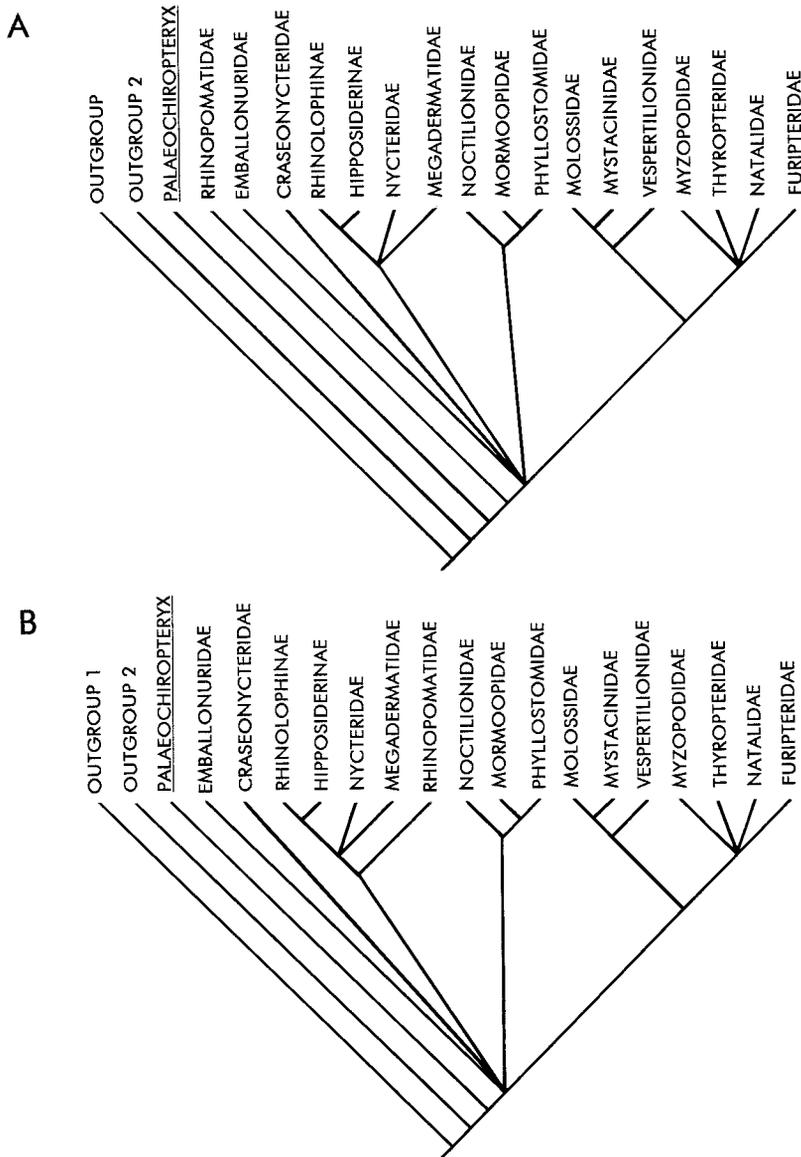


Fig. 16. Two alternative hypotheses of interfamilial relationships suggested by Novacek (redrawn from Novacek, 1991: figs. 6, 7). The original caption for **A** read "This cladogram . . . is based on discussions in Koopman (1984). The position of *Palaeochiropteryx* . . . follows Novacek (1987). Note the remote branch position of Rhinopomatidae." the caption for **B** read "as in [the previous figure] modified by relocation of Rhinopomatidae as a sister taxon of Rhinolophoidea (following Pierson, 1986)."

together with Myzopodidae, Thyropteridae, and Furipteridae, which Van Valen (1979) reduced in rank to subfamily level.

Novacek (1980a) and Luckett (1980a) published cladograms of bat relationships based on analyses of single organ systems.

Novacek focused on morphology of the auditory region; Luckett concentrated on morphology and development of fetal membranes. Primarily because the tree derived from auditory characters (fig. 9) differed significantly from all previous hypotheses of

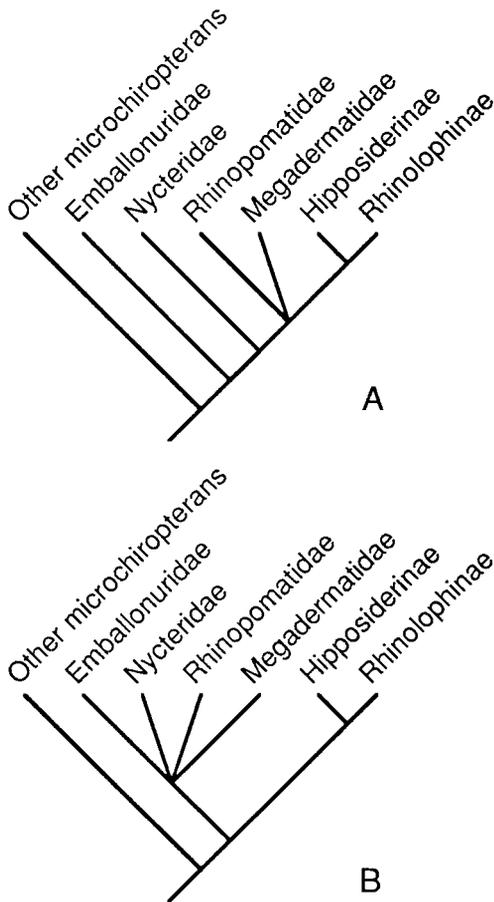


Fig. 17. Two alternative hypotheses of yinochiropteran relationships based on hyoid musculoskeletal morphology (redrawn from Griffiths et al., 1992: figs. 10, 11). Both trees were equally parsimonious in the context of the hyoid data presented by Griffiths and Smith (1991) and Griffiths et al. (1992), but these authors preferred tree A on the basis of hypothesized patterns of transformation in two characters.

higher-level relationships, Novacek (1980a) warned against using that cladogram (or any other derived from a single organ system) as a basis for a new phylogenetic reconstruction or classification. Luckett's (1980a) study was unable to resolve many relationships (fig. 10), but provided some support for monophyly of Noctilionoidea and a close relationship between Megadermatidae and a clade containing Vespertilionidae and Thyropteridae. Monophyly of Vespertilionidae sensu Koopman and Jones (1970) was apparently

assumed by both Novacek (1980a) and Luckett (1980a).

Eisenberg (1981) published a phylogeny of bats in his book on mammalian radiations. Eisenberg's (1981: 147) tree (fig. 11) differed only slightly from that presented by Smith (1976; see fig. 7). Like Smith (1976), Eisenberg depicted each of the microchiropteran superfamilies as monophyletic. However, Eisenberg placed Emballonuroidea, Rhinolophoidea, and Phyllostomatoidea (= Noctilionoidea) together in an unresolved clade with Vespertilionoidea as the sister-group, rather than identifying Emballonuroidea and Rhinolophoidea as sister-taxa as had Smith (1976).

Gopalakrishna and Chari (1983) described fetal membrane development in *Miniopterus*, a taxon generally placed in its own subfamily in Vespertilionidae. Based on their findings, which indicated major differences between miniopterines and other vespertilionids, Gopalakrishna and Chari recommended removal of *Miniopterus* to its own family, Miniopteridae.

Pierson (1986) proposed a series of phylogenetic hypotheses based on an analysis of transferrin immunological distance data (fig. 13). Her results differed significantly from those of previous studies in many areas, including (1) placing Rhinopomatidae within Rhinolophoidea, (2) associating Mystacinidae with Noctilionoidea rather than Vespertilionoidea, (3) placing Furipteridae and Natalidae at the base of the microchiropteran tree, and (4) grouping *Tomopeas* and *Miniopterus* with Molossidae rather than with Vespertilioninae. In the context of Pierson's trees, Yinochiroptera is monophyletic, but Yangochiroptera and the four superfamilies are not. One of the more striking results of Pierson's (1986) immunological study—the placement of Mystacinidae—was explored in greater depth in Pierson et al. (1986), which also included a discussion of some morphological features.

Hill and Harrison (1987) reviewed craniodental morphology and structure of the baculum in selected vespertilionids, and proposed a new generic classification of those forms traditionally included in Vespertilioninae (e.g., by Miller, 1907). Hill and Harrison (1987) included Myotini and Antrozoini

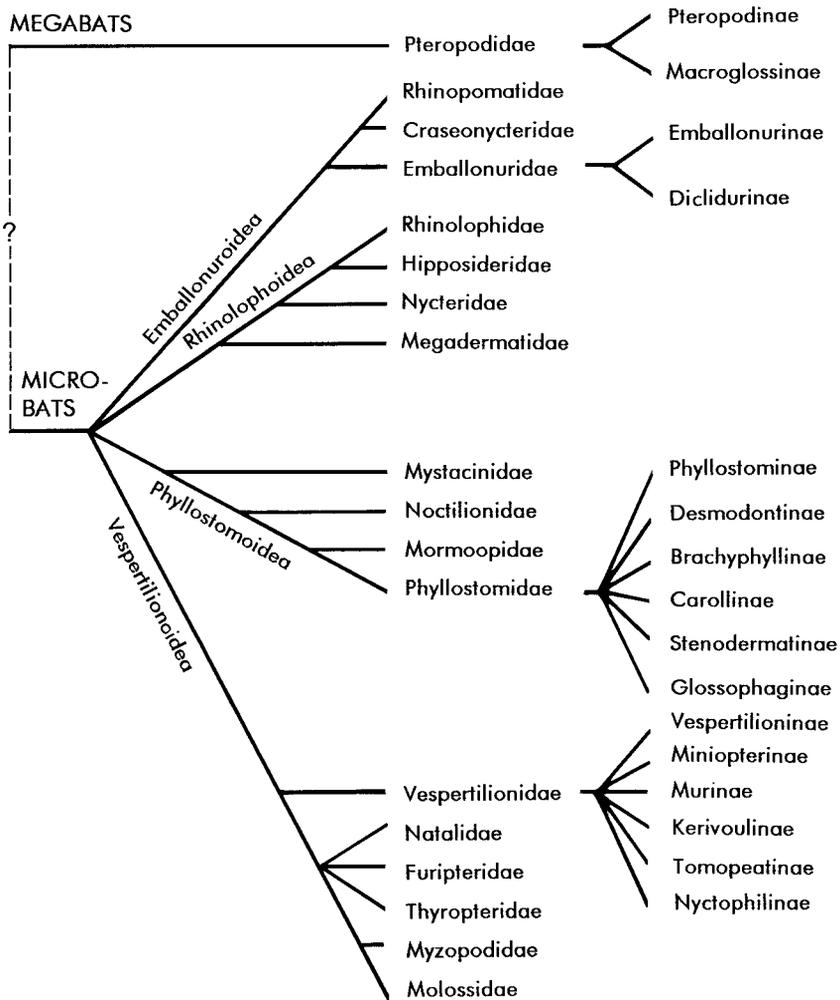


Fig. 18. Fenton's (1992) phylogeny of bat families with Altringham's (1996) addition of subfamilies (redrawn from Fenton [1992: p. 10] and Altringham [1996: fig. 1.12]). Fenton's (1992) caption read "A family tree or phylogeny shows the presumed evolutionary relationships between the living families of bats. The families are grouped according to superfamilies and suborders." Altringham's (1996) caption read "An evolutionary tree for the bats to subfamily level. Considerable uncertainty surrounds some parts of this tree, in particular the relationships between megabats and microbats, and the detailed classification of the Phyllostomidae and Vespertilionidae."

as tribes within Vespertilioninae, and recognized Nyctophininae as a distinct subfamily.

Tiunov (1989) examined variation in morphology of the tongue and male accessory glands (e.g., prostate, seminal vesicles, Cowper's gland, ampullary glands) in a number of Old World species, and discussed the phylogenetic implications of these data. Based on observed differences, Tiunov con-

curred with Gopalakrishna and Chari's (1983) recommendation that Miniopteridae should be recognized as a family distinct from Vespertilionidae. In contrast, Tiunov found no differences between rhinolophines and hipposiderines, and therefore recommended that they be placed in a single family, Rhinolophidae.

Baker et al. (1991a) analyzed variation in rDNA restriction sites in a study designed to

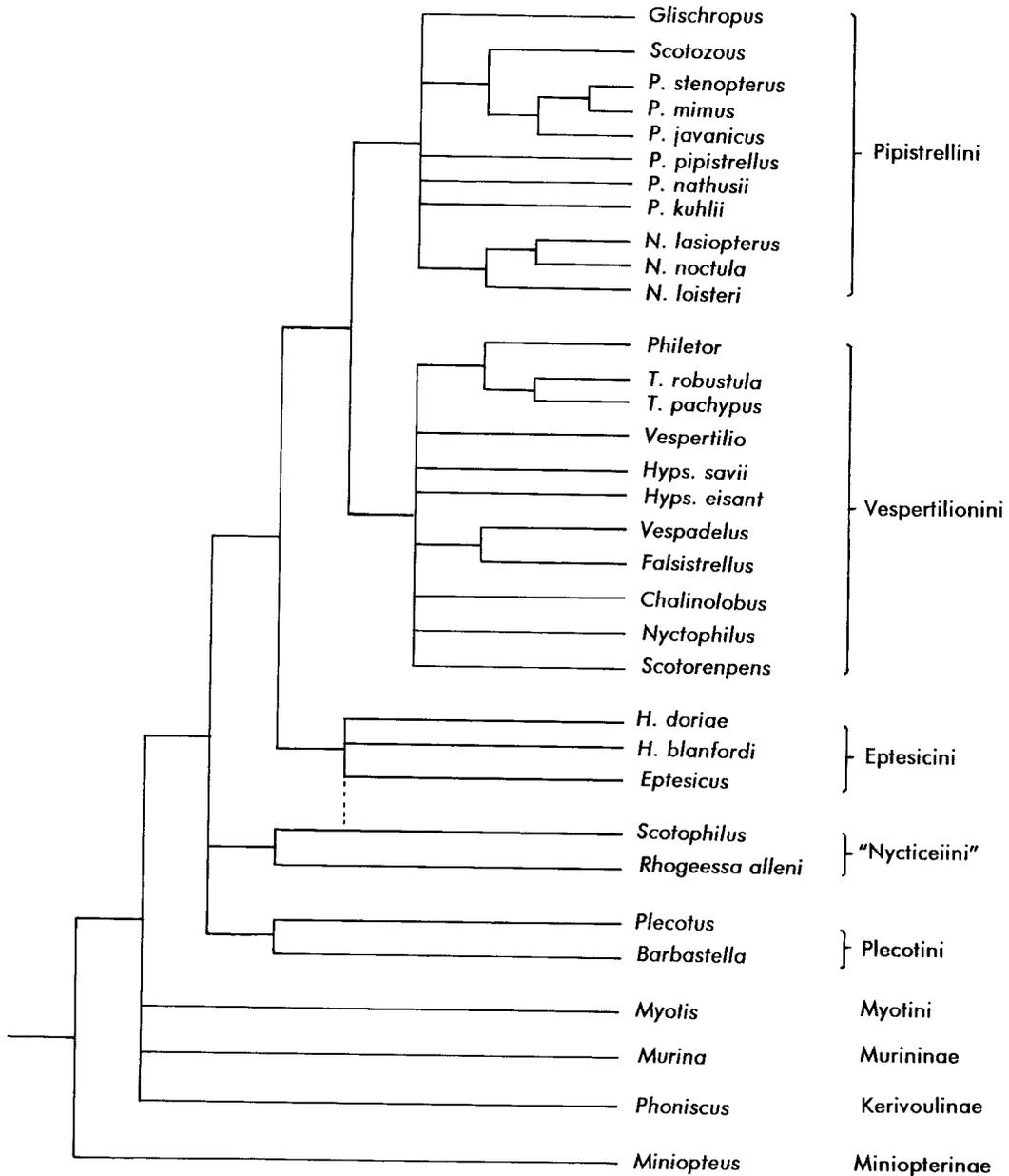


Fig. 19. Volleth and Heller's hypothesis of relationships among vespertilionids (redrawn from Volleth and Heller, 1984: fig. 7). The original caption read "Cladogram of Vespertilionidae based on karyological features . . . Where the names of species are lacking, only one species was studied (12 cases). From karyologically heterogeneous genera all species studied are shown. The dotted line between *Eptesicus* and *Scotophilus* indicates a second possibility for the relations of Eptesicini . . . [that tribe] could be grouped together with *Scotophilus* . . . [Abbreviations:] *H.* = *Hesperopternus*, *Hyps.* = *Hypsugo*, *Ny.* = *Nyctalus*, *P.* = *Pipistrellus*, *T.* = *Tylonycteris*."

test bat monophyly (see below). Although their data set could not resolve subordinal or interfamilial relationships of bats, support was found for several groups, including Yinochiroptera, Noctilionoidea, and a clade containing Mormoopidae and Noctilionidae.

In the 1980s and early 1990s, a significant controversy arose in chiropteran systematics regarding bat monophyly. The history of this controversy was reviewed by Simmons (1994) and will not be repeated here. Although bat diphyly has been proposed by several authors (e.g., Smith and Madkour, 1980; Hill and Smith, 1984; Pettigrew, 1986, 1991a, 1991b, 1994, 1995; Pettigrew and Jamieson, 1987; Pettigrew et al., 1989; Rayner, 1991b; Pettigrew and Kirsch, 1995), a growing body of data provides very strong support for bat monophyly. Data supporting chiropteran monophyly include morphological features from many organ systems (Luckett, 1980a, 1993; Wible and Novacek, 1988; Kovtun, 1989; Thewissen and Babcock, 1991, 1993; Kay et al., 1992; Novacek, 1992, 1994; Beard, 1993; Simmons, 1993a, 1994, 1995; Wible and Martin, 1993; Simmons and Quinn, 1994; Miyamoto, 1996), DNA-DNA hybridization data (Kirsch et al., 1995; Hutcheon and Kirsch, 1996; Kirsch, 1996), and sequence data from numerous mitochondrial and nuclear genes (Adkins and Honeycutt, 1991, 1993, 1994; Mindell et al., 1991; Ammerman and Hillis, 1992; Bailey et al., 1992; Stanhope et al., 1992, 1993, 1996; Honeycutt and Adkins, 1993; Knight and Mindell, 1993; Novacek, 1994; Allard et al., 1996; Miyamoto, 1996; Porter et al., 1996). Bat monophyly now represents one of the most strongly supported phylogenetic hypotheses within Mammalia (Simmons, 1994; Miyamoto, 1996).

Novacek (1991) used two novel phylogenies as a framework for discussing evolution of cochlear features in bats (fig. 16). These trees were not derived from an explicit character analysis, but were instead based on consideration of the morphological characters discussed in Koopman (1984) and Novacek (1987) as well as Pierson's (1986) immunological results (see caption to fig. 16). Both of Novacek's (1991) trees indicated paraphyly of Yinochiroptera and Emballonuroidea, left monophyly of Yangochiroptera

unresolved, and suggested monophyly of the remaining three superfamilies. Monophyly of Vespertilionidae (including kerivoulines, tomopeatines, and miniopterines) was not discussed.

Griffiths and his colleagues used osteomyological characters of the hyoid region to explore relationships among various groups of yinochiropteran bats (Griffiths and Smith, 1991; Griffiths et al., 1992). Griffiths et al. (1992) presented two alternative phylogenies (fig. 17), neither of which supported monophyly of Emballonuroidea or Rhinolophoidea. The only clade that appeared in both trees was Rhinolophidae + Hipposideridae.

Gopalakrishna and Badwaik (1992) discussed fetal membrane structure and used phenetic similarity to evaluate phylogenetic relationships among bat families. They concluded that

... similarities between Molossidae and Pteropodidae and differences between Molossidae and Vespertilionidae suggest a closer relationship between Pteropodidae and Molossidae than between Molossidae and Vespertilionidae. It is, therefore, suggested on purely embryological grounds that Molossidae be separated from the Super-family Vespertilionidae and be placed somewhere between Pteropodidae and Emballonuridae (Gopalakrishna and Badwaik, 1992: 7).

Fenton (1992) provided a phylogeny of bat families in his semipopular book on bats, but did not discuss the source of this hypothesis. The same topology was reproduced by Fenton (1995). This tree (fig. 18) was developed to summarize possible relationships of bats as reflected in numerous systematic studies and classifications (e.g., Hill, 1974; Pierson et al., 1986); it was not based on any new data or data analyses (Fenton, personal commun.). Altringham (1996) reproduced Fenton's tree (again with no mention of source), modifying it only by adding branches for each subfamily (fig. 18).

Volleth and Heller (1994) provided the first cladistic hypothesis of relationships among genera of Vespertilionidae *sensu lato* (fig. 19). Using data from G-banded chromosomes, they identified homologous arms and presented a cladogram based on an analysis of derived chromosomal features (e.g., translocations, Robertsonian fusions, fissions). They concluded that (1) Miniopterinae is the sister-group to a clade containing

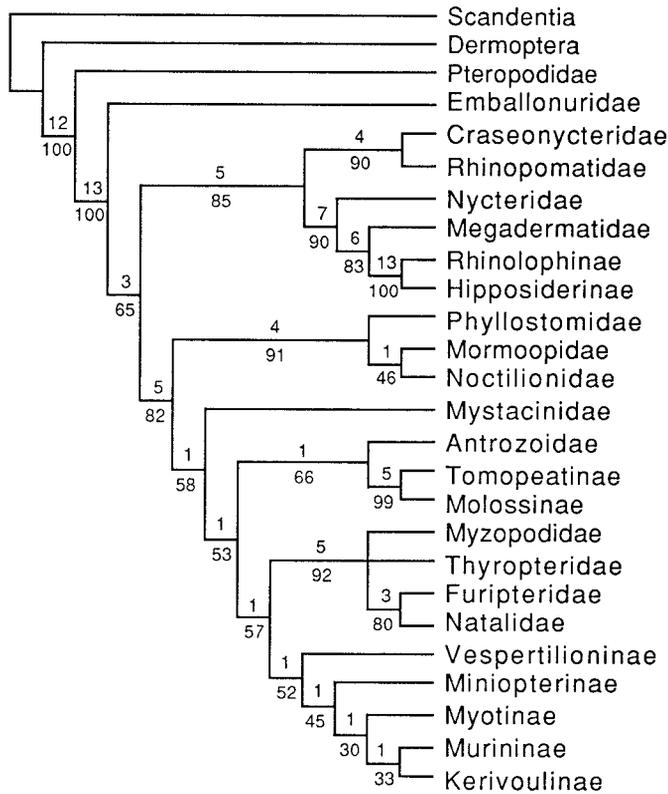


Fig. 20. Results of Simmons' (1998) analysis of higher-level relationships based on morphology and rDNA restriction sites. The original caption of this figure read "Strict consensus of two equally most-parsimonious trees (608 steps each; CI = 0.410, RI = 0.592) found in a heuristic analysis . . . The numbers below internal branches indicate the percentage of bootstrap replicates in which each clade appeared; numbers above the branches are decay values (the minimum number of additional steps required to collapse each clade)."

Kerivoulinae + Murininae + Vespertilioninae; (2) Myotini falls outside a clade containing the remaining vespertilionines; (3) *Nyctophilus* is a member of Vespertilionini; (4) Vespertilionini and Pipistrellini are sister-taxa; and (5) Eptesicini (including *Hesperoptenus*), "Nycticeini," and Plecotini fall outside the Vespertilionini + Pipistrellini clade. *Antrozous*, *Tomopeas*, *Lasiurus*, and other New World taxa were omitted from Volleth and Heller's study.

Sudman et al. (1994), drawing in part upon the unpublished work of Barkley (1984), investigated relationships of *Tomopeas* (the only member of Tomopeatinae) to vespertilionids and molossids using protein electrophoresis, cytochrome *b* gene sequences, and morphological characters. They con-

cluded that these data support a close relationship between *Tomopeas* and molossids rather than vespertilionids, and recommended that Tomopeatinae be transferred from Vespertilionidae to Molossidae.

Kirsch and his colleagues (Pettigrew and Kirsch, 1995; Hutcheon and Kirsch, 1996; Kirsch, 1996; Kirsch and Hutcheon, 1997; Hutcheon et al., in press; Kirsch and Pettigrew, in press; Pettigrew and Kirsch, in press) reported results of a series of DNA-DNA hybridization studies of relationships among a set of taxa including both megachiropterans and microchiropterans. Surprisingly, these experiments suggested that Rhinolophoidea and Pteropodidae may be sister-taxa, implying microchiropteran paraphyly. However, this result has been questioned by

the authors themselves, who have suggested that base compositional bias might be responsible for producing a false phylogenetic signal linking two A-T rich clades (Pteropodidae and Rhinolophoidea; Hutcheon and Kirsch, 1996; Kirsch, 1996; Kirsch and Hutcheon, 1997; Hutcheon et al., in review; Kirsch and Pettigrew, in review; Pettigrew and Kirsch, in review). Although topology of other parts of the tree remains suspect, many recovered groupings are congruent with those identified in previous studies. As noted by Hutcheon et al. (in press), "a tree as startling as ours obviously must be verified by additional studies . . ."

The most recent comprehensive attempt to resolve higher-level relationships among extant family-level lineages of bats was that of Simmons (1998). She assembled a data set of 192 discrete characters including many new morphological characters, all of the relevant morphological data discussed by most previous workers (e.g., Van Valen, 1979; Luckett, 1980a; Novacek, 1980a, 1991; Barkley, 1984; Griffiths and Smith, 1991; Griffiths et al., 1992), and the rDNA restriction site data presented by Baker et al. (1991a). To test vespertilionid monophyly and evaluate relationships of its subfamilies, Vespertilionidae *sensu lato* was split into seven subgroups for analysis: Vespertilioninae, Myotinae, Miniopterinae, Murininae, Kerivoulinae, Antrozoinae, and Tomopeatinae. Parsimony analyses of the resulting data set produced a well-resolved tree (fig. 20) in which many nodes were strongly supported. Major results included the following: (1) Emballonuridae appears to be the sister-group of all other microchiropterans, therefore Emballonuroidea and Yinochiroptera (as traditionally recognized) are not monophyletic; (2) Rhinopomatidae and Craseonycteridae are sister-taxa; (3) Rhinolophoidea, Noctilionoidea, Vespertilionoidea, and Yangochiroptera each appear to be monophyletic; (4) Vespertilionidae *sensu lato* is not monophyletic; Antrozoinae and Tomopeatinae are more closely related to Molossidae than to other vespertilionids; and (5) Myzopodidae, Thyropteridae, Natalidae, and Furipteridae form a clade.

Simmons (1998) proposed a number of nomenclatural changes (table 2) based on her

TABLE 2
Higher-level Classification of Recent Bats
Proposed by Simmons (1998)

Order Chiroptera
Suborder Megachiroptera
Family Pteropodidae
Suborder Microchiroptera
Infraorder incertae sedis
Superfamily Emballonuroidea
Family Emballonuridae
Infraorder Yinochiroptera
Superfamily Rhinopomatoidea
Family Craseonycteridae
Family Rhinopomatidae
Superfamily Rhinolophoidea
Family Nycteridae
Family Megadermatidae
Family Rhinolophidae
Subfamily Rhinolophinae
Subfamily Hipposiderinae
Infraorder Yangochiroptera
Superfamily incertae sedis
Family Mystacinidae
Superfamily Noctilionoidea
Family Noctilionidae
Family Mormoopidae
Family Phyllostomidae
Superfamily Molossoidea
Family Antrozoidae
Family Molossidae
Subfamily Tomopeatinae
Subfamily Molossinae
Superfamily Vespertilionoidea
Family Vespertilionidae
Subfamily Vespertilioninae
Subfamily Miniopterinae
Subfamily Myotinae
Subfamily Murininae
Subfamily Kerivoulinae
Superfamily Nataloidea
Family Myzopodidae
Family Thyropteridae
Family Furipteridae
Family Natalidae

phylogenetic results, restricting Emballonuroidea to Emballonuridae, placing Rhinopomatidae and Craseonycteridae in Rhinopomatoidea, restricting Yinochiroptera to Rhinopomatoidea + Rhinolophoidea, raising Antrozoinae to family rank as Antrozoidae, referring Tomopeatinae to Molossidae, recognizing Antrozoidae + Molossidae as a new superfamily Molossoidea, recognizing Myzopodidae + Thyropteridae + Natalidae

+ Furipteridae as a new superfamily Nata-loidea, and restricting Vespertilionidae to Vespertilioninae + Miniopterinae + Myotinae + Murinae + Kerivoulinae. Noting that several of the latter subfamilies might eventually be raised to family rank, Simmons (1998) restricted Vespertilionoidea to Vespertilionidae as defined above, pending further study.

GOALS OF THE CURRENT STUDY

The data set developed by Simmons (1998)—which of course includes many characters originally described by others (see appendix 2)—includes more than 80 craniodental and postcranial osteological characters. This provides a unique opportunity to evaluate the evolutionary relationships of the archaic Eocene taxa in the context of a phy-

logeny of extant lineages, and to investigate methodological issues involving fossil taxa and missing data in phylogenetic analyses. The goals of the current study are as follows: (1) to determine the relationships of *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* to each other and to family-level lineages of extant bats; (2) to evaluate the effects of including fossil genera on perceived relationships among extant forms; (3) to evaluate the effects of including soft-tissue and molecular characters in a study including both fossil and extant groups; (4) to document patterns of character transformation in the basal part of the chiropteran tree; and (5) to consider the implications of these data for theories concerning the early evolution of echolocation and foraging strategies in Microchiroptera.

MATERIALS AND METHODS

TAXONOMIC SAMPLING AND MONOPHYLY

The present study consists of a phylogenetic analysis of 24 family-level lineages of extant bats, two ordinal-level extant outgroup taxa (Scandentia, Dermoptera), and four Eocene fossil bat genera (*Icaronycteris*, *Archaeonycteris*, *Palaeochiropteryx*, *Hassianycteris*; see appendix 1 for specimens examined). The extant lineages are the same as those analyzed by Simmons (1998); taxonomic names used for bat clades follow the classification proposed by Simmons (1998; table 2). Monophyly of Vespertilioninae (including Nyctophilinae) was assumed for practical reasons following Volleth and Heller (1994) and Simmons (1998). Monophyly of each of the other extant bat lineages used as OTUs (operational taxonomic units) is well established (see Simmons [1998] and references cited therein). Each of the fossil genera also appears to be monophyletic (table 3), with the possible exception of *Icaronycteris*.

In the absence of apomorphic traits, most workers have diagnosed *Icaronycteris* on the basis of primitive features that have been modified in all other bats (Jepsen, 1966, 1970; Novacek, 1987). Although Jepsen

(1966, 1970) noted 14 characters of *Icaronycteris* that he considered as “primitive” or “generalized” relative to the conditions seen in extant bats, close examination of these features by Novacek (1987) reduced this list considerably. Novacek identified only four primitive features apparently found in *Icaronycteris* that have been lost or modified in all other known fossil and extant bats: (1) unfused sternal elements, (2) relatively short radius, (3) complete phalangeal formula (2-3-3-3) on the digits of the wings, and (4) head and neck of femur set at an angle to the shaft. Our examination of additional specimens of extant bats plus material of *Icaronycteris* that was not available to Jepsen or Novacek indicate that two more of these features should be removed from the list.

Our observations indicate that sternal elements are typically unfused in juvenile, subadult, and some young adult bats. Novacek (1987) noted that the holotype of *Icaronycteris index* (PU 18150) might have unfused sternal elements simply because it was a young individual. This was confirmed by our examination of UW 21481a–b (fig. 21), a previously undescribed specimen of *Icaronycteris index* from Wyoming.² The sternal el-

² We identified UW 21481a–b as *Icaronycteris index*

ements in this individual are fused with the exception of the joints between the manubrium and mesosternum and between the mesosternum and xiphisternum. Sutures are visible between three mesosternal elements, but the remaining mesosternal elements are fully fused (fig. 22). This degree of fusion is similar to that found in young adult bats of many extant families. Because UW 21481a–b and PU 18150 are similar in all other respects, we conclude that PU 18150 was a young adult *Icaronycteris*, whereas UW 21481a–b represents a somewhat older individual. A similar pattern of variation is also seen in some of the Messel bats. For example, all mesosternal elements are fused in some specimens of *Archaeonycteris trigonodon* (e.g., SMF Me 80/1379), while all sutures are still visible in others (e.g., SMF Me 963a). *Icaronycteris* therefore appears to have had an ontogenetic pattern of sternal fusion similar to that seen in *Archaeonycteris* and many extant bats.

based on morphology and collection locality. Based on comparisons with Jepsens original stereophotographs (many of which remain unpublished), we found that UW 21481a–b appears identical to the holotype of *Icaronycteris index* PU 18150 in virtually all respects (although see text for a discussion of sternal fusion). Forearm length in UW 21481a–b is 47.5 mm; forearm length in PU 18150 is 48.0 mm. Measurements of skull length, tibia length, and length of various wing elements in UW 21481a–b are within ± 2 mm of those reported by Jepsen (1966) for PU 18150. This range of variation is well within that seen in extant species of similar body size (e.g., Swanepoel and Genoways, 1979). UW 21481a–b was collected from early Eocene sediments of the Green River Formation of Wyoming, the same deposits from which PU 18150 was collected (Jepsen, 1966). Because detailed dental comparisons between PU 18150 and UW 21481a–b were precluded by preservation of the latter specimen, it remains possible that UW 21481a–b represents a species of *Icaronycteris* distinct from *index*; however, we found no data to support such an interpretation. Accordingly, we refer UW 21481a–b to *Icaronycteris index* Jepsen, 1966.

Grande (1980: fig. III.26) figured a badly preserved bat fossil from Middle Eocene deposits of the Green River Formation of Colorado that he noted “probably represents an undescribed species.” Unfortunately, this specimen is in a private collection and has never been described. This record suggests, however, that bat species other than *Icaronycteris index* may have been present in western North America in the Eocene.

Another feature cited by Jepsen (1966, 1970) and Novacek (1987) as a primitive character of *Icaronycteris* is the orientation of the head and neck of femur, which they described as set at an angle to the long axis of the shaft (although not to the extent seen in terrestrial mammals). Novacek (1987: 13) noted that in this trait *Icaronycteris* is “clearly more conservative than living mega- and microchiropterans, where the head is nearly aligned with the shaft and the neck is very short or absent.” However, our comparisons of the femur of *Icaronycteris* with those of extant bats indicate that Novacek was misled by the angle of presentation of the femur in PU 18150, which provides an oblique view of the head and neck (fig. 23). We found that this view accentuates a relatively small degree of offset of the femoral head. Comparisons of the femur of PU 18150 and UW 21481a–b with those of extant megachiropterans and noctilionoids of similar body size indicate that the head and neck of the femur of *Icaronycteris* are set at the same angle (relative to the shaft of the femur) as seen in many extant bats. Indeed, the proximal femur of *Rousettus aegyptiacus* is virtually identical to that of *Icaronycteris* when viewed from the same angle. *Icaronycteris* thus cannot be considered more primitive than extant bats in terms of femur morphology.

Our survey thus limits the list of primitive features found in *Icaronycteris* (but modified in all other known bats) to the following: (1) relatively short radius, and (2) complete phalangeal formula (2-3-3-3) on the digits of the wings. Novacek (1987) noted that relative length of the radius had never been quantified, but this was subsequently done by Habersetzer and Storch (1987). They found that the ratio of humerus length to radius length was somewhat larger (and the radius therefore relatively shorter) in *Icaronycteris* compared to other Eocene bats, although the difference between the range of values for *Icaronycteris* (0.715–0.732) and *Archaeonycteris* (0.680–0.715) is not great.

The diagnosis of *Icaronycteris* therefore rests on just two plesiomorphic features. However, it seems unlikely that multiple lineages are represented in this group (at least among the four specimens that we examined) because the range of variation in size and

TABLE 3
Apomorphies^a Diagnosing Genera of Eocene Bats

Icaronycteris (one species, *I. index*)

- No apomorphies

Archaeonycteris (three species, *A. trigonodon*, *A. pollex*, *A. brailloni*)

- Ectoflexus deeply retracted between parastyle and metastyle on M1 and M2
- Ventral process of manubrium of sternum oriented at approximately 90° to axis of body of manubrium
- Posterior xiphisternum narrow, without lateral flare
- Dorsal ischial tuberosity present

Palaeochiropteryx (two species, *P. tupaiodon* and *P. spiegelii*)

- Metaconule present on M1 and M2
- Length of postparacrista equals length of premetacrista on M3
- Ventral accessory process present on cervical vertebra 5
- Infraspinous fossa of scapula relatively broad
- Ventral projection present on anteromedial flange of scapula

Hassianycteris (four species, *H. messelensis*, *H. magna*, *H. revilliodi*, and *H. joeli*)

- Protoconid and hypoconid on molar teeth exceptionally tall and robust
- Last lower premolar not molariform, metaconid lacking and talonid short
- First upper premolar reduced to tiny peg or absent
- Mandible deep, thickened dorsoventrally
- Radius unusually long and strongly curved
- Trochiter extends well beyond level of head humerus
- Metacarpal of digit V relatively short compared to metacarpals III and IV

^a Not found in any other Eocene taxon. Membership in extant families is precluded by documented or inferred absence of derived characters diagnostic of those taxa (for a list of characters diagnosing extant lineages see Simmons, 1998: tables 1, 2). Sources: Russell and Sigé, 1970; Smith and Storch, 1981; Habersetzer and Storch, 1987, 1989; Storch and Habersetzer, 1988; personal obs.).

shape of skeletal elements among referred individuals appears to fall within limits characteristic of extant species (see footnote 2). We have therefore assumed monophyly of *Icaronycteris* for the purposes of the current study, although we recognize that the European material referred to *?Icaronycteris menui* and *?Icaronycteris* sp. may represent one or more different clades.

OUTGROUPS

Only one outgroup is necessary to root a phylogenetic tree (Nixon and Carpenter, 1993), but at least two outgroups are usually included in cladistic analyses to establish character polarities and to permit testing of ingroup monophyly (Maddison et al., 1984). Ideally, outgroups should comprise the nearest sister-taxa to the ingroup because the probability of homoplasy increases with time since divergence from a common ancestor. The identity of the sister-group of bats is still the subject of considerable debate, and recent

congruence studies have failed to resolve existing conflicts between morphological data and several molecular data sets (e.g., Allard et al., 1996; Miyamoto, 1996; Stanhope et al., 1996). Nevertheless, practical considerations require that a choice of outgroups be made to facilitate analyses of relationships and character evolution within Chiroptera. A close relationship between Chiroptera and Dermoptera (colugos or flying lemurs) is strongly supported by morphological data (Wible and Novacek, 1988; Novacek, 1992, 1994; Simmons, 1993a, 1994, 1995; Szalay and Lucas, 1993; Wible, 1993; Simmons and Quinn, 1994; Miyamoto, 1996; Griffiths, MS), 12S rDNA sequences (sampled from more than 150 species representing 20 orders; Vrana, 1994), and combined morphological data and cytochrome oxidase II (COII) gene sequences (Novacek, 1994). Accordingly, Simmons (1998) used Dermoptera as an outgroup for investigating interrelationships of bats. Morphological synapomor-



Fig. 21. New specimen of *Icaronycteris index* (UW 21481a–b) from the Green River Formation, Wyoming. Photograph by C. Tarka.

phies supporting monophyly of Volitantia (Dermoptera + Chiroptera) are listed in table 4. Scandentia (tree shrews), which together with Primates form the sister-group of the Volitantia in optimal morphological trees (Novacek, 1992, 1994; Miyamoto, 1996),

was included as an additional outgroup by Simmons (1998). Monophyly of extant Dermoptera and monophyly of Scandentia are each strongly supported (Zeller, 1986; MacPhee et al., 1989; Beard, 1993; Wible and Zeller, 1994).

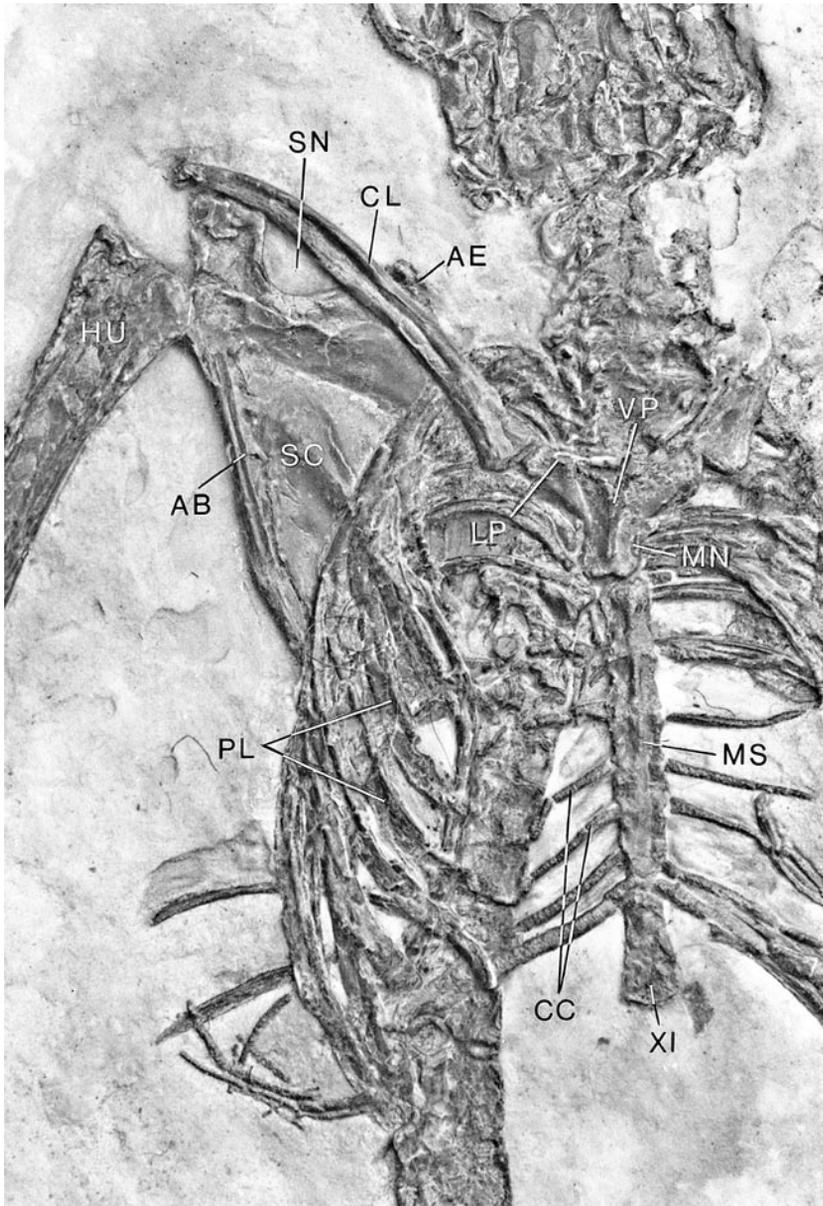


Fig. 22. *Icaronycteris index* (UW 21481a-b). Close-up ventral view of the ribcage, sternum, and right shoulder region. AB, axillary border of scapula; CC, costal cartilages; CL, clavicle; HU, humerus; LP, lateral process of manubrium of sternum; MN, manubrium of sternum; MS, mesosternum; PL, posterior laminae of ribs; SC, scapula; SN, suprascapular notch; VP, ventral process of manubrium of sternum; XI, xiphisternum. Photograph by C. Tarka.

Several DNA nucleotide sequence data sets (epsilon β -globin, interphotoreceptor retinoid binding protein [IRBP], COII, von Willebrand factor [vWF]) have produced alternative hypotheses of mammalian interor-

dinal relationships when analyzed alone and in combined analyses (Bailey et al., 1992; Stanhope et al., 1992, 1993, 1996; Adkins and Honeycutt, 1993, 1994; Novacek, 1994; Allard et al., 1996; Miyamoto, 1996; Porter

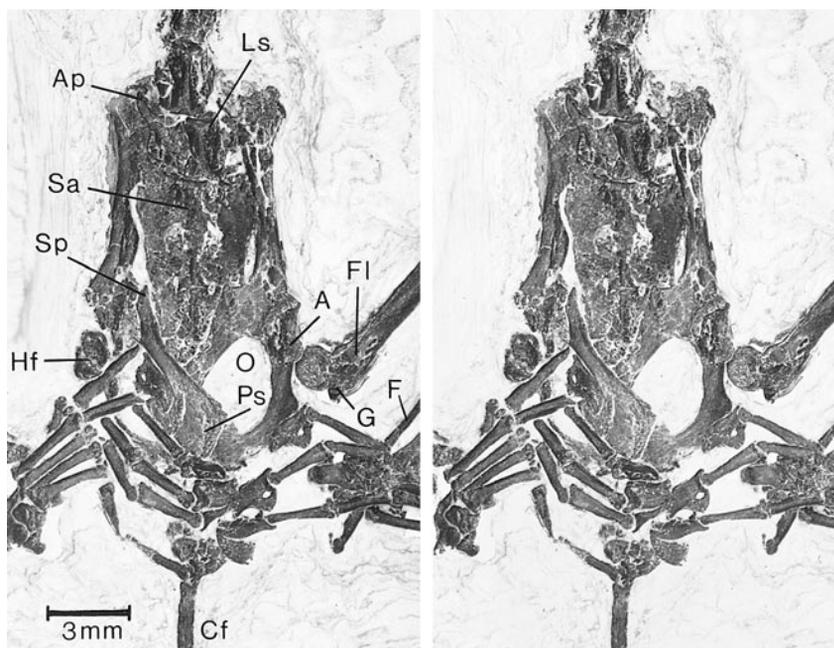


Fig. 23. *Icaronycteris index* (holotype; PU 18150). Stereophotographs of close-up ventral view of pelvic region. From Jepsen (1970: fig. 16); reprinted and labels revised by Novacek (1987: fig. 8). A, acetabulum; Ap, anterolateral process of seventh lumbar vertebra; Cf, fourth caudal vertebra; F, fibula; Fl, lesser trochanter of femur; G, greater trochanter of femur; Hf, head of femur; Ls, seventh lumbar vertebra; O, obturator foramen; Ps, pubic symphysis; Sa, sacrum; Sp, pubic spine.

et al., 1996). Rather than placing Dermoptera and Scandentia as close relatives of Chiroptera (i.e., in a monophyletic Archonta), these studies have alternatively suggested that Insectivora, Carnivora, Artiodactyla, a clade comprising Artiodactyla + Cetacea, an Artiodactyla + Cetacea + Perissodactyla clade, or a Carnivora + Perissodactyla clade might be the sister-taxon of bats. We considered including some or all of these orders in our study, but preliminary examinations of character variation indicated that all of these taxa exhibited high degrees of taxonomic polymorphism with respect to the characters in our data set, thus limiting their value as outgroups for the current study.

Simmons (1998) demonstrated that outgroup choice does not appear to be critical for determining ingroup relationships of bats, at least when morphological data are employed. She obtained identical tree topologies for Chiroptera regardless of whether both outgroups, one outgroup, or no outgroups were included (in the latter case, the

tree was rooted using Pteropodidae). These results indicate that morphological character data for the ingroup taxa are highly structured, and lead us to suspect that the same tree topology would be obtained no matter what eutherian group was used to root the tree. Accordingly, we chose to retain the outgroups used by Simmons (1998) rather than expanding the study to include additional outgroup taxa.

Although choice of outgroups may not be critical for determining ingroup relationships within Chiroptera, it can significantly affect assessments of character polarity. We therefore note that the polarity assessments discussed below are based on the assumption that Scandentia and Dermoptera are appropriate outgroups for investigating patterns of morphological character evolution in bats. This assumption was accepted in the current study because (1) as noted above, considerable morphological and some molecular data support a close relationship between bats, dermopterans, and tree shrews;

TABLE 4
**Morphological Synapomorphies^a of Volitantia (Chiroptera + Dermoptera)
 Identified by Simmons (1995)**

- 1) Tooth enamel with horseshoe-shaped prisms with associated minor boundary planes (seams)^b
- 2) Fenestra cochleae (round window) faces directly posteriorly^c
- 3) Subarcuate fossa greatly expanded and dorsal semicircular canal clearly separated from endocranial wall of squamosal^c
- 4) Tegmen tympani reduced, tapered to a round process, does not form roof over mallear-incudal articulation or entire ossicle chain^d
- 5) Ramus infraorbitalis of the stapedia artery passes through the cranial cavity dorsal to the alisphenoid^{e,f}
- 6) Neural spines on cervical vertebrae 3–7 weak or absent^c
- 7) Ribs flattened, especially near vertebral ends^{c,s}
- 8) Forelimbs markedly elongated^c
- 9) Proximal displacement of the areas of insertion for the pectoral and deltoid muscles; coalesced single proximal humeral torus^s
- 10) Presence of humeropatagialis muscle^c
- 11) Reduction of proximal ulna^c
- 12) Modification of distal radius and ulna: fusion of distal ulna to distal radius; distal radius transversely widened, manus effectively rotated 90°; deep grooves for carpal extensors on dorsal surface of distal radius; disengagement and reduction of the ulna from anterior humeral contact^{f,s}
- 13) Fusion of scaphoid, centrale, and lunate into scaphocentralunate^s
- 14) Patagium continuously attached between digits of manus^{c,s}
- 15) Elongation of the fourth and fifth pedal rays^s
- 16) Ungual phalanges both proximally and distally deep, compressed mediolaterally^s
- 17) Presence of a tendon-locking mechanism on digits of feet^t

^a Features listed have been discussed by other authors as noted. Dermoptera is defined here to include extant gliding lemurs (*Galeopithecidae* = *Cynocephalus*) + extinct *Paromomyidae*. This grouping is equivalent to *Eudermoptera sensu* Beard (1993). Several fossil taxa included in *Dermoptera* by Beard (*micromomyids*, *plesiadapids*, *carpolestids*, and *saxonellids*) are excluded here due to ambiguity concerning their relationships (Simmons, 1993a).

^b Lester et al. 1988.

^c Wible and Novacek 1988.

^d Wible and Martin 1993.

^e Wible 1993.

^f Simmons 1994.

^s Szalay and Lucas 1993.

^t Simmons and Quinn 1994.

(2) dermopterans and tree shrews exhibit many character states that are widely regarded as plesiomorphic for *Eutheria* (Slaughter, 1970; Cartmill and MacPhee, 1980; Novacek, 1980b, 1986; 1990; Novacek and Wyss, 1986), thus providing an appropriate guide to polarity of many characters used in this study (see character descriptions for further comments); (3) at least with respect to nondental skeletal characters, dermopterans constitute a plausible morphotype for a gliding chiropteran ancestor with specializations for underbranch hanging behavior (Winge, 1941; Smith, 1977; Hill and Smith, 1984; Rayner, 1986; Szalay and Lucas, 1993; Simmons and Quinn, 1994; Simmons, 1995); and (4) tree

shrews similarly constitute a plausible morphotype for a scansorial arboreal ancestral form (Novacek, 1980b; Szalay and Drawhorn, 1980). Nevertheless, it must be noted that our polarity assessments may require further modification as better resolution of interordinal relationships is achieved.

Monophyly of Chiroptera was assumed in the current study based on the studies previously cited (see above). Morphological features identified by Simmons (1994) as synapomorphies of Chiroptera are listed in table 5. Because bat monophyly was assumed a priori, characters relevant only to bat monophyly (e.g., most of the features in table 5) were not included in the data set used in the current study.

TABLE 5
Morphological Synapomorphies of Chiroptera Identified by Simmons (1994)

-
- 1) Deciduous dentition does not resemble adult dentition; deciduous teeth with long, sharp, recurved cusps
 - 2) Palatal process of premaxilla reduced; left and right incisive foramina fused in midsagittal plane
 - 3) Postpalatine torus absent
 - 4) Jugal reduced and jugolacrimal contact lost
 - 5) Two entotympanic elements in the floor of the middle-ear cavity: a large caudal element and a small rostral element associated with the internal carotid artery
 - 6) Tegmen tympani tapers to an elongate process that projects into the middle-ear cavity medial to the epitympanic recess
 - 7) Proximal stapedia artery enters cranial cavity medial to the tegmen tympani; ramus inferior passes anteriorly dorsal to the tegmen tympani
 - 8) Modification of scapula: reorientation of scapular spine and modification of shape of scapular fossae; reduction in height of spines presence; of a well-developed transverse scapular ligament
 - 9) Modification of elbow: reduction of olecranon process and humeral articular surface on ulna; presence of ulnar patella; absence of olecranon fossa on humerus
 - 10) Absence of supinator ridge on humerus
 - 11) Absence of entepicondylar foramen in humerus
 - 12) Occipitopollicalis muscle and cephalic vein present in leading edge of propatagium
 - 13) Digits II–V of forelimb elongated with complex carpometacarpal and intermetacarpal joints, support enlarged interdigital flight membranes (patagia); digits III–V lack claws
 - 14) Modification of hip joint: 90° rotation of hindlimbs effected by reorientation of acetabulum and shaft of femur; neck of femur reduced; ischium tilted dorsolaterally; anterior pubes widely flared and pubic spine present; absence of m. obturator internus
 - 15) Absence of m. gluteus minimus
 - 16) Absence of m. sartorius
 - 17) Vastus muscle complex not differentiated
 - 18) Modification of ankle joint: reorientation of upper ankle joint facets on calcaneum and astragalus; trochlea of astragalus convex, lacks medial and lateral guiding ridges; tuber of calcaneum projects in plantolateral direction away from ankle and foot; peroneal process absent; sustentacular process of calcaneum reduced, calcaneo-astragal and sustentacular facets on calcaneum and astragalus coalesced; absence of groove on astragalus for tendon of m. flexor digitorum fibularis
 - 19) Presence of calcar and m. depressor ossis styloformis
 - 20) Entocuneiform proximodistally shortened, with flat, triangular distal facet
 - 21) Elongation of proximal phalanx of digit I of foot
 - 22) Embryonic disc oriented toward tubo-uterine junction at time of implantation
 - 23) Differentiation of a free, glandlike yolk sac
 - 24) Preplacenta and early chorioallantoic placenta diffuse or horseshoe-shaped, with definitive placenta reduced to a more localized discoidal structure
 - 25) Definitive chorioallantoic placenta endotheliochorial
 - 26) Cortical somatosensory representation of forelimb reverse of that in other mammals
-

THE DATA SET

The basis of our study was the morphology + rDNA restriction site data set originally developed by Simmons (1998) to address family-level relationships among extant bats. Although nucleotide sequence data hold great promise for resolving bat phylogeny, sampling has been poor in previous studies with respect to the taxonomic levels under consideration here. As noted by Simmons (1998), taxonomic sampling in amino acid and nucleotide sequence data sets has been

restricted to fewer than half of the extant families, and no published data set includes representatives of more than 7 of the 24 extant taxa included in the present study (e.g., Pettigrew et al., 1989; Adkins and Honeycutt, 1993; Stanhope et al., 1993, 1996; Porter et al., 1996). Accordingly, nucleotide sequence data are not included in our data set.

The data set used in our study (see appendices 2, 3) comprises 195 morphological characters, 12 rDNA restriction site characters, and one character based on the number

of R-1 tandem repeats in the mtDNA d-loop region. Although fundamentally similar to that presented by Simmons (1998), our data set includes corrections, some new observational data (e.g., hyoid and shoulder myology data for Antrozoidae), several modified character definitions (e.g., an additional state defined for character 21; characters 75–77 jointly replace a single character defined by Simmons, 1998), and a number of entirely new characters (i.e., characters 19, 125–127, 138, 143, 154–157, 192, 208).

Multistate characters were coded hierarchically following methods described by Simmons (1993a), except in cases where so doing would result in uninformative characters. For example, if “absent” represented one condition in a multistate transformation, we defined two characters: (A) a present/absent character (e.g., character 86); and (B) a character describing variations in form of the structure when it is present (e.g., character 87). This method preserves homology information without requiring ordered character transformations (Simmons, 1993b). However, if the “absent” condition occurs in only one taxon in the analysis, a present/absent character would not be informative. In these cases, we defined a multistate character including “absent” as one of the character states (e.g., character 91).

The complete data set used in this study, including character state descriptions and references for data sources, is available electronically via the World Wide Web at <ftp://ftp.amnh.org/pub/mammalogy>.

CHARACTERS EXAMINED IN FOSSIL BATS

As a result of imperfect preservation, the Eocene specimens available for study (see appendix 1 for list of specimens examined) permitted us to score *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* for most but not all of the hard-tissue characters in the data set. Below, we present our observations concerning the characters that we could score in these taxa, as well as the range of variation seen among extant lineages with respect to these features. Character descriptions and complete references for all characters (including soft-tissue fea-

tures and rDNA restriction sites) are summarized in appendix 2. The character order established by Simmons (1998) is retained to facilitate comparison between that data set and the modified version used in this study; gaps in the numerical sequence given below reflect characters that could not be scored in any of the fossil taxa. Higher-level taxonomic names employed below are sensu Simmons (1998; table 2).

SKULL AND DENTITION

Character 9: *Premaxilla articulates with maxilla via sutures (0); or premaxilla fused to maxilla (1); or premaxilla articulates with maxilla via ligaments, premaxilla freely movable (2).* The articulation between the maxilla and the premaxilla consists of a simple sutured joint in *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. Although Smith and Storch (1981: 158) noted in the original description of *Hassianycteris messelensis* that “the premaxillary appears to have a strong nasal branch which appears to have been fused to the maxillary,” examination of new material (e.g., SMF ME 1469b) led us to conclude that the premaxilla was not fused to the maxilla in *Hassianycteris*. Instead, the premaxilla–maxilla articulation appears to have consisted of a simple suture in this taxon, as in the other Eocene forms. Among extant bats, a similar sutured joint is seen only among megachiropterans (e.g., *Pteropus*, *Rousettus*). In contrast, the premaxilla is fully fused to the maxilla and the sutures are obliterated in adults of some megachiropteran species (e.g., *Hypsignathus*) and all yangochiropteran bats. Emballonurids and yinochiropterans exhibit yet another derived condition, one in which the premaxilla articulates with the maxilla via ligaments that allow the premaxilla to be freely movable. The articulation between the maxilla and the premaxilla consists of a simple suture in both outgroups and most other mammals. In this context, the state seen in the Eocene fossil bats apparently represents the primitive condition.

Character 10: *Nasal branches of premaxillae well developed (0); or reduced or absent (1).* The nasal branches of the premaxillae are defined as those portions of the pre-

maxillae that lie on the face adjacent to the external narial opening. The nasal branches of the premaxillae are relatively well developed in *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*, as they are in most extant bats. In contrast, the nasal branches of the premaxillae in rhinolophoids are either entirely absent or are reduced to tiny splints of bone. The nasal branches of the premaxillae are well developed in both outgroups, suggesting that the state seen in the Eocene fossil bats is primitive.

Character 11: *Palatal branches of premaxillae well developed (0); or reduced or absent (1).* The palatal branches of the premaxillae are defined as those portions of the premaxillae that contribute to the anterior palate. The palatal branches of the premaxillae are relatively well developed in *Icaronycteris* and many extant bats (Nycteridae, Rhinolophidae, Phyllostomidae, Noctilionidae, Mormoopidae, Mystacinidae, Myzopodidae, Thyropteridae, Natalidae, some Molossinae). In contrast, the palatal branches of the premaxillae are either reduced to tiny splints of bone or are entirely absent in other extant lineages. This reduction is apparently a derived condition since well developed palatal branches are present in both outgroups and most other mammals.

The condition of the anterior palate in *Archaeonycteris* and *Palaeochiropteryx* could not be determined from available specimens. We found that the palatal branches of the premaxillaries are not visible in specimens prepared in dorsal view, and that the mandibular rami obscure the palate in all specimens prepared in ventral view. Accordingly, these forms are scored “?” for this character.

Smith and Storch (1981: 154, 164) noted that in *Hassianycteris* the “palatal branch [of the premaxilla] not well developed, premaxillaries not fused [at midline],” and that “the apparent shape and reduction of the premaxillary is quite reminiscent of the derived condition of this element in emballonurids.” However, the source(s) of these observations were not discussed, and we were unable to confirm them during our microscopic examination of specimens. Smith and Storch apparently described these features based on radiographs, although the published versions are too fuzzy to be of use. In both published

radiographs (Smith and Storch, 1981: figs. 1, 2), an image of the anterior dentition is superimposed on the anterior palate. Considering the complex nature of this region and the high density of the dental images, any observations of palatal morphology in these specimens must be viewed with caution. We considered scoring *Hassianycteris* as having a reduced palatal branch of the premaxilla based on the report by Smith and Storch (1981), but subsequently noted that reduction and lack of fusion of the palatal branches were omitted from Habersetzer and Storch’s (1987) diagnosis of *Hassianycteridae* (which contains only *Hassianycteris*). Given the prominence of these features in Smith and Storch’s original diagnosis of *Hassianycteris*, we can only conclude that there is considerable uncertainty about the structure of the premaxilla in these bats. Accordingly, we score *Hassianycteris* as “?” for this character.

Character 15: *Hard palate extends posteriorly into interorbital region (0); or terminates either at or anterior to level of zygomatic roots (1).* The hard palate, which forms a bony separation between the oral and nasal passages, terminates posteriorly at the mesopterygoid fossae. Position of the posterior edge of the hard palate varies independently of the posterior extent of the molar toothrow, and is apparently linked to the structure of the nasal passages and soft tissues of the pharyngeal region. The hard palate extends posteriorly into the interorbital region in *Archaeonycteris*, *Palaeochiropteryx*, one of the outgroups (Scandentia), and many extant bats (Pteropodidae, some Emballonuridae, some Hipposiderinae, some Phyllostomidae, Mormoopidae, Noctilionidae, Mystacinidae, Myzopodidae, Thyropteridae, some Furipteridae, Natalidae, Antrozoidae, Tomopeatinae, some Molossidae, and Vespertilionidae). In contrast, the hard palate terminates either at or anterior to the level of the zygomatic roots in the other outgroup (Dermoptera) and all remaining extant bats. Lack of agreement between the two outgroups precludes a priori determination of the primitive condition for this character. The position of the posterior end of the hard palate in *Icaronycteris* and *Hassianycteris* could not be determined due to the position of the

mandibular rami in all available specimens, so these forms are scored “?” for this character.

Character 16: *Two upper incisors in each side of jaw (0); or one incisor (1); or upper incisors absent (2).* Because of difficulties associated with determining homologies of the anterior dental loci among different bat lineages (reviewed by Slaughter, 1970), we chose to score the number of teeth in various dental regions (i.e., upper incisors, lower incisors, upper premolars, lower premolars) rather than attempting to score presence/absence of teeth at specific loci. Although some potentially informative patterns may be overlooked by this method, this approach preserves that homology information of which we are most confident and permits scoring of all taxa (including the outgroups) for each character.

The size of one or more teeth in a number of species has been reduced to the point where these teeth are considered vestigial (Slaughter, 1970). This is particularly common in the premolar dentition. In some instances there is within-species (and even within-individual) polymorphism with respect to presence/absence of vestigial teeth (e.g., the anterior upper premolar in *Rhinolophus clivosus*, the middle lower premolar in *Chrotopterus auritus*). In our experience, older individuals frequently lack such teeth, while they are often present in younger animals. This pattern suggests that vestigial teeth are often lost during the lifetime of the individual. Consequently, we have scored the taxa in question as having the higher dental formula in cases of within-species polymorphism in presence/absence of vestigial teeth.

Two upper incisors are present on each side of the jaw in *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. This is the same upper incisor formula as seen in many extant bats (some Pteropodidae, some Emballonuridae, Nycteridae, some Phyllostomidae, Mormoopidae, Noctilionidae, Nataloidea, some Vespertilioninae, Miniopterinae, Myotinae, Murininae, and Kerivoulinae). In contrast, only one incisor is present on each side of the upper jaw in some Pteropodidae, some Emballonuridae, Rhinopomatoidea, Rhinolophidae, some Phyllostomidae, Mystacinidae, Molossoidea, and some Vesperti-

lioninae. The upper incisors are entirely absent in some Pteropodidae and Megadermatidae. Both outgroups have two upper incisors on each side of the jaw. In this context, the state seen in *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* apparently represents the primitive condition. We were unable to unambiguously determine the number of upper incisors in *Icaronycteris*, so this taxon is scored “?” for this character.

Character 17: *Three lower incisors in each side of jaw (0); or two incisors (1); or one incisor (2); or incisors absent (3).* Three lower incisors are present on each side of the jaw in *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. This is the same lower incisor formula seen in many extant bats (some Emballonuridae, Nycteridae, Nataloidea, some Antrozoidae, some Molossinae, and Vespertilionidae). Two lower incisors are present on each side of the lower jaw in some Pteropodidae, some Emballonuridae, Rhinopomatoidea, Megadermatidae, Rhinolophidae, some Phyllostomidae, Mormoopidae, some Antrozoidae, Tomopeatinae, and some Molossinae. A single lower incisor is present on each side in some Pteropodidae, some Phyllostomidae, Noctilionidae, Mystacinidae, and some Molossinae. Finally, the lower incisors are entirely absent in some Pteropodidae and some Phyllostomidae. Both outgroups have three lower incisors on each side. In this context, the state seen in the Eocene bat genera apparently represents the primitive condition.

Character 18: *Three upper premolars in each side of jaw (0); or two premolars (1); or one premolar (2).* Three upper premolars are present on each side of the jaw in *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx magna*. *Hassianycteris messelensis* has only two upper premolars (fig. 24), apparently having lost the tiny peg-like anterior premolar seen in *H. magna*. Among extant bats, three upper premolars are present in some Pteropodidae, some Phyllostomidae, Myzopodidae, Thyropteridae, Natalidae, some Myotinae, and Kerivoulinae. In contrast, two upper premolars are present on each side of the jaw in some Pteropodidae, Emballonuridae, some Megadermatidae, Rhinolophinae, some Hipposiderinae, some Phyllostomidae, Mormoopidae,

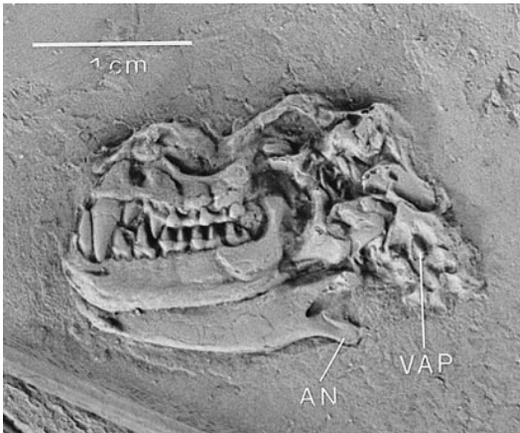


Fig. 24. *Hassianycteris messelensis* (SMF ME 1414a). Closeup lateral view of skull. Note the robust dentary and dentition, and the absence of the first upper premolar. A vestigial first upper premolar is present in *H. magna*. AN, angular process of dentary; VAP, ventral accessory process of vertebra (C3?). Scale bar = 10 mm. From Habersetzer and Storch (1987: fig. 5). Photo by E. Pantak (Senckenbergmuseum).

Mystacinidae, Furipteridae, some Molossinae, some Vespertilioninae, Miniopterinae, some Myotinae, and Murininae. A single upper premolar is present on each side in Rhinopomatoidea, Nycteridae, some Megadermatidae, some Hipposiderinae, some Phyllostomidae, Noctilionidae, Antrozoidae, Tomopeatinae, some Molossinae, and some Vespertilioninae. Among the outgroups, Scandentia has three upper premolars, while Dermoptera has two. Lack of agreement between the two outgroups precludes a priori determination of the primitive condition for this character.

Character 19: *Middle upper premolar with three roots (0); or with two roots (1); or with one root (2).* Among bats with three upper premolars, the middle premolar (usually designated P3) may have either one, two, or three roots. P3 has three roots in *Icaronycteris*. In contrast, this tooth has only two roots in *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. Among extant bats, P3 is triple-rooted only in Natalidae. P3 has two roots in Pteropodidae, some Phyllostomidae, Thyropteridae, and some Kerivoulinae. P3 is single-rooted in some Phyllostomidae, Myzopodidae, Myotinae, and some Kerivouli-

nae. Three roots are present on P3 in both outgroups, suggesting that the triple-rooted condition seen in *Icaronycteris* is primitive. The double-rooted condition seen in the other Eocene taxa is apparently derived. Because it is thought that P3 is often the first tooth lost from the premolar dentition in species with a reduced number of teeth (Slaughter, 1970), we scored this character only in forms that retain three upper premolars (state "0" of character 18 above). Accordingly, Emballonuridae, Yinochiroptera, Mormoopidae, Noctilionidae, Mystacinidae, Furipteridae, Molossoidea, Vespertilioninae, Miniopterinae, and Murininae are scored "-" for this character.

Character 20: *Three lower premolars in each side of jaw (0); or two premolars (1).* Three premolars are present on each side of the lower jaw in *Icaronycteris*, *Archaeonycteris*, *Hassianycteris* and *Palaeochiropteryx*. Among extant bats, three lower premolars are present in Rhinolophinae, some Phyllostomidae, Mormoopidae, Nataloidea, some Vespertilioninae, Miniopterinae, some Myotinae, and Kerivoulinae. Only two lower premolars are present in all other lineages. Among the outgroups, Scandentia has three lower premolars, while Dermoptera has two. Lack of agreement between the two outgroups precludes a priori determination of the primitive condition for this character.

Character 21: *Lower first and second molars with primitive tribosphenic arrangement of cusps and cristids (0); or nyctalodont (1); or myotodont (2); or teeth modified for fruit and/or nectar or blood feeding, cusps and cristids not distinct (3).* Menu and Sigé (1971) discussed molar morphology in bats, and distinguished two forms of the talonid of m1 and m2 that they termed "nyctalodonty" and "myotodonty." In both morphotypes, the hypoconulid lies adjacent to the entoconid on the lingual edge of the tooth, having shifted lingually from the midline position (where it is more or less equidistant from the labial and lingual borders of the tooth) characteristic of primitive therian tribosphenic molars. Nyctalodonty is defined by the position of the postcrisid, which connects the hypoconid with the hypoconulid in nyctalodont forms. Myotodonty is distinguished by an alternative arrangement in which the post-

crisid bypasses the hypoconulid to connect instead with the entoconid. The postcrisid is relatively high and forms a sharp shearing edge in both conditions, but no crisid runs between the entoconid and hypoconulid.

Although it is easy to classify molar morphology of most extant bats, Menu and Sigé (1971) noted that problems arise when Eocene bats are considered because the hypoconulid is located in the midline position in some taxa, always connected to the hypoconid and sometimes connected to the entoconid by low cristids. The posterior edge of the talonid is thus dominated by a large conical cusp (the hypoconulid) rather than by a shearing crest (the postcrisid). This morphology, termed "archaic" by Menu and Sigé (1971), appears in numerous Late Cretaceous and Paleocene mammals, including forms thought to represent the earliest members of several eutherian radiations (e.g., primates, insectivores; Menu and Sigé, 1971). This apparently represents the primitive tribosphenic condition.

Possible differences in function of the three talonid types discussed above have not yet been examined. Nyctalodont and myotodont teeth are at least superficially similar in terms of the length and height of the postcrisid, which may indicate an increased reliance on shearing as compared to the primitive tribosphenic condition. Increased shearing has been associated with specializations for feeding on hard-shelled beetles (Freeman, 1979) and on soft-bodied prey (Strait, 1993). Freeman (1979) found that molossid bats that feed on beetles have relatively larger teeth with longer shearing cusps than do molossids that feed on soft-bodied prey. Alternatively, Strait (1993) found that mammalian insectivores that feed predominantly on soft-bodied prey (e.g., moths and caterpillars) have relatively longer shearing crests (summed across the entire molar) than do close relatives that have more generalized feeding habits and consume large quantities of hard-bodied beetles. Whatever the relationship between shearing and prey type, these studies suggest that variation in talonid form may be indicative of differences in dietary habits. However, there does not seem to be any obvious correlation between feeding habits and talonid type in extant bats. For example,

rhinolophids that feed on soft-bodied prey (e.g., *Rhinolophus blasii*) and those that feed on hard-bodied prey (e.g., *Hipposideros commersoni*) both have nyctalodont teeth (Strait, 1993). It therefore seems premature to draw any functional conclusions from transformations in talonid structure in bats.

The first lower molars exhibit the primitive tribosphenic arrangement of the talonid cusps and cristids in *Archaeonycteris*. In contrast, the lower molars are nyctalodont in *Hassianycteris*. Both nyctalodont and myotodont conditions appear in *Palaeochiropteryx*, although never in the same individual. Both nyctalodont and myotodont specimens have been referred to *Palaeochiropteryx tupaiodon* (e.g., by Russel and Sigé, 1970), raising the possibility of within-species polymorphism. However, we are unaware of any cases of within-species polymorphism in this character in extant bats. This suggests that *P. tupaiodon* may be a composite species, a hypothesis that will require testing with additional data. Meanwhile, we score *Palaeochiropteryx* as exhibiting both nyctalodonty and myotodonty.

Van Valen (1979) claimed that the lower molars of *Icaronycteris* are nyctalodont, an observation that was subsequently cited by other authors (e.g., Gingerich, 1987). We disagree with Van Valen's assessment. Our observations indicate that *Icaronycteris index* had primitive tribosphenic lower molars. The European specimens referred to *?Icaronycteris* by Russell et al. (1973) include both nyctalodont and primitive tribosphenic morphotypes. However, this material consists of isolated teeth only, and we consider the affinities of these specimens to each other and to *Icaronycteris index* to be uncertain at best. Accordingly, we score *Icaronycteris* as exhibiting only the primitive tribosphenic condition.

Among the extant families, the primitive tribosphenic condition of the talonid is seen in fossil members of Hipposiderinae (i.e., *Palaeophyllophora*) and Megadermatidae (i.e., *Necromantis*; Beard et al., 1992). Nyctalodonty occurs in Emballonuridae, Rhinopomatoidea, Nycteridae, extant Megadermatidae, Rhinolophinae, extant Hipposiderinae, some Phyllostomidae, Mormoopidae, Furipteridae, Natalidae, some Molossinae, some

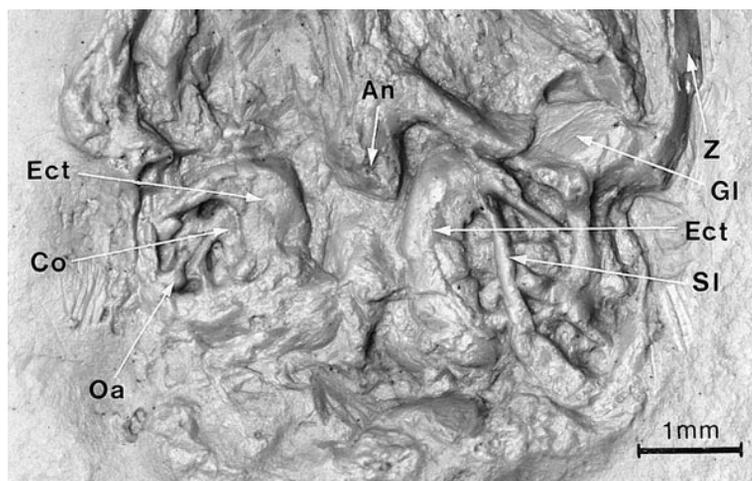


Fig. 25. *Icaronycteris index* (UW 2244). Ventral view of the basicranium and posterior lower jaws. From Novacek (1987: fig. 2). An, angular process of dentary; Co, cochlea; Ect, ectotympanic; Gl, glenoid fossa; Oa, orbicular apophysis; Sl, stylohyal; Z, zygomatic arch.

Vespertilioninae, Miniopterinae, some Myotinae, and Murininae. In contrast, myotodonty is found in some Phyllostomidae, Noctilionidae, Mystacinidae, Myzopodidae, Thyropteridae, Antrozoidae, Tomopeatinae, some Molossinae, some Vespertilioninae, some Myotinae, and Kerivoulinae. In Pteropodidae and some Phyllostomidae the teeth are modified for fruit and/or nectar or blood feeding and the cusps and cristids are not distinct. Among the outgroups, Scandentia exhibits the primitive tribosphenic condition, but we could not score Dermoptera owing to its unique dental morphology. Although polarity cannot be ascertained unambiguously, the data suggest that the primitive tribosphenic condition is primitive for bats.

Character 22: *Lower jaw with elongate angular process (0); or without elongate angular process (1).* The angular region of the lower jaw in mammals is the site of insertion of jaw adductor muscles including m. masseter pars superficialis, m. masseter pars profundus, m. zygomaticomandibularis, m. mandibuloauricularis, and m. pterygoideus internus (= medial pterygoid; Turnbull, 1970). In many “generalized” eutherian mammals and some specialized carnivores, a bony extension of the angle—termed the angular process—lies between the insertions of m. pterygoideus internus and m. masseter. These muscles insert both on the angular process

and on a common raphe dorsal, posterior, and ventral to the angular process (Turnbull, 1970). This pattern of muscle insertion is seen in bats that have an elongate angular process (Storch, 1968; Kallen and Gans, 1972). Both m. masseter and m. pterygoideus internus act to close and protrude the lower jaw. M. masseter also pulls the ipsilateral dentary (the dentary on the same side of the skull as the muscle) laterally, while m. pterygoideus internus pulls the ipsilateral dentary lingually (Storch, 1968; Kallen and Gans, 1972).

The lower jaw has an elongate angular process in *Icaronycteris* (figs. 25, 26), *Archaeonycteris*, *Hassianycteris* (fig. 24), and *Palaeochiropteryx* (fig. 27). This is similar to the condition seen in most bats. In contrast, the angular process is either very short (relative to its dorsoventral width) or is effectively absent in Pteropodidae, Craseonycteridae, and some Nycteridae. An elongate angular process is present in Scandentia but not in Dermoptera. Lack of agreement between the two outgroups precludes a priori determination of the primitive condition for this character. However, occurrence of an elongate angular process in many presumably primitive eutherians (e.g., leptictids, *Asioryctes*, lipotyphlans) suggests that presence of an elongate angular process may be primitive for Eutheria.

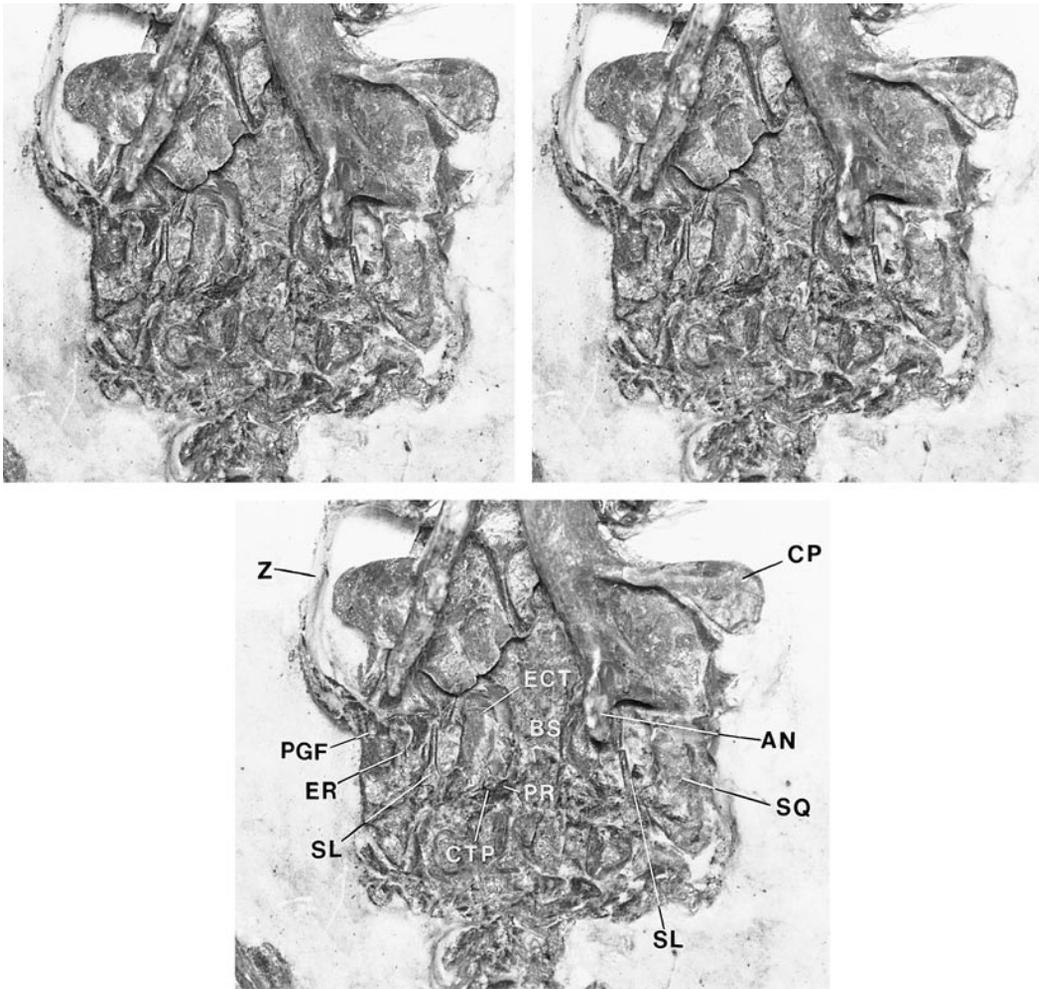


Fig. 26. *Icaronycteris index* (UW 21481a–b). Stereophotographs of a ventral view of the basicranial region (top) with labelled key photograph (bottom center). AN, angular process of dentary, BS, basisphenoid; CP, coronoid process of dentary; CTP, caudal process of tympanic; ER, epitympanic recess; PGF, postglenoid foramen; PR, periotic; SL, tylohyal; SQ, squamosal; Z, zygomatic arch. Photographs by C. Tarka.

Character 23: *Angular process projects at or below level of occlusal plane of toothrow, well below coronoid process (0); or angular process projects above level of occlusal plane of toothrow, at same level as the coronoid process (1).* The angular process, when present, extends from the posteroventral “corner” of the lower jaw. The angular process projects at or below the level of the occlusal plane of the toothrow (well below the coronoid process) in *Icaronycteris* (figs. 25, 26), *Archaeonycteris*, *Hassianycteris* (fig. 24), and *Palaeo-*

chiropteryx (fig. 27). This is similar to the condition seen in most extant bats and both outgroups. In contrast, the angular process projects above the level of the occlusal plane of the toothrow (roughly at the same level as the coronoid process) in Myzopodidae, Thyropteridae, and Furipteridae. In this context, the condition in the Eocene fossil bats appears to be primitive. This character cannot be evaluated in taxa that lack an angular process (e.g., taxa scored “1” for **22**); these forms are therefore scored “-” for this character).

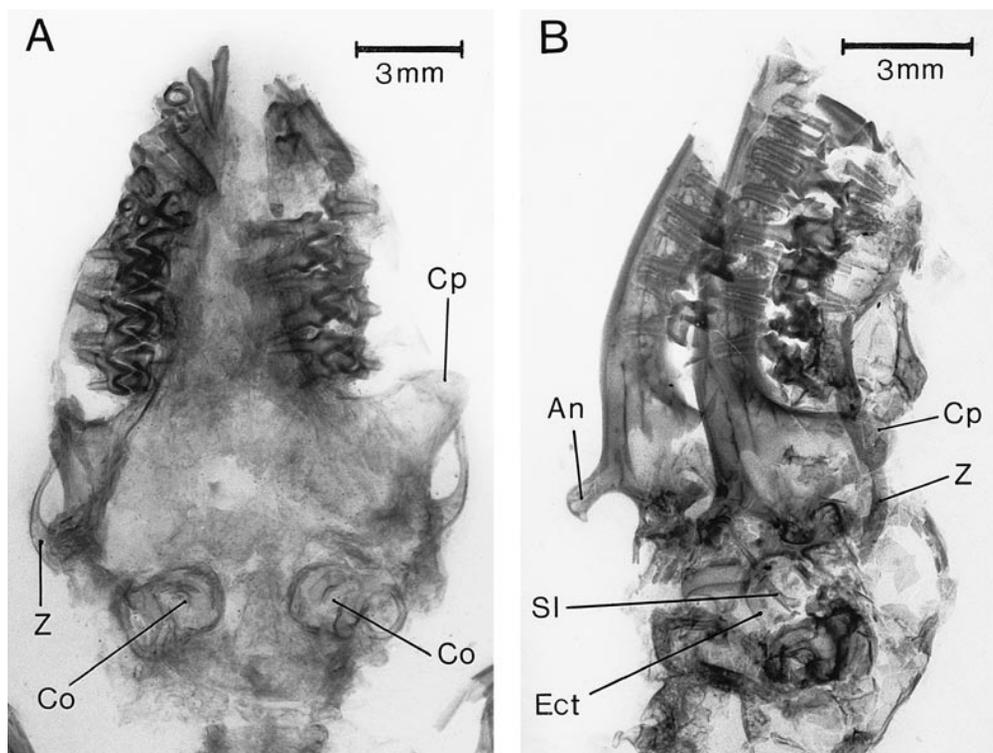


Fig. 27. *Palaeochiropteryx tupaiodon*, positive prints of radiographs; from Novacek (1987: fig. 4). **A.** Dorsoventral view of the skull of SMF ME 788b. **B.** Lateral view of SMF ME 1127. An, angular process of dentary; Co, cochlea; Cp, coronoid process of dentary; Ect, ectotympanic; Sl, stylohyal;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

Character 24: *Postorbital process present (0); or absent (1).* The postorbital process is a laterally projecting process of the frontal that forms part of the posterodorsal rim of the orbit. A postorbital process is present in *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. Among extant forms, a postorbital process is present only in Pteropodidae, Emballonuridae, Nycteridae, and Megadermatidae. All other extant bats lack a postorbital process. A postorbital process is present in both outgroups, suggesting that presence of this structure represents the primitive condition. We were not able to ascertain whether this process is present in *Icaronycteris*; this taxon is therefore scored “?” for this feature.

Character 25: *Pars cochlearis of petrosal sutured to basisphenoid (0); or loosely attached to basisphenoid via ligaments and/or thin splints of bone (1).* The petrosal of all

extant microchiropterans (with the exception of some Emballonuridae) is not fused with or sutured to the basisphenoid. Instead, the pars cochlearis is loosely attached to the basisphenoid via ligaments and/or thin splints of bone (fig. 28). This condition (sometimes referred to as “cochlear isolation”) is thought to function in reducing bone conduction of laryngeal vibrations (Henson, 1970; Van Valen, 1979). Although there is some variation in the degree of isolation of the cochlea as judged by the relative sizes of the openings that surround the periotic (the anterolateral pyriform fenestra, anteromedial to medial parts of the basicochlear fissure, and posteromedial jugular foramen; Novacek, 1991), this “loosely attached” condition clearly differs from the typical mammalian pattern in which the periotic is firmly sutured to the surrounding bones of the basicranium including the basisphenoid.

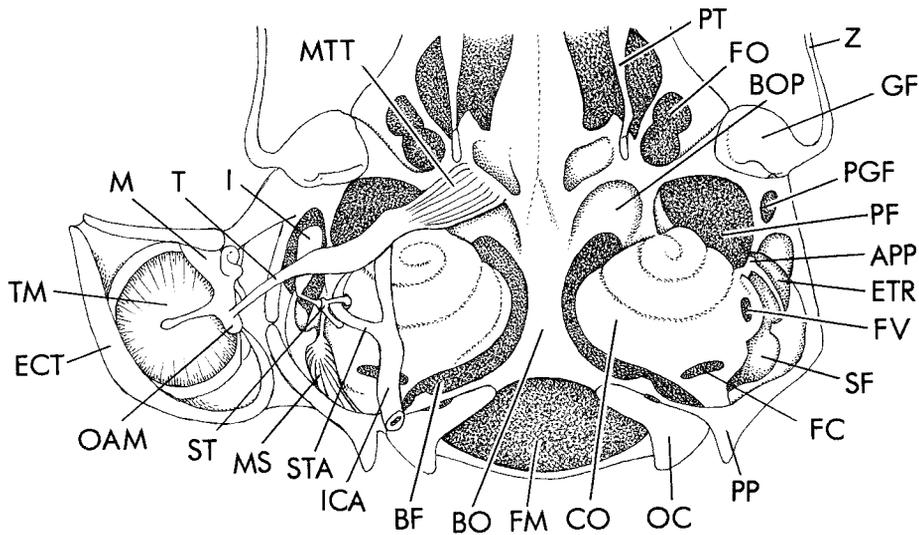


Fig. 28. *Nyctalus noctula* (Vespertilioninae; redrawn from Henson, 1970: fig. 9). Ventral view of the basicranium and auditory region showing major osteological features, blood vessels, and muscles. The ectotympanic and malleus have been reflected laterally on the right side of the skull. APP, anterior process of petrosal; 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.

Based on observed gaps and patterns of breakage in the basicranium of preserved specimens of *Archaeonycteris* and *Palaeochiropteryx*, it appears that the periotic was loosely attached to the basisphenoid (and the cochlea relatively isolated) in these taxa. In contrast, the periotic is sutured to the basisphenoid in Pteropodidae and some Emballonuridae. A similar condition is seen in both outgroups and most other mammals, suggesting that the “sutured” condition is primitive, and that the “loosely attached” condition seen in *Archaeonycteris* and *Palaeochiropteryx* is derived. We were unable to determine the type of periotic connection in *Icaronycteris* and *Hassianycteris*; these taxa are therefore scored “?” for this character.

Character 26: Cochlea not enlarged (0); or moderately enlarged (1); or greatly enlarged (2). Much has been written about cochlear size and echolocation in bats, with most authors agreeing that cochlear enlargement (specifically enlargement of the basal

turn) is a specialization for perceiving the echoes of high-frequency echolocation signals (Henson, 1970; Segall, 1971; Bruns et al., 1983–1984; Novacek, 1985a, 1987, 1991; Habersetzer and Storch, 1992). By plotting maximum external cochlear width against skull length, Novacek (1985a, 1987, 1991) found that extant Microchiroptera and Megachiroptera have nonoverlapping distributions, with microchiropterans having consistently larger cochleae. The megachiropteran condition (i.e., a relatively small cochlea) was interpreted as the primitive condition because it also occurs in many other small to medium-sized mammals (Novacek, 1985a, 1987, 1991).

Novacek (1985a, 1987, 1991) also estimated cochlear width and skull length of *Icaronycteris* and *Palaeochiropteryx*, and found that these fossil taxa fell within the range of variation observed in extant Microchiroptera. Because an enlarged cochlea is derived and is associated with use of sophisticated echo-

location,³ these observations led Novacek (1985a, 1987, 1991) to conclude that *Icaronycteris* and *Palaeochiropteryx* were echolocating bats closely related to extant Microchiroptera.

In another study of relative cochlear size in bats, Habersetzer and Storch (1992) suggested that Novacek's (1985a, 1987, 1991)

³ We recognize two categories of echolocation systems based on the information that is obtained from resulting echoes. We use the term "sophisticated echolocation" to describe systems that can be used for orientation in cluttered environments (e.g., within vegetation or under the forest canopy) and for detection, tracking, and evaluation of moving objects including prey. Calls associated with sophisticated echolocation are produced in the larynx and are often (but not always) highly structured in terms of call length, frequency, and type of modulation. Call structure, duration, and pulse interval may be intentionally varied by the animal depending on the circumstances (e.g., searching for prey, approaching prey, attacking prey), and call structure is often species specific. There is a strong correlation between call type and flight/foraging strategies, in part because the information content of returning echoes varies depending on call structure and pulse interval. However, all sophisticated echolocators apparently record and process information of several types, including relative timing of pulse and echo (including different arrival times at the right and left ears), differences in intensity between pulse and echo, and (in some cases) frequency shifts between pulse and echo. Sophisticated echolocation apparently provides the animal with a detailed acoustic map of its environment, a map that changes moment by moment depending on movement of both the echolocator and the objects in its environment. This form of echolocation occurs in all extant microchiropterans but not in megachiropterans.

In contrast, we use the term "primitive echolocation" to refer to less complex systems in which echoes of broadband clicks produced by the animal (by tongue-clicks, voice, or some other means) are used to obtain general information about the animals surroundings. Pulses of sound used in primitive echolocation systems are always broadband, low in intensity, short in duration, and never exhibit structured changes in frequency over time. The data used by the animal appears to consist only of differences in timing of pulse and returning echo. The information obtained using primitive echolocation is probably limited to detection of relatively large, stationary obstacles (e.g., cave walls); this form of echolocation is not useful for detecting and tracking prey or orientation in cluttered environments. See discussion under "Evolution of Echolocation and Foraging Strategies" for references and more information about the taxonomic distribution of different echolocation systems.

methods were biased by his use of skull length as a measure of body size, because skull length also reflects dietary habits and structure of the dentition. Habersetzer and Storch alleviated this problem by using basicranial width (measured between the outermost bony margins of the semicircular canals) as an indicator of size, and also adopted a more precise method of measuring cochlear width. Using radiographs, they measured cochlear width from the end of the first half turn of the cochlea to the end of the second half turn, thus guaranteeing homologous measurements that excluded the promontorium and vestibular system. Using these methods, Habersetzer and Storch obtained results different from those of Novacek (1985a, 1987, 1991). Rather than having completely nonoverlapping distributions, they found that Microchiroptera (represented by more than 200 species) and Megachiroptera (more than 70 species) exhibited a narrow zone of overlap in relative cochlear size (fig. 29). Some microchiropterans with unusually small cochleae for their body sizes (e.g., *Phyllostomus hastatus*, *Leptonycteris nivalis*, *Carollia perspicillata*, *Megaderma lyra*, *Megaderma spasma*) fell within or on the border of the smallest polygon containing nonecholocating megachiropterans (Habersetzer and Storch, 1992). The observed pattern of distribution (fig. 29) was interpreted as evidence that cochlear size in bats varies essentially continuously from Megachiroptera (with the smallest cochleae, lacking sophisticated echolocation) through Rhinolophidae (with the largest cochlea and highly sophisticated echolocation), with cochlear size mirroring the functional significance of the acoustic sense.

Habersetzer and Storch (1992) also measured cochlear and basicranial width in *Archaeonycteris trigonodon*, *A. pollex*, *Palaeochiropteryx tupaiodon*, *P. spiegelii*, *Hassianycteris messelensis*, and *H. revilliodi*, and compared the resulting measurements with data from extant forms. They found that both species of *Archaeonycteris* had a relatively small cochlea, falling in the zone of overlap between Megachiroptera and Microchiroptera, close to the point representing *Megaderma spasma*. In contrast, both species of *Palaeochiropteryx* and both species of *Hassi-*

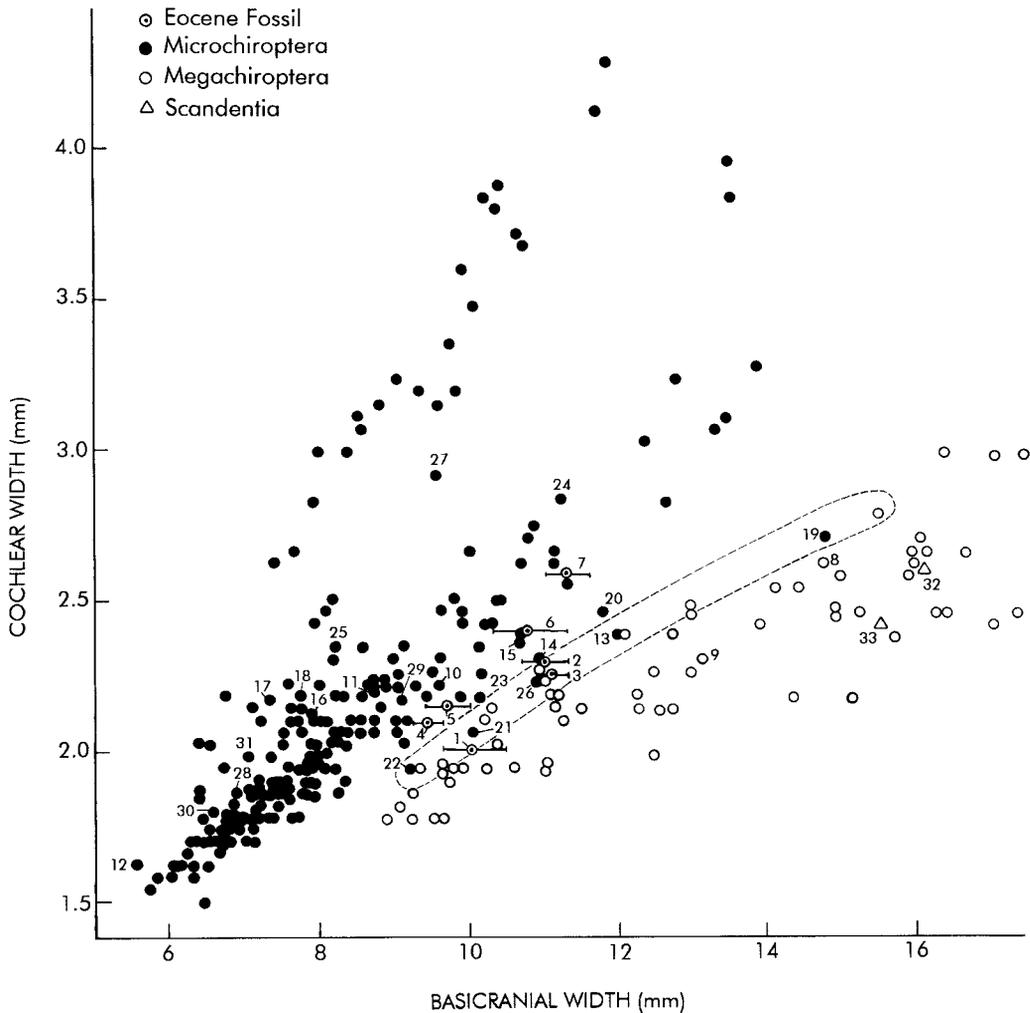


Fig. 29. Plot of the oblique diameter (width) of the cochlea versus basicranial width; see text for discussion. This graph was redrawn from Habersetzer and Storch (1992: fig. 4) and several new data points were added. The zone of overlap between Megachiroptera and Microchiroptera is enclosed with a dashed line. Numbered data points refer to the following taxa: 1, *Icaronycteris index*; 2, *Archaeonycteris trigonodon*; 3, *Archaeonycteris pollex*; 4, *Palaeochiropteryx tupaiodon*; 5, *Palaeochiropteryx spiegelii*; 6, *Hassianycteris revilliodi*; 7, *Hassianycteris messelensis*; 8, *Rousettus aegypticus*; 9, *Rousettus leschenaulti*; 10, *Rhinopoma microphyllum*; 11, *Rhinopoma hardwickei*; 12, *Craseonycteris thonglongyai*; 13, *Megaderma lyra*; 14, *Megaderma spasma*; 15, *Nycteris grandis*; 16, *Nycteris macrotis*; 17, *Nycteris thebaica*; 18, *Nycteris hispida*; 19, *Phyllostomus hastatus*; 20, *Trachops cirrhosus*; 21, *Leptonycteris nivalis*; 22, *Carollia perspicillata*; 23, *Desmodus rotundus*; 24, *Noctilio albiventris*; 25, *Mormoops megalophylla*; 26, *Mystacina robusta*; 27, *Myzopoda aurita*; 28, *Thyroptera tricolor*; 29, *Antrozous pallidus*; 30, *Tomopeas ravus*; 31, *Kerivoula pelucida*; 32, *Tupaia glis*; 33, *Tupaia javanica*. Values for *Cynocephalus variegatus* (not shown on graph): basicranial width = 28.1; cochlear width = 3.85.

anycteris had a relatively larger cochlea, falling slightly above the zone of overlap in the lower edge of the vespertilionid range.

In our attempts to score cochlear size as a phylogenetic character, we evaluated the studies of both Novacek (1985a, 1987, 1991) and Habersetzer and Storch (1992) and found evidence that led us to prefer the approach adopted by the latter authors. As previously noted, skull length (as used by Novacek) is correlated with diet and is not a good measure of body size. For example, long-nosed nectar-feeding phyllostomids such as *Leptonycteris* have skull lengths equivalent to those seen in bats more than twice their body mass. Basicranial width (as measured by Habersetzer and Storch, 1992) is much less subject to this bias. We also found Novacek's method of measuring cochlear size somewhat problematic. He measured the maximum width of the cochlea in a plane perpendicular to the long axis of the skull (Novacek, personal commun.). We examined many of the same specimens used by Novacek, and found that the region of maximum width of the cochlea varied in location depending on cochlear shape, orientation, size of the fenestra cochleae, and thickness of the bone forming the cochlear wall lateral to the fenestra cochleae. Accordingly, Novacek's measurements may not have been taken from homologous points in all taxa, and may have regularly overestimated size of the cochlea in taxa with a large fenestra cochleae with a thickened lateral wall. In contrast, Habersetzer and Storch's (1992) measure of cochlear width (taken across the second half of the basal turn of the cochlea) has several advantages, including (1) it is based on homologous points and is not affected by differences in size of the fenestra cochleae or thickness of the lateral wall of the cochlea in that region; and (2) it is biologically meaningful because it measures the width of the basal turn of the cochlea, which is the region where echolocation calls are perceived (Henson, 1970; Burns et al., 1983–1984; Habersetzer and Storch, 1992).

Using the figures reported by Habersetzer and Storch (1992) for several species (e.g., *Trachops cirrhosus*, *Megaderma spasma*), we found that we could reproduce their measurements quite closely using calipers ap-

plied to specimens from which the bullae and ear ossicles had been removed. This method allowed us to plot cochlea width/basicranial width for several taxa not mentioned in their study, including outgroup taxa (*Tupaia*, *Cynocephalus*) and several extant bats not explicitly mentioned by them (e.g., *Nycteris* [additional species], *Noctilio*, *Mystacina*, *Myzopoda*, *Thyroptera*, *Furipterus*, *Antrozous*, *Tomopeas*, *Kerivoula*).

We estimated cochlear width and basicranial width for *Icaronycteris* based on UW 2244 (fig. 25). Basicranial width was estimated by doubling the observed width of the left half of the basicranium, which is less distorted than the right side. To obtain cochlear width, we estimated the width of the basioccipital, width of both epitympanic recesses, and width of portions of the squamosal exposed lateral to the ear region. These measurements were summed and the total subtracted from basicranial width. The resulting value was divided by 2 to provide an estimate of width of the cochlea. This method assumes that the basicapsular fenestra, if present, was not of significant width.

To reflect the variation seen in cochlear size in bats (and the correlation between width of the basal turn of the cochlea and use of sophisticated echolocation), we adopted a tripartite scoring scheme for this feature based on figure 29. Three states are recognized: cochlea not enlarged, cochlea moderately enlarged, and cochlea greatly enlarged.

Taxa that fall below the zone of overlap between Megachiroptera and Microchiroptera (as plotted in fig. 29) were scored as having a cochlea that is not enlarged. This condition is seen in most Pteropodidae, and our estimates of values for Scandentia and Dermoptera (also Habersetzer and Storch's [1992] calculations for small primates, insectivores, and rodents) indicate that a relatively small cochlea is the primitive condition. None of the extant members of these groups use sophisticated echolocation comparable to that seen in extant microchiropterans (see discussion under "Evolution of Echolocation and Foraging Strategies" below).

Taxa were scored as having a moderately enlarged cochlea when they fell within the zone of overlap between Megachiroptera and Microchiroptera as outlined in figure 29. Two

fossil bats fall in this zone: *Icaronycteris* and *Archaeonycteris*. Among extant taxa, this condition is seen in some Pteropodidae, some Megadermatidae, some Phyllostomidae, and at least one member of Mystacinidae (*Mystacina robusta*, now extinct). Some of these forms (e.g., the megachiropterans) do not use echolocation, but others do (e.g., the microchiropterans). However, none of the latter are typical aerial insectivores. Instead, most apparently rely on passive acoustic cues and/or vision to detect large invertebrate or small vertebrate prey that is captured by gleaning or landing on the prey, or they feed on fruit or nectar detected by vision or olfaction (Norberg and Rayner, 1987; Habersetzer and Storch, 1992). *Mystacina tuberculata* apparently combines all of these foraging strategies with some aerial hawking for flying insects (Daniel, 1976, 1979, 1990; B. Lloyd and S. Parsons, personal commun.). However, nothing is known of the foraging behavior of *Mystacina robusta*, which was the only mystacinid available for our study.

Taxa were scored as having a greatly enlarged cochlea when they fell above the zone of overlap between Megachiroptera and Microchiroptera as plotted in figure 29. This condition is seen in two fossil taxa (*Hassianycteris* and *Palaeochiropteryx*) and in all extant microchiropteran groups except some Megadermatidae, some Nycteridae, some Phyllostomidae, and Mystacinidae. All extant forms with a greatly enlarged cochlea (as defined here) use sophisticated echolocation, and most are expert aerial hawkers (Norberg and Rayner, 1987; Habersetzer and Storch, 1992).

Character 27: *Cochlea cryptocochlear* (0); or *phanerocochlear* (1). Novacek (1985b, 1991) described variation in cochlear structure among bats and recognized two distinct patterns of petrosal ossification and adult cochlear morphology. The “phanerocochlear” state occurs when the petrosal wall is thin and poorly ossified, resulting in a condition where the cochlear labyrinth is clearly visible externally in the adult (Novacek, 1985b, 1991). In contrast, a “cryptocochlear” condition occurs when strong petrosal ossification produces a thicker encasement of bone around the cochlea, hiding the cochlear

labyrinth from external view in adults (Novacek, 1985b, 1991).

Novacek (1991) hypothesized that the differences between the cryptocochlear and phanerocochlear conditions resulted from differing rates of ossification of the cochlea, with phanerocochlear forms having a slower rate of bone deposition (paedomorphosis). An alternative explanation is that these different cochlear conditions may result from differential growth rates of the cochlear labyrinth (whose growth requires bone resorption from the inner side of the cochlear wall) and the outer wall of the periotic (whose growth requires bone deposition in the area of the promontorium). The cochlea of most embryonic mammals has a very thin, transparent promontorial wall (Novacek, 1991). In the cryptocochlear condition, growth of the cochlear labyrinth apparently does not keep pace with growth of the outer wall of the promontorium during ontogeny. Resorption on the inner surface does not compensate for deposition on the outer surface, and thus a thick cochlear wall forms as development progresses. This stands in contrast to the phanerocochlear condition, in which both processes (resorption and deposition) appear to keep pace throughout development, resulting in a thin, transparent promontorium that resembles that seen in the embryo. Although a reduction in rate of external bone deposition (paedomorphosis) is possible, it seems much more likely that an increase in growth rate of the cochlear labyrinth (peramorphosis) is responsible. This developmental hypothesis is supported by the observation that many cryptocochlear microchiropterans (e.g., Megadermatidae, Nycteridae, some Phyllostomidae) exhibit cochlear widths that fall in the zone of overlap with megachiropterans (i.e., a “moderately enlarged” cochlea), while most phanerocochlear microchiropterans have what we term a “greatly enlarged” cochlea (see character 26 above). However, some exceptions exist. For example, hipposiderines have a very large cochlea relative to most other microchiropterans (Habersetzer and Storch, 1992), but many have a cryptocochlear cochlea. Accordingly, we treat cochlear enlargement and form of the cochlear wall (cryptocochlear or phanerocochlear) as separate characters.

As judged from comparisons of radiographs of fossil and extant forms published by Habersetzer and Storch (1989, 1992) and Habersetzer et al. (1994), *Palaeochiropteryx* and *Hassianycteris* apparently exhibit the phanerochlear condition. This conclusion was supported by our microscopic examinations of several specimens (SMF Me 1205, Me 1494) in which the cochlear wall easily transmits light. Among extant bats, the phanerochlear condition occurs in Emballonuridae, Rhinopomatoidea, some Nycteridae, some Rhinolophinae, some Hipposiderinae, some Phyllostomidae, some Mormoopidae, Mystacinidae, Nataloidea, Antrozoidae, Tomopeatinae, some Molossinae, Vespertilioninae, Miniopterinae, Myotinae, and Muriniinae. In contrast, the cryptocochlear condition is seen in Pteropodidae, some Nycteridae, Megadermatidae, some Rhinolophinae, some Hipposiderinae, some Phyllostomidae, some Mormoopidae, Noctilionidae, some Molossidae, and Kerivoulinae. Both outgroups are also cryptocochlear, suggesting that this condition is primitive. Accordingly, the phanerochlear condition seen in *Palaeochiropteryx* and *Hassianycteris* is derived. We were unable to ascertain which condition is present in *Icaronycteris* and *Archaeonycteris*; these taxa are therefore scored “?” for this character.

Character 28: *Lateral process of ectotympanic weak or absent (0); or well developed, forms tubular external auditory meatus (1).* The ectotympanic in bats is a ring-shaped or horseshoe-shaped bone that supports the tympanic membrane (fig. 28). In most bats, the medial edge of the ectotympanic is expanded and encloses part of the middle ear, thus forming a partial bulla that encloses the primary tympanic cavity as defined by Klaauw (1931). In some bats, an additional lateral outgrowth of the ectotympanic forms the floor of a bony enclosure of what Klaauw (1931) termed the “recessus meatus acousti externi” (external auditory meatus). The lateral process of the ectotympanic is absent in *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. This is similar to the condition seen in most extant bats. In contrast, the lateral process of the tympanic is well developed and forms the floor of a tubular external auditory meatus in some

Pteropodidae, Nycteridae, Megadermatidae, and some Phyllostomidae. In both outgroups, the lateral process of the tympanic is poorly developed or absent. Accordingly, the condition seen in the Eocene fossil bats appears to be primitive.

Character 30: *Epitympanic recess shallow and broad (0); or deep, often constricted in area (1).* The epitympanic recess (= recessus epitympanicus, atticus tympanicus, or aditus ad antrum) is that part of the primary tympanic cavity that contains the middle ear ossicles (Klaauw, 1931). In bats, the epitympanic recess lies in the dorsolateral roof of the middle ear space, and it effectively houses only the incus and the joint between the incus and malleus (fig. 28). The stapes lies just medial to the recess in articulation with the fenestra ovalis of the periotic, and most of the malleus is located in a more ventrolateral position in the tympanic cavity.

The epitympanic recess is shallow and broad in *Icaronycteris* (fig. 26) and *Palaeochiropteryx*. Among extant bats, this condition is seen in Pteropodidae, Emballonuridae, Rhinopomatidae, Megadermatidae, Phyllostomidae, Myzopodidae, Nataloidea, Molossoidea, and Vespertilionidae. In contrast, the epitympanic recess is deep and often constricted in area in Craseonycteridae, Nycteridae, Rhinolophidae, Mormoopidae, Noctilionidae, and Mystacinidae. The epitympanic recess is shallow and broad in both outgroups, suggesting that the similar condition seen in *Icaronycteris* and *Palaeochiropteryx* is relatively primitive. We were not able to observe the epitympanic recess in *Archaeonycteris* and *Hassianycteris*; these taxa are therefore scored “?” for this character.

Character 31: *Fossa for m. stapedius indistinct (0); or shallow and broad (1); or deep, constricted in area, often a crescent-shaped fissure (2).* The fossa for the origin of m. stapedius is located in the posterior roof of the middle ear space (fig. 28). When well-defined, it occupies a cavity dorsal to the crista parotica. The fossa for m. stapedius is apparently deep and constricted in *Palaeochiropteryx*. Among extant bats, a similar condition is seen in Emballonuridae, Rhinopomatoidea, Phyllostomidae, Noctilionidae, Molossoidea, some Vespertilioninae, Miniopterinae, Muriniinae, and Kerivoulinae. In

these forms, the fossa for m. stapedius is often a deep, crescent-shaped fissure that lies lateral to the posterolateral surface of the cochlea. In contrast, the fossa for m. stapedius is comparatively shallow and broad in Megadermatidae, Myzopodidae, Thyropteridae, Furipteridae, some Vespertilioninae, and Myotinae. The fossa for m. stapedius is poorly developed (not distinguishable from the remainder of the roof of the middle ear) in Nycteridae, Rhinolophidae, Mormoopidae, Mystacinidae, and Natalidae. The fossa for m. stapedius is similarly indistinct in both outgroups, suggesting that the presence of a deep fossa in *Palaeochiropteryx* is a relatively derived condition. We were unable to determine the condition of the fossa for m. stapedius in *Icaronycteris*, *Archaeonycteris*, and *Hassianycteris*; these taxa are therefore scored “?” for this character.

Character 32: *Fenestra cochleae* small or of moderate size, maximum diameter <20% of the external width of the first half-turn of the cochlea (0); or enlarged, maximum diameter >25% of the external width of the first half turn of the cochlea (1). The fenestra cochleae (= fenestra rotundum) is a membrane-covered opening in the tympanic wall of the petrosal. It faces posteriorly or posterolaterally, and separates the scala tympani (at the base of the cochlear labyrinth) from the middle ear cavity (fig. 28). The fenestra cochleae appears relatively large in *Hassianycteris* and *Palaeochiropteryx*, where it has a maximum diameter >25% of the external width of the first half turn of the cochlea. Among extant bats, a similarly large fenestra cochleae is seen in Pteropodidae, Rhinopomatoidea, Noctilionoidea, and Mystacinidae. In contrast, the fenestra cochleae is of small or moderate size (<20% of the external width of the first half turn of the cochlea) in Emballonuridae, Rhinolophoidea, Nataloidea, Molossoidea, and Vespertilionidae. The fenestra cochleae is similarly small in both outgroups, suggesting that the relatively enlarged fenestra cochleae seen in *Hassianycteris* and *Palaeochiropteryx* is relatively derived. We were unable to determine the condition of the fenestra cochleae in *Icaronycteris* and *Archaeonycteris*; these taxa are therefore scored “?” for this character.

Character 35: *Orbicular apophysis* small

or absent (0); or large (1). The orbicular apophysis is a dense osseous protrusion that lies at the end of the body of the malleus, distal to the base of the manubrium of the malleus (fig. 28). The function of the orbicular apophysis remains uncertain, although several hypotheses have been proposed. The principal axis of rotation of the malleus runs through the long axis of the gonial process, perpendicular to the transverse body of the malleus (Fleisher, 1978, 1980; Wilson and Bruns, 1983). Fleischer (1978, 1980) suggested that the orbicular apophysis might function as the center for a second mode of vibration at high frequencies, in which the malleus vibrates around an axis running through the transverse body of the malleus, perpendicular to the gonial process. This hypothesis implies that complex motions of the malleus are possible, perhaps including flexion at the malleus-incus joint if the short process of the incus were constrained (Wilson and Bruns, 1983). However, Wilson and Bruns (1983) found no evidence of a change in the rotational axis with increasing frequency in their experimental study of middle-ear mechanics in *Rhinolophus*, suggesting that rotational movement of the malleus occurs only around the primary (gonial) axis of rotation or that rotation around both axes occurs at all frequencies.

A second hypothesis proposed by Fleischer (1978, 1980) is that presence of an orbicular apophysis serves to shift the center of mass of the malleus-incus complex away from the axis of rotation of the ossicle system, thus lowering its natural resonant frequency. Fleischer (1978: 34) suggested that presence of an orbicular apophysis, which is correlated with minute size of the ossicle chain and rigid fusion of the gonial process to the ectotympanic, may be necessary to tune the middle ear because “without the orbicular apophysis, the natural frequency of the malleus-incus complex might simply be too high, even for bats.” However, Wilson and Bruns (1983) argued that this explanation was unlikely since the extra mass would have been better employed for this purpose if it were applied to stiffening the manubrium of the malleus. They also noted that the resonating frequency of the membrane ossicle system was not sharply tuned to the CF fre-

quency used by the bat in their study, *Rhinolophus ferrumequinum*.

Wilson and Bruns (1983: 12) suggested alternative hypotheses for function of the orbicular apophysis in bats:

... the middle-ear may be acting as a transmission line with distributed mass and stiffness. In an ideal transmission line ... a signal is transmitted without loss even at high frequencies, but with a delay (phase shift proportional to frequency) depending on length ... Considering the dimensions involved, the major source of delay [of transmission of sound through the middle ear] would appear to be transverse motion of the manubrium ... On this hypothesis the orbicular apophysis might help to match transverse vibration along the manubrium into a torsional vibration along the transversal segment of the malleus. Alternatively, it might play a similar role to a telephone line loading coil which, contrary to intuition, improved high-frequency transmission.

In other words, the orbicular apophysis may improve the ability of the middle ear to transmit high-frequency sounds with a minimum time delay. Unfortunately, Wilson and Bruns (1983) did not explain how this "matching" of transverse to torsional vibrations occurs.

Another possible function for the orbicular apophysis may be in the system employed by echolocating bats to avoid self-deafening by "freezing" the middle-ear ossicle during the emission of echolocation calls (for descriptions of this mechanism, see Henson, 1964, 1965, 1966, 1967a, 1970; Jen and Suga, 1976; Fenton et al., 1995). One component of this system is *m. tensor tympani*, which inserts onto the transverse body of the malleus just proximal to the orbicular apophysis. In bats that use short FM (frequency modulated) calls for echolocation, contraction of *m. tensor tympani* begins 6–8 msec before the onset of vocalization, and relaxation occurs very rapidly, within 2–8 msec after vocalization (Jen and Suga, 1976). Possible roles that the orbicular apophysis may play in this system (e.g., in changing the speed with which the ear ossicles freeze and return to full sensitivity) have not been explored.

The orbicular apophysis is relatively large in *Icaronycteris* (fig. 25), *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. A similar condition is seen in all known extant Microchiroptera. In contrast, the orbicular apophysis is small or absent in Pteropodidae

and both outgroups. This suggests that the large orbicular apophysis seen in the Eocene bats is a derived condition.

Character 74: *Stylohyal occurs as gently curved bar with no enlargement or other modification to the lateral edge or cranial tip (0); or with cranial tip slightly expanded (1); or with bifurcated tip (2); or with large, flat expansion or "foot" on lateral cranial tip (3); or with very large, flat, axe-shaped enlargement at tip (4); or lateral half of entire stylohyal swollen (5).* The stylohyal is the distalmost element of the anterior cornu of the hyoid apparatus. It typically consists of an elongate bar that extends between the hyoid apparatus and the ear region of the skull. In *Icaronycteris* (figs. 25, 26), *Archaeonycteris*, and *Palaeochiropteryx* (fig. 27) the distal stylohyal (the end nearest the skull) has as a slightly expanded, paddle-shaped tip. Among extant bats, a similar condition is seen in some Emballonuridae, Craseonycteridae, and all Yangochiroptera with the exception of Myzopodidae. In contrast, the distal stylohyal has a bifurcated tip in some Emballonuridae and Rhinopomatidae. The stylohyal has a large, flat, lateral expansion or "foot" in Rhinolophoidea, and a very large, axe-shaped enlargement (which extends both laterally and medially) at its tip in Myzopodidae. Only three extant bat groups—Pteropodidae, Nycteridae, and Megadermatidae—lack any enlargement or modification of the distal tip of the stylohyal. In these forms, the stylohyal consists of a simple, curved bar. Among the outgroups, the stylohyal is a simple, curved bar in Scandentia, but Dermoptera has a unique stylohyal that is laterally swollen throughout much of its length. Although there is disagreement between the two outgroups used in the current study, comparisons with the stylohyal of other mammalian orders (Klaauw, 1931; Sprague, 1943) indicate that the primitive form of the stylohyal is a simple, curved bar. This suggests that the expanded distal tip seen in *Icaronycteris*, *Archaeonycteris*, and *Palaeochiropteryx* represents a derived condition. We were unable to determine the condition of the stylohyal in *Hassianycteris*, which is therefore scored "?" for this character.

ANTERIOR AXIAL SKELETON

Character 75: *Posteriorly directed ventral accessory processes not present on centra of cervical vertebrae 2 and 3 (0); or ventral accessory processes present on C2 and C3 (1).* Ventral accessory processes are paired projections from the posteroventral edges of the vertebral centra (fig. 24). These processes, which may be fused across the midline to form a single large projection, articulate with corresponding facets on successive vertebrae. Many mammals have ventral accessory processes on the axis (C2), but these processes rarely occur on other vertebrae except in bats. Presence of ventral accessory processes on multiple vertebrae apparently facilitates extensive dorsiflexion of the neck in many bats, allowing greater freedom of movement of the head while roosting (Crerar and Fenton, 1984).

Posteriorly directed ventral accessory processes are present on the centra of cervical vertebrae 2 and 3 in *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. Among extant bats, similar accessory processes are present on C3 in some Pteropodidae and all Microchiroptera. Accessory processes are absent from these vertebrae in some Pteropodidae and both outgroups. In this context, presence of accessory processes on C2 and C3 in the Eocene bats apparently represents a derived condition.

Character 76: *Posteriorly directed ventral accessory processes not present on centrum of cervical vertebra 4 (0); or ventral accessory processes present on C4 (1).* Posteriorly directed ventral accessory processes are absent on C4 in *Icaronycteris*, but are present on C4 in *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. Among extant bats, ventral accessory processes are present on C4 in all Microchiroptera, but are absent from this vertebra in Pteropodidae and both outgroups. In this context, absence of ventral accessory processes in *Icaronycteris* appears to represent the primitive condition, while presence of accessory processes on C4 in the other Eocene bats is a derived condition.

Character 77: *Posteriorly directed ventral accessory processes not present on centrum of cervical vertebra 5 (0); or ventral*

accessory processes present on C5 (1). Posteriorly directed ventral accessory processes are absent from C5 in *Icaronycteris*, *Archaeonycteris*, and *Hassianycteris*, but are present on C5 in *Palaeochiropteryx*. Among extant bats, ventral accessory processes are present on C5 in all Microchiroptera, but are absent from this vertebra in Pteropodidae and both outgroups. In this context, absence of ventral accessory processes (state "0") in *Icaronycteris*, *Archaeonycteris*, and *Hassianycteris* appears to represent the primitive condition, while presence of accessory processes on C5 in *Palaeochiropteryx* is a derived condition.

Character 78: *Seventh cervical vertebra not fused to first thoracic vertebra (0); or C7 and T1 at least partially fused (1).* There is no evidence of fusion between the seventh cervical and first thoracic vertebrae in *Icaronycteris*, *Archaeonycteris*, and *Palaeochiropteryx*. This condition is similar to that seen in extant Pteropodidae, Emballonuridae, Rhinopomatidae, some Nycteridae, Phyllostomidae, some Mormoopidae, Noctilionidae, Mystacinidae, Myzopodidae, Antrozoidae, and Vespertilionidae. In contrast, the centra, zygapophyses, and transverse processes of C7 and T1 are partially to fully fused in adult Craseonycteridae, some Nycteridae, Megadermatidae, Rhinolophidae, some Mormoopidae, Thyropteridae, Furipteridae, Natalidae, and Molossidae. Sutures may be visible between C7 and T1 in some young adults, but synovial joints are lacking. These vertebrae are not fused in either outgroup, nor are they fused in most other mammals. In this context, lack of C7–T1 fusion in the Eocene bats apparently represents the primitive condition. We were unable to determine the condition of C7 and T1 in *Hassianycteris*; this taxon is therefore scored "?" for this character.

Character 79: *First and second thoracic vertebrae not fused (0); or T1 and T2 fused (1).* There is no evidence of fusion between the first and second thoracic vertebrae in *Icaronycteris* and *Palaeochiropteryx*. This condition is similar to that seen in most extant bats. In contrast, the centra, zygapophyses, and transverse processes of T1 and T2 are fused in adult Hipposiderinae and Thyropteridae. Sutures may be visible between T1 and T2 in some young adults, but synovial

joints are lacking. T1 and T2 are not fused in either outgroup, nor are they fused in most other mammals. In this context, lack of T1–T2 fusion in *Icaronycteris* and *Palaeochiropteryx* apparently represents the primitive condition. We were unable to determine the condition of T1 and T2 in *Archaeonycteris* and *Hassianycteris*; these taxa are therefore scored “?” for this character.

Character 80: *Anterior ribs not fused to vertebrae (0); or first rib fused to vertebrae (1); or at least first five ribs fused to vertebrae (2).* The anterior ribs are not fused to vertebrae in *Icaronycteris*, *Hassianycteris*, and *Palaeochiropteryx*. Among extant bats, a similar condition is seen in Pteropodidae, Emballonuridae, Rhinopomatidae, Nycteridae, Megadermatidae, and Yangochiroptera. In contrast, the first rib is fused to the vertebral column in Craseonycteridae, and at least the first five ribs are fused to vertebrae in Rhinolophidae. No fusion is seen between ribs and vertebrae in the outgroups and most other mammalian groups. This suggests that the lack of fusion seen in the Eocene bats is primitive. We were unable to determine if rib fusion was present or absent in *Archaeonycteris*; this taxon is therefore scored “?” for this character.

Character 81: *Width of first rib similar to other ribs (0); or first rib at least twice the width of other ribs (1).* The width of the first rib is similar to that of the other ribs in *Icaronycteris* and *Palaeochiropteryx*. This condition is also seen in most extant bats. In contrast, the first rib is at least twice the width of the other ribs in Rhinolophoidea. The width of the first rib is similar to that of the other ribs in both outgroups and most other mammals, suggesting that this condition, which is seen in the Eocene bats, is primitive. We were unable to determine the width of the first rib in *Archaeonycteris* and *Hassianycteris*; these taxa are therefore scored “?” for this character.

Character 82: *First costal cartilage not ossified or fused with manubrium or first rib (0); or first costal cartilage ossified and fused to manubrium (where it appears to form a winglike lateral process of the manubrium) and fused to first rib (1).* The manubrium is the anteriormost element of the sternum. It lies at the junction of the proxi-

mal clavicles (with which it articulates anterolaterally), the costal cartilages of rib 1 (with which it articulates posterolaterally), and the mesosternum (with which it articulates posteriorly). The manubrium extends laterally only to the level of the clavicular joint in *Icaronycteris* (fig. 22), *Archaeonycteris* (fig. 3), *Hassianycteris*, and *Palaeochiropteryx*, and there is no evidence of fusion of the first costal cartilage to the manubrium or first rib. This is similar to the condition seen in most extant bats. In contrast, the manubrium has a winglike projection on each side that extends laterally well beyond the clavicular joint in Rhinopomatoidea, Megadermatidae, and Rhinolophidae. In these forms, this winglike lateral projection is fused directly to the first rib. It seems likely that these manubrial “wings” are formed by ossification and fusion of the first costal cartilage (which is typically broad and has a similar shape) with the body of the manubrium. Manubrial wings are lacking and the first rib is not fused to the manubrium or ribs in both outgroups and most mammals, suggesting that the condition seen in the Eocene bats is primitive.

Character 83: *Second costal cartilage articulates with sternum at manubrium–mesosternum joint (0); or second rib articulates with manubrium, no contact between rib (or costal cartilage) and mesosternum (1).* The second costal cartilage articulates with the sternum at the manubrium–mesosternum joint in *Icaronycteris* (figs. 21, 22), *Archaeonycteris* (fig. 3), *Hassianycteris*, and *Palaeochiropteryx*. This condition is similar to that seen in most extant bats. In contrast, in Rhinolophoidea the second rib articulates with the manubrium and there is no contact between rib (or costal cartilage) and mesosternum. The second costal cartilage articulates with the sternum at the manubrium–mesosternum joint in both outgroups. This suggests that the condition seen in the Eocene bats is relatively primitive.

Character 84: *Second rib articulates with sternum via costal cartilage (0); or second rib fused to sternum, costal cartilage absent or ossified (1).* The second rib articulates with the sternum via a costal cartilage in *Icaronycteris* (figs. 21, 22), *Archaeonycteris* (fig. 3), *Hassianycteris*, and *Palaeochiropteryx*.

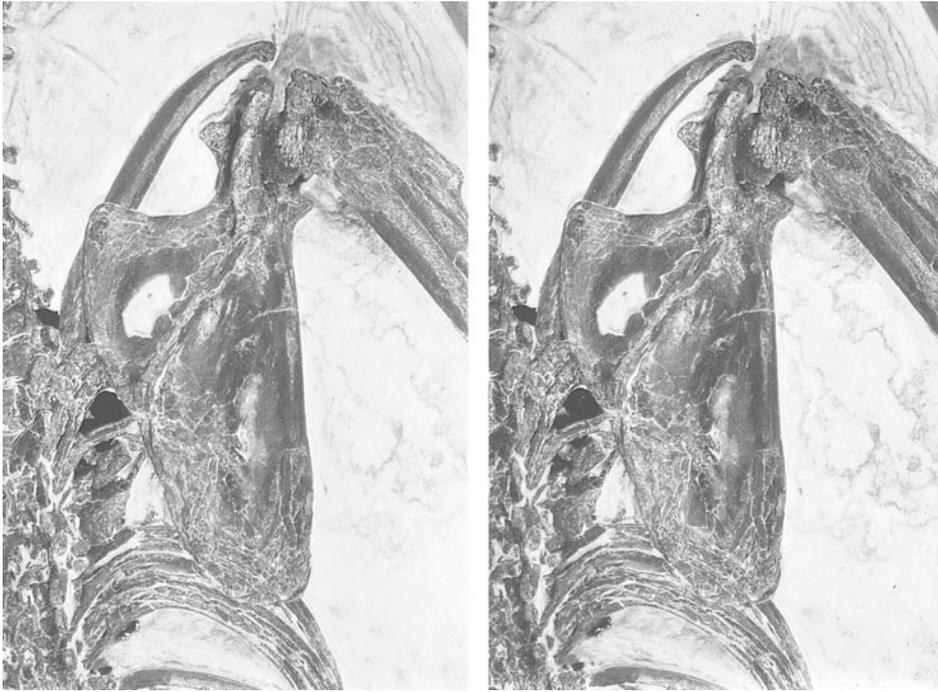


Fig. 30. *Icaronycteris index* (holotype; PU 18150). Stereophotographs of close-up dorsal view of the shoulder region. From Jepsen (1970: fig. 9); reprinted from original negatives.

teryx. This condition is similar to that seen in most extant bats. In contrast, in Rhinolophidae the second rib is fused to the sternum and the costal cartilage is absent or ossified. In these forms, an extensive sheet of thin bone runs between the second rib and the lateral process of the manubrium. The second rib articulates with the sternum via a costal cartilage in both outgroups and most other mammals, suggesting that the condition seen in the Eocene bats is relatively primitive.

Character 85: *Mesosternum articulates with at least five costal cartilages posterior to second rib (0); or articulates with four costal cartilages posterior to second rib (1); or articulates with only three costal cartilages posterior to second rib (2)*. The mesosternum articulates with at least five costal cartilages posterior to the second rib in *Icaronycteris* (figs. 21, 22), *Archaeonycteris* (fig. 3), *Hassianycteris*, and *Palaeochiropteryx*. Among extant lineages, a similar condition is seen in some Pteropodidae, some Phyllostomidae, Mormoopidae, Noctilionidae, Mystacinidae, Myzopodidae, Natalidae,

Molossidae, some Vespertilioninae, and some Myotinae. In contrast, the mesosternum articulates with only four costal cartilages posterior to the second rib in some Pteropodidae, Craseonycteridae, Rhinolophoidea, and some Phyllostomidae. This number is further reduced to three costal cartilages in some Vespertilioninae, Murininae, and Kerivouliinae. The mesosternum articulates with five or more costal cartilages in both outgroups, suggesting that the condition seen in the Eocene bats is relatively primitive.

Character 86: *Ribs with no anterior laminae (0); or anterior laminae present (1)*. Anterior laminae are thin plates of bone that run along the leading edges of ribs anterior to the main body of the rib in some bats. These structures, which are often nearly transparent, appear to provide an increased area for muscle attachment. Anterior laminae are absent in *Icaronycteris* (figs. 22, 30), but are present in *Palaeochiropteryx*. Among extant forms, anterior laminae are absent in some Emballonuridae, Rhinolophidae, some Phyllostomidae, Mystacinidae, Antrozoidae,

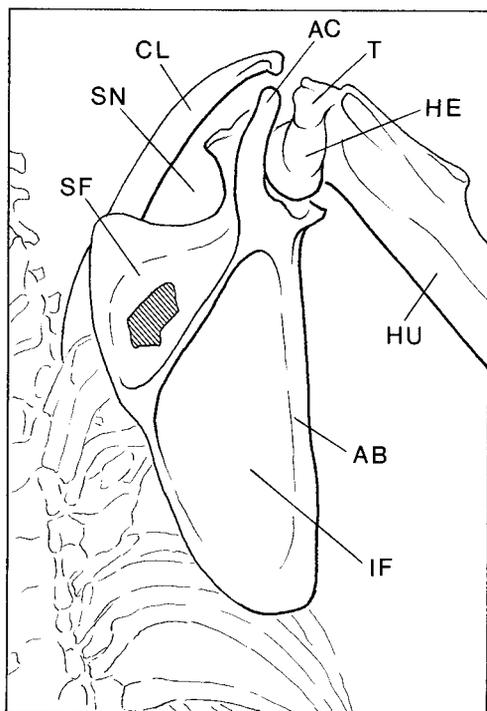


Fig. 30 (continued). Key to stereophotographs on preceding page. AB, axillary border of scapula; AC, acromion process of scapula; CL, clavicle; HE, head of humerus; HU, humerus; IF, infraspinous fossa of scapula; SF, supraspinous fossa of scapula; SN, suprascapular notch of scapula; T, trochiter.

Tomopeatinae, and some Molossinae. Anterior laminae are present in some Pteropodidae, some Emballonuridae, Rhinopomatoidea, Nycteridae, Megadermatidae, some Phyllostomidae, Mormoopidae, Noctilionidae, Nataloidea, some Molossinae, and Vespertilionidae. Both outgroups lack anterior laminae, suggesting that absence of anterior laminae in *Icaronycteris* is relatively primitive, while presence in *Palaeochiropteryx* is relatively derived. We were unable to adequately determine presence/absence of these structures in *Archaeonycteris* and *Hassianycteris*; these taxa are therefore scored “?” for this character.

Character 87: *Anterior laminae on ribs narrow, lamina width less than that of main body of rib (0); or anterior laminae wide, equal to or wider than main body of rib (1).* The anterior laminae on the ribs of bats may

be either relatively narrow (lamina width less than that of the main body of the rib) or wide (equal to or wider than the main body). The anterior laminae are narrow in *Palaeochiropteryx*. Among extant bats, narrow anterior laminae are found in Pteropodidae, Emballonuridae, Craseonycteridae, Phyllostomidae, Myzopodidae, Molossidae, Vespertilioninae, Myotinae, Murininae, and Kerivoulinae. Wide anterior laminae are seen in Rhinopomatidae, Nycteridae, Megadermatidae, Mormoopidae, Noctilionidae, Thyropteridae, Furpteridae, Natalidae, and Miniopterinae. This character cannot be evaluated for taxa that lack anterior laminae (state “0” of character 86 above); these forms (including *Icaronycteris*) are scored “-” for this character. Because both outgroups lack anterior laminae, the polarity of this character cannot be determined a priori. As noted above, we were unable to adequately determine presence/absence of anterior laminae in *Archaeonycteris* and *Hassianycteris*; these taxa are therefore scored “?” for this character.

Character 88: *Ribs with no posterior laminae (0); or posterior laminae present (1).* Posterior laminae are thin plates of bone that run along the trailing edges of ribs posterior to the main body of the rib. Like the anterior laminae, these structures may be nearly transparent, and they appear to provide an increased area for muscle attachment. Posterior laminae are present in *Icaronycteris* (figs. 22, 30), *Hassianycteris* (fig. 4), and *Palaeochiropteryx* (fig. 2), and they are also present in most extant bats. Posterior laminae are absent in Mystacinidae and some Molossinae. Posterior laminae are also absent in both outgroups, suggesting that their presence in *Icaronycteris* and *Palaeochiropteryx* is derived. We were unable to adequately determine presence/absence of these structures in *Archaeonycteris*; this taxon is therefore scored “?” for this character.

Character 89: *Posterior laminae on ribs narrow, lamina width less than that of main body of rib (0); or posterior laminae wide, equal to or wider than main body of rib (1).* Like the anterior laminae, posterior laminae may be either relatively narrow (lamina width less than that of the main body of the rib) or wide (equal to or wider than the main body). The posterior laminae are narrow in

Icaronycteris (figs. 22, 30) but are wide in *Hassianycteris* and *Palaeochiropteryx*. Among extant bats, narrow posterior laminae are found in Pteropodidae, some Emballonuridae, Craseonycteridae, Phyllostomidae, Noctilionidae, Natalidae, Molossoidea, and some Vespertilioninae. Wide posterior laminae are seen in some Emballonuridae, Rhinopomatidae, Rhinolophoidea, Mormoopidae, Myzopodidae, Thyropteridae, Furipteridae, some Vespertilioninae, Miniopterinae, Myotinae, Murininae, and Kerivoulinae. This character cannot be evaluated for taxa that lack posterior laminae (state "0" of character 88 above); these forms are scored "-" for this character. Because both outgroups lack posterior laminae, polarity of this character cannot be determined a priori. As noted above, we were unable to adequately determine presence/absence of anterior laminae in *Archaeonycteris* and *Hassianycteris*; these taxa are scored "?" for this character.

Character 90: *Anterior face of manubrium small (0); or broad, defined by elevated ridges (1)*. In addition to its role in connecting the body of the sternum to the clavicles and anterior ribs, the manubrium is also an important site of muscle origin for parts of the m. pectoralis complex, which provides the majority of the power for the downstroke of the wings (Vaughan, 1959, 1970b; Norberg, 1970; Strickler, 1978; Hermanson and Altenbach, 1983, 1985). The anterior face of the manubrium provides the point of origin for part of the anterior division of m. pectoralis, which rotates the humerus and helps to pull it downward and forward and during the downstroke when the wing is protracted against the force of the airstream (Vaughan, 1959, 1970b; Norberg, 1970; Strickler, 1978; Hermanson and Altenbach, 1983, 1985). The anterior face of the manubrium of the sternum is relatively small and poorly defined in *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. This condition is similar to that seen in most extant bats. In contrast, the anterior face of the manubrium is a broad, triangular surface that extends onto the lateral processes and is defined by three elevated ridges in some Pteropodidae, Megadermatidae, Rhinolophidae, some Phyllostomidae, Natalidae, and some Molossinae. Among the outgroups, the anterior face of

the manubrium is small in Scandentia but is broad and triangular in Dermoptera. Lack of agreement between the outgroups precludes a priori determination of the primitive condition for this character. We were unable to determine the form of the anterior face of the manubrium in *Icaronycteris*; this taxon is therefore scored "?" for this character.

Character 91: *Ventral process of manubrium absent (0); or ventral process present, distal tip blunt or rounded (1); or ventral process present, distal tip laterally compressed (2)*. The ventral process of the manubrium provides the anterior attachment point for a series of ligamentous sheets that run down the midline of the sternum (Vaughan, 1959, 1970b; Norberg, 1970, 1972a; Strickler, 1978; Hermanson and Altenbach, 1983, 1985). The ventral process, together with these ligamentous sheets, forms the origin for the m. pectoralis complex (Vaughan, 1959, 1970b; Norberg, 1970; Strickler, 1978; Hermanson and Altenbach, 1983, 1985). The distal tip of the ventral process of the manubrium is blunt and somewhat rounded in *Icaronycteris* (figs. 21, 22) and *Archaeonycteris* (fig. 3). The ventral process in these forms is triangular in cross section and points somewhat posteriorly. In contrast, the tip of the ventral process is laterally compressed (keel-like) in *Hassianycteris* and *Palaeochiropteryx*. In cross section, the ventral process in these forms is lens-shaped with the long axis running anteroposteriorly. Among extant bats, a ventral process with a blunt or rounded tip is found in Rhinopomatidae, Megadermatidae, Rhinolophinae, some Hipposiderinae, some Phyllostominae, Mystacinidae, Antrozoidae, Tomopeatinae, some Molossinae, and some Vespertilioninae. A laterally compressed ventral process is seen in Pteropodidae, Emballonuridae, Craseonycteridae, Nycteridae, some Hipposiderinae, some Phyllostominae, Mormoopidae, Noctilionidae, Nataloidea, some Molossinae, some Vespertilioninae, Miniopterinae, Myotinae, Murininae, and Kerivoulinae. Among the outgroups, a blunt ventral process occurs in Dermoptera, but the ventral process is absent in Scandentia. Although the outgroup evidence is ambiguous, this distribution suggests that a ventral process with a blunt, rounded tip (as in *Icaronycteris* and

Archaeonycteris) may be primitive, while the laterally compressed, keel-like condition seen in *Hassianycteris* and *Palaeochiropteryx* appears to be derived.

Character 92: *Angle between axis of ventral process and body of manubrium acute (0); or approximately 90° (1); or obtuse (2); or ventral process bilobed with one acute and one obtuse process (3).* The axis of the ventral process is defined as the long axis of the thickened base and central body of the process. The orientation of the axis of the ventral process (as seen in lateral view) varies among bats. In some taxa, the angle between the ventral process and the body of the manubrium is acute, and the ventral process appears to project posteroventrally. In other forms, the angle is approximately 90° (so that the ventral process projects ventrally) or obtuse (ventral processes projects anteroventrally). Although a full range of variation between these conditions is theoretically possible, we found that most species could be easily placed in one of the categories defined above. The only exceptions were a few taxa that have a bilobed ventral process with one acute and one obtuse lobe.

Our examinations of the Eocene fossils indicated that the ventral process is obtuse in *Icaronycteris* (figs. 21, 22) and *Palaeochiropteryx*, and is oriented at approximately 90° in *Archaeonycteris* (fig. 3). Among extant forms, an obtuse ventral process is seen in some Pteropodidae, some Emballonuridae, Noctilionidae, some Mormoopidae, some Mystacinidae, Myzopodidae, Molossoidea, and Vespertilioninae. The ventral process is oriented at approximately 90° in some Pteropodidae, some Emballonuridae, Rhinopomatoidea, some Phyllostomidae, some Mormoopidae, Thyropteridae, Myotinae, Murinae, and Kerivoulinae. An acute ventral process occurs in Megadermatidae, Rhinolophidae, some Phyllostomidae, and Natalidae. The ventral process is bilobed in Nycteridae, Furipteridae, and Miniopterinae. Among the outgroups, an obtuse ventral process occurs in Dermoptera. This feature cannot be evaluated in taxa that lack a ventral process on the manubrium (state "0" of character 91 above). Scandentia, whose members lack a ventral process, is therefore scored "-" for this character. Although the

outgroup evidence is ambiguous, presence of an obtuse ventral process in Dermoptera suggests that this condition, which is also seen in *Icaronycteris* and *Palaeochiropteryx*, may be primitive. The approximate 90° angle of the ventral process in *Archaeonycteris* would thus be interpreted as a derived condition. We were unable to determine the angle of the ventral process in *Hassianycteris*; this taxon is therefore scored "?" for this character.

Character 93: *Length of manubrium posterior to lateral processes >2.5 times transverse width (0); or length <2 times transverse width (1).* The length of the manubrium posterior to the lateral processes is less than twice the transverse width of this portion of the manubrium in *Icaronycteris* (figs. 21, 22), *Archaeonycteris* (fig. 3), *Hassianycteris*, and *Palaeochiropteryx*. This condition is similar to that seen in most extant bats. In contrast, the manubrium is relatively elongated (posterior portion >2.5 times transverse width) in Nycteridae, some Phyllostomidae, and Molossoidea. Both conditions occur among the outgroups—the manubrium is relatively short in Dermoptera but is elongate in Scandentia. Accordingly, the primitive condition of this feature cannot be determined a priori.

Character 94: *Mesososternum narrow, mean width less than half the distance between clavicles at sternoclavicular joint (0); or mesososternum broad, mean width greater than three-fourths the distance between clavicles (1).* The mesososternum (= body of sternum) articulates with the manubrium anteriorly and with the xiphisternum posteriorly. The relative width of the mesososternum in a bat can be estimated by comparing mean mesososternal width with the transverse distance between the right and left clavicles at their joints with the manubrium.⁴ The mesososternum is relatively narrow (mesososternal width less than half the interclavicular distance) in *Icaronycteris* (figs. 21, 22), *Archaeonycteris*,

⁴ Modifications of the manubrium and ribs in a number of taxa (e.g., rhinolophoids) preclude meaningful size comparisons of the mesososternum with these elements. Accordingly, we chose to compare width of the mesososternum with the interclavicular distance because our observations suggest that the distance between the clavicles is correlated principally with body size.

Hassianycteris, and *Palaeochiropteryx*. This is similar to the condition seen in Pteropodidae, Emballonuridae, Rhinopomatoidea, Megadermatidae, Rhinolophidae, Noctilionoidea, Mystacinidae, Myzopodidae, Molossoidea, and some Vespertilionidae. In contrast, the mesosternum is broad (width greater than three-fourths the interclavicular distance) in Nycteridae, Thyropteridae, Furipteridae, Natalidae, some Vespertilioninae, Miniopterinae, Myotinae, Murininae, and Kerivoulinae. The mesosternum is relatively narrow in both outgroups, suggesting that the narrow condition seen in the Eocene bats is relatively primitive.

Character 95: *Xiphisternum without keel (0); or with prominent median keel (1)*. The xiphisternum lacks a median longitudinal keel on its ventral surface in *Icaronycteris* (fig. 22), *Archaeonycteris*, and *Palaeochiropteryx*. This condition is seen among extant bats in Pteropodidae, Rhinopomatidae, Hipposiderinae, some Phyllostomidae, Noctilionidae, Myzopodidae, Molossoidea, and some Vespertilioninae. In contrast, a prominent, ventrally projecting median keel is present on the xiphisternum in Emballonuridae, Craseonycteridae, Nycteridae, Megadermatidae, Rhinolophidae, some Phyllostomidae, Mormoopidae, Mystacinidae, Thyropteridae, Furipteridae, Natalidae, some Vespertilioninae, Miniopterinae, Myotinae, Murininae, and Kerivoulinae. A xiphisternal keel is absent in both outgroups, suggesting that absence of a keel is relatively primitive. We were unable to determine if a xiphisternal keel is present in *Hassianycteris* due to distortion and flattening of the sternal region in all available specimens; this taxon is therefore scored “?” for this character.

Character 96: *Posterior xiphisternum with wide lateral flare (0); or not laterally flared (1)*. The posterior xiphisternum has a wide lateral flare in *Icaronycteris* (fig. 22), *Hassianycteris*, and *Palaeochiropteryx*. This flare is produced by a steady increase in width of the xiphisternum from the anterior to the posterior end of the element. In contrast, the xiphisternum is not flared (and width of the posterior end is approximately equal to the width of the anterior end) in *Archaeonycteris*. Among extant forms, a lateral flare is present in some Pteropodidae, some

Emballonuridae, Rhinopomatoidea, Nycteridae, Megadermatidae, Hipposiderinae, Noctilionoidea, Mystacinidae, Thyropteridae, Molossoidea, and Vespertilionidae. There is no lateral flare in some Pteropodidae, some Emballonuridae, Rhinolophinae, Myzopodidae, and Furipteridae. Both outgroups have a xiphisternum with a wide lateral flare. This pattern suggests that the flared morphology seen in *Icaronycteris*, *Hassianycteris*, and *Palaeochiropteryx* may be relatively primitive, while absence of a xiphisternal flare in *Archaeonycteris* may represent a relatively derived condition.

PECTORAL GIRDLE

Character 97: *Acromion process without medial shelf (0); or with shelf that projects medially over supraspinous fossa or medial base of acromion process (1)*. The distal half of the medial surface of the acromion process serves as the attachment point for one end of the transverse scapular ligament (= dorsal scapular ligament), which stretches between the acromion and the anteromedial rim of the scapula dorsal to m. supraspinatus (Vaughan, 1959, 1970b; Norberg, 1970; Strickler, 1978; Hermanson and Altenbach, 1983, 1985). In various bats the transverse scapular ligament provides an increased attachment area for m. supraspinatus (which elevates, extends, and rotates the humerus), m. acromiodeltoideus (which elevates the humerus), and m. spinodeltoideus (which elevates and flexes the humerus; Vaughan, 1959, 1970b; Norberg, 1970; Strickler, 1978; Hermanson and Altenbach, 1983, 1985). Presence of a medial shelf on the distal acromion is probably correlated with changes in the extent and orientation of the transverse scapular ligament and in the origins of those parts of m. supraspinatus and m. acromiodeltoideus that originate directly from the acromion process.

The acromion process of the scapula lacks a medial shelf in *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. This is similar to the condition seen in most extant bats. In contrast, the acromion process has a shelflike projection that extends medially over the supraspinous fossa or medial base of the acromion process in Thyropteridae, Furipteridae, Natalidae, some Vesperti-

lioninae, Miniopterinae, and Kerivoulinae. No medial shelf is seen in either outgroup, suggesting that absence of a medial shelf on the acromion process is the primitive condition.

Character 98: *Tip of acromion process without anterior projection (0); or with triangular anterior projection (1).* The tip of the acromion process lacks an anterior projection in *Icaronycteris*, *Hassianycteris*, and *Palaeochiropteryx*. The acromion similarly lacks such a projection in Pteropodidae, Emballonuridae, Yinochiroptera, Phyllostomidae, Natalidae, and Murininae. In contrast, a triangular anterior projection is present just ventral and medial to the tip of the acromion process in Mormoopidae, Noctilionidae, Mystacinidae, Myzopodidae, Thyropteridae, Furipteridae, Molossoidea, Vespertilioninae, Miniopterinae, Myotinae, and Kerivoulinae. This projection curves slightly ventrally in some taxa. No anterior projection is present on the acromion process in the outgroups; this suggests that absence of an anteroventral projection in the Eocene forms may be primitive. We were not able to determine if an anteroventral process is present in *Archaeonycteris*; this taxon is therefore scored “?” for this character.

Character 99: *Distal acromion process without posterolateral projection (0); or with triangular posterolateral projection (1).* The entire lateral surface of the acromion process serves as part of the origin of m. acromiodeltoideus, a muscle that elevates and rotates the humerus and provides important control during the upstroke of the wing (Vaughan, 1959, 1970b; Strickler, 1978). Presence of a posterolateral projection on the distal acromion may serve to increase the area of attachment for m. acromiodeltoideus, and may affect the moment arm for at least some of the fibers in this muscle.

The acromion process lacks a posterolateral projection in *Icaronycteris*, *Archaeonycteris*, *Palaeochiropteryx*, and some specimens of *Hassianycteris* (e.g., SMF Me 1500). This condition is similar to that seen in most extant bats. In contrast, a triangular posterolateral projection is present on the distal acromion process in extant Molossidae and some specimens of *Hassianycteris* (e.g., SMF Me 1540a). Both specimens of *Hassi-*

anycteris are similar in size; accordingly, this variation may represent either within-species polymorphism (within *H. messelensis*) or taxonomic polymorphism (it may differentiate *H. messelensis* from a previously unidentified specimen of *H. revilliodi*). We are unaware of any within-species polymorphism in this character in extant bat species, so we favor the latter interpretation.

No posterolateral projection is present on the acromion process in the outgroups, suggesting that absence of a posterolateral projection in the Eocene bats is primitive. Presence of a triangular posterolateral projection on the acromion in some *Hassianycteris* is apparently a derived condition.

Character 100: *Dorsal articular facet (for trochiter of humerus) absent from scapula (0); or present (1).* A secondary articulation between the humerus and scapula occurs in many bats when the humerus is abducted and an enlarged trochiter (= greater tuberosity) contacts a dorsal articular facet on the scapula. As discussed by Vaughan (1959, 1970b), Hill (1974), Strickler (1978), Hill and Smith (1984), Altenbach and Hermanson (1987), and Schlosser-Strum and Schleimann (1995), this secondary articulation forms a critical part of a “locking mechanism” in the shoulder. Functional explanations for the shoulder-locking mechanism are diverse and, in some cases, contradictory (see discussion in Schlosser-Strum and Schleimann, 1995). One possibility is that this mechanism functions in part to arrest the upstroke of the wing, thus facilitating long-range, fast flight (1) by providing a longer recovery period for critical flight muscles between wing beats, and (2) by reducing the amount of force that must be exerted by many of the same muscles (Vaughan, 1959, 1970b; Hill, 1974; Strickler, 1978; Hill and Smith, 1984). An alternative view based on new morphological and experimental evidence suggests that the secondary shoulder joint serves to increase the moment arm of m. pectoralis and reduce pronatory movements of the abducted forearm during the downstroke (Altenbach and Hermanson, 1987; Schlosser-Strum and Schliemann, 1995).

The dorsal articular facet is situated on the dorsal surface of the scapula immediately anteromedial to the glenoid fossa. *Icaronycteris*

lacks a dorsal articular facet. In contrast, a dorsal articular facet is present in *Hassianycteris* and *Palaeochiropteryx*. Most extant bats have a dorsal articular facet; exceptions include Pteropodidae, some Emballonuridae, Rhinopomatidae, and Noctilionidae. Both outgroups and most other mammals do not have a secondary articulation between the humerus and scapula, and therefore lack a dorsal articular facet on the scapula. This suggests that absence of a dorsal articular facet in *Icaronycteris* represents a relatively primitive condition. We were unable to determine if a dorsal articular facet occurs in *Archaeonycteris*; this taxon is therefore scored “?” for this character.

Character 101: *Dorsal articular facet faces dorsolaterally and consists of small groove on anteromedial rim of glenoid fossa (0); or faces dorsolaterally and consists of an oval facet on anteromedial rim of glenoid fossa (1); or faces dorsally and consists of a large, flat facet clearly separated from glenoid fossa (2).* In *Palaeochiropteryx*, the dorsal articular facet consists of a small, dorsolaterally facing groove on the anteromedial rim of the glenoid fossa of the scapula. In contrast, the dorsal articular facet consists of an oval, dorsolaterally facing facet on the anteromedial rim of the glenoid fossa in *Hassianycteris*. Among extant bats, the “small groove” condition is seen in Emballonuridae, Nycteridae, and some Hipposiderinae. An oval, dorsolaterally facing dorsal articular facet on the anteromedial rim of the glenoid fossa is found in Craseonycteridae, some Megadermatidae, some Phyllostomidae, Mormoopidae, Thyropteridae, Furipteridae, and Natalidae. In contrast, the dorsal articular facet is a large, flat facet that faces dorsally and is clearly separated from the glenoid fossa in some Megadermatidae, Rhinolophinae, some Hipposiderinae, some Phyllostomidae, Mystacinidae, Myzopodidae, Molossoidea, and Vespertilionidae. This character cannot be scored in taxa that lack a dorsal articular facet or those in which presence/absence of a dorsal articular facet has not been determined. Both outgroups, Pteropodidae, and *Icaronycteris* lack a dorsal articular facet; these taxa are scored “-” for this character. *Archaeonycteris* is scored “?” to reflect insufficient information for this taxon. This

character cannot be polarized a priori because both outgroups lack a dorsal articular facet.

Character 102: *Infraspinous fossa of scapula narrow, length ≥ 2 times width (0); or wide, length ≤ 1.5 times width (1).* The infraspinous fossa provides the site of origin for m. infraspinatus and m. teres major, muscles that act to flex, rotate, and (in the case of m. infraspinatus) abduct the humerus (Vaughan, 1959, 1970b; Norberg, 1970; Strickler, 1978; Hermanson and Altenbach, 1983, 1985). The width of the infraspinous fossa is measured from the junction of the scapular spine and the vertebral border of the scapula to the axillary border in a line perpendicular to the long axis of the fossa (which is defined by the line of maximum length). The infraspinous fossa is narrow (length greater than or equal to twice the width) in *Icaronycteris* (figs. 22, 30), *Archaeonycteris*, and *Hassianycteris*. In contrast, the infraspinous fossa is relatively wide (length ≤ 1.5 times width) in *Palaeochiropteryx* (fig. 2). Among extant forms, a narrow infraspinous fossa is seen in Pteropodidae, Rhinopomatoidea, Rhinolophoidea, some Mormoopidae, Myzopodidae, Thyropteridae, some Molossinae, and Murininae. A wide infraspinous fossa occurs in Phyllostomidae, Noctilionidae, some Mormoopidae, Mystacinidae, Furipteridae, Natalidae, Antrozoidae, Tomopeatinae, some Molossinae, Vespertilioninae, Miniopterinae, Myotinae, and Kerivoulinae. The infraspinous fossa in both outgroups is narrow, suggesting that a narrow fossa is relatively primitive and that the wide infraspinous fossa in *Palaeochiropteryx* represents a derived condition.

Character 103: *Infraspinous fossa with one facet (0); or two facets (2); or three facets (2).* Faceting of the infraspinous fossa, which effectively serves to increase the surface area without increasing the outline dimensions of the fossa, is thought to function to increase the area of origin for m. infraspinatus and m. subscapularis (Vaughan, 1959; see discussion of m. subscapularis function below under character 106). Faceting may also reflect compartmentalization or subdivision of fibers of these muscles into units with distinct functions, although this has yet to be investigated.

The infraspinous fossa has two facets in *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. The smaller of these (the medial facet) lies posterior to the scapular spine and faces posterolaterally; the larger lateral facet, which is convex, lies more posteriolaterally and faces dorsally. Among extant bats, two facets are found in some Pteropodidae, Rhinopomatoidea, Nycteridae, some Phyllostomidae, Mystacinidae, Furipteridae, Natalidae, Antrozoidae, Tomopeatinae, some Vespertilioninae, and Myotinae. In contrast, the infraspinous fossa has three facets in some Pteropodidae, Emballonuridae, Megadermatidae, Rhinolophidae, some Phyllostomidae, Mormoopidae, Noctilionidae, Myzopodidae, Thyropteridae, Molossinae, some Vespertilioninae, Myotinae, Murininae, and Kerivoulinae. In these forms, the facet just posterior to the scapular spine is called the posteromedial facet; this appears to be homologous to the medial facet found in the same position in bats that have only two facets. The larger lateral facet is further subdivided into an intermediate facet and a posterolateral facet. The posterolateral facet lies along the lateral edge of the scapula and faces posterolaterally; the intermediate facet lies between the posteromedial and posterolateral facets and faces anteromedially. The infraspinous fossa is not subdivided in the outgroups. In these forms, there is only a single, large convex facet in the infraspinous fossa. Accordingly, it is not possible to determine a priori the primitive condition for bats (two facets or three facets).

Character 105: *Lateral or posterolateral facet of infraspinous fossa restricted, does not extend into infraglenoid region anteriorly or wrap around intermediate facet at posterior (caudal) angle of scapula (0); or posterolateral facet more extensive, extends into infraglenoid region and wraps around caudal end of intermediate facet (1).* In *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*, the extent of the lateral facet of the infraspinous fossa is relatively restricted; this facet does not extend into the infraglenoid region or wrap around the medial facet at the posterior (caudal) angle of the scapula. A similar condition is seen in most extant bats regardless of the number of facets in the infraspinous fossa. In contrast,

the posterolateral facet is more extensive in Megadermatidae and Rhinolophidae. In these forms (which have three facets), the posterolateral facet extends into the infraglenoid region anterolaterally, and it wraps around the caudal end of the intermediate fossa posteriorly. This character cannot be evaluated in taxa that have only one infraspinous facet, which precludes useful scoring of this character in the outgroups; these taxa are scored “-” for this feature. Accordingly, the primitive condition for bats cannot be reconstructed a priori.

Character 106: *Thick lip present along axillary border of scapula (0); or thick lip with bladelike lateral edge present (1); or thick lip absent, axillary border flat or slightly upturned (2).* The axillary border of the scapula provides part of the site of origin of *m. subscapularis*, which adducts and extends the humerus (although a more important function may be to stabilize and provide fine control of the wing), and *m. teres minor*, which is a weak flexor of the humerus (Vaughan, 1959, 1970b; Norberg, 1970; Strickler, 1978; Hermanson and Altenbach, 1983, 1985). Morphology of the edge of the scapula along its axillary (lateral/posterolateral) border varies among bats. A thick lip is present along the axillary border of the scapula in *Icaronycteris* (fig. 30), *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. The bone itself is fairly thin; the appearance of a thickened lip is produced by an abrupt fold near the axillary border. This condition is similar to that seen among extant Pteropodidae, some Emballonuridae, Mystacinidae, Thyropteridae, Molossoidea, Vespertilioninae, Miniopterinae, Myotinae, and Kerivoulinae. In contrast, the axillary border of the scapula is characterized by a thick lip with a bladelike lateral edge in some Emballonuridae, Noctilionoidea, and Myzopodidae. No thickening is seen along the axillary border in the remaining lineages of bats; instead, the edge of the scapula is flat or slightly upturned, and the abrupt fold is absent. Both outgroups exhibit a simple, thick lip (state “0”) on the axillary border, suggesting that this is the primitive condition.

Character 107: *Pit for attachment of clavicular ligament absent from scapula (0); or present anterior and medial to glenoid fossa*

(1). The clavicular ligament extends between the base of the coracoid process and the clavicle. There is no evidence of a pit for attachment of the clavicular ligament on the scapula in *Icaronycteris* and *Hassianycteris*, and the same is true in most extant bat lineages. In contrast, a distinct pit for the clavicular ligament is present anterior and medial to the glenoid fossa in some Emballonuridae, Rhinolophoidea, some Phyllostomidae, and Mormoopidae. When a dorsal articular facet is present, the pit for the clavicular ligament is located medial to this structure. The pit for the clavicular ligament is absent in both outgroups, suggesting that absence of this structure represents the primitive condition. We were unable to determine if a pit for the clavicular ligament is present in *Archaeonycteris* and *Palaeochiropteryx*; these taxa are therefore scored “?” for this character.

Character 108: *Anteromedial edge of scapula without projections or flanges (0); or with triangular anteromedial flange (1)*. The anteromedial flange is a roughly triangular flange that projects ventrally from the anteromedial edge of the scapula (medial to the suprascapular notch) in some bats (Vaughan, 1959, 1970a; Norberg, 1970; Strickler, 1978; Hermanson and Altenbach, 1983, 1985). The dorsal aspect of the scapular edge in this region serves as the origin of the transverse scapular ligament, while part of the origins of *m. subscapularis* and the anterior division of *m. serratus anterior* occupy its ventral surface (Vaughan, 1959, 1970b; Norberg, 1970; Strickler, 1978; Hermanson and Altenbach, 1983, 1985). Projections from the border of the scapula in this region apparently simultaneously serve to provide an increased area of attachment for the transverse scapular ligament and an increased area for muscle origins. Presence of a large, triangular anteromedial flange is correlated with relatively large size of *m. subscapularis* (Vaughan, 1959), which is one of the principal adductors and extensors of the humerus. *M. subscapularis* plays an important role in the downstroke during flight and also helps to support the weight of the anterior part of the body in terrestrial locomotion (Vaughan, 1959, 1970b; Strickler, 1978).

The anteromedial rim of the scapula lacks projections or flanges in *Icaronycteris*, *Ar-*

chaeonycteris, and *Hassianycteris*. In contrast, a triangular anteromedial flange is present on the medial superior (anterior) border of the scapula in *Palaeochiropteryx*. Among extant bats, the anteromedial flange is absent in Pteropodidae, Emballonuridae, Rhinolophoidea, Yinochiroptera, Noctilionoidea, Mystacinidae, Myzopodidae, Thyropteridae, and Furipteridae. A large, triangular anteromedial flange is present in Myzopodidae, Natalidae, Molossoidea, and Vespertilionoidea. Absence of this flange in both outgroups (and most other mammals) indicates that absence of this structure is the primitive condition.

Character 109: *Coracoid process stout and of moderate length (0); or very long and thin (1)*. The coracoid process of the scapula is the site of origin of the coracoid head (= short head) of *m. biceps brachii*. *M. biceps brachii* is a two-part muscle that flexes and rotates the forearm, adducts the wing, and helps to hold the forearm rigidly outstretched against the opposing action of *m. triceps* during much of the downstroke (Vaughan, 1959, 1970b; Norberg, 1970; Strickler, 1978; Hermanson and Altenbach, 1983, 1985). Length of the coracoid process plays a role in function of *m. biceps brachii* because a long coracoid process enables the coracoid head of the biceps to act as an adductor of the wing by placing its origin below the line of the long axis of the humerus; the greater the displacement from this axis, the greater the mechanical advantage of the biceps as an adductor (Vaughan, 1959, 1966).

The coracoid process of the scapula is stout (wider than the clavicle) and of moderate length in *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. This condition is similar to that seen in most extant bats. In contrast, the coracoid is very long and thin (distal half not as wide as clavicle) in Furipteridae, Natalidae, Tomopeatinae, and some Molossinae. Both outgroups exhibit the “short and stout” morphology, suggesting that this is the primitive condition for the coracoid process.

Character 110: *Coracoid process curves ventrolaterally (0); or curves ventrally (1); or curves ventromedially (2)*. The direction of curvature of the coracoid process varies considerably among bats (fig. 31). Orienta-

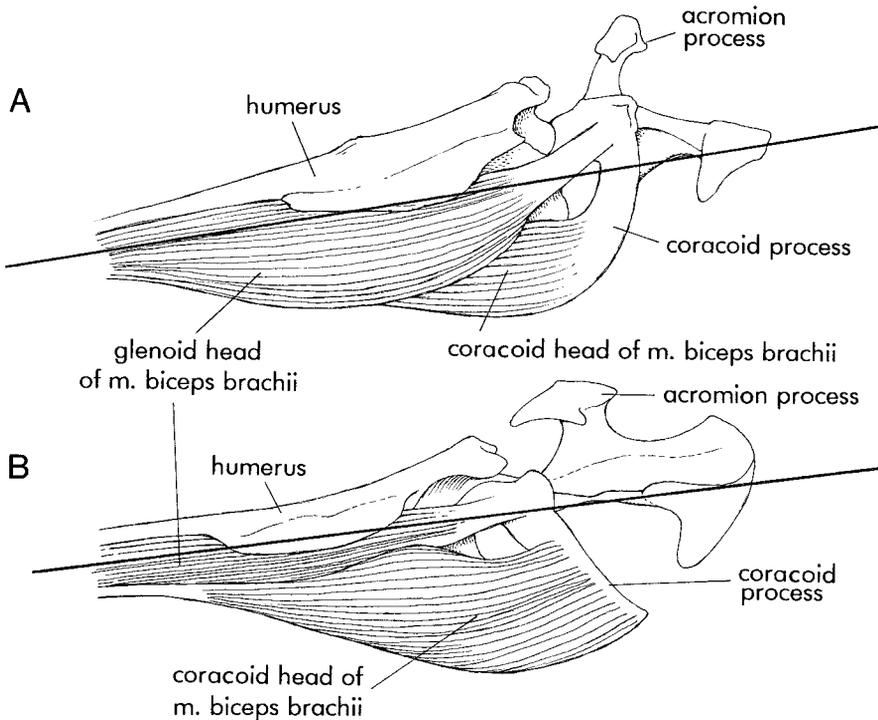


Fig. 31. Anterior view of the shoulder girdle showing the curvature of the coracoid process of the scapula, and the relative sizes of the coracoid and glenoid heads of *m. biceps brachii* (redrawn from Vaughan, 1970b: fig. 10). **A.** *Antrozous pallidus* (Antrozoidae). **B.** *Eumops perotis* (Molossidae).

tion of the coracoid process affects the function of *m. biceps brachii*, whose coracoid head originates from this process. Ventrolateral curvature of the coracoid places the coracoid head of *m. biceps brachii* well lateral to the long axis of the humerus throughout the first half of the downstroke, providing mechanical advantage that facilitates brachial adduction (Vaughan, 1959, 1966). The greatest mechanical advantage of *m. biceps brachii* as a brachial adductor occurs when the humerus reaches a horizontal position (fig. 31A), because the origin of the coracoid head of *m. biceps brachii* is at its maximum displacement from the long axis of the humeral shaft (Vaughan, 1959, 1966). Efficiency of the biceps is reduced when the wing is depressed because the long axis of the humeral shaft approaches the coracoid process, thus reducing the distance between origin and insertion of the coracoid head (Vaughan, 1959, 1966).

In contrast, ventromedial curvature of the

coracoid process takes the origin of *m. biceps brachii* out of the way of the lesser tuberosity of the humerus, allowing more space for the origin and a large belly for the muscle (fig. 31B; Vaughan, 1959, 1966). The site of origin is only slightly offset from the long axis of the humeral shaft at the top of the upstroke, which means that the biceps is probably not an effective adductor at the top of the upstroke (Vaughan, 1959, 1966). However, the angle between the origin of the coracoid head and its insertion decreases continuously through the downstroke, increasing the relative offset of the coracoid process from the axis of the humeral shaft and thus increasing mechanical advantage. Efficiency of *m. biceps* as an adductor thus increases continuously throughout the downstroke and peak efficiency is probably reached at the bottom of the downstroke (Vaughan, 1959, 1966).

The coracoid process curves ventrolaterally in *Icaronycteris*, *Archaeonycteris*, *Has-*

sianycteris, and *Palaeochiropteryx*. This condition is similar to that seen in most extant bats. In contrast, the coracoid process curves ventrally (i.e., remains with in a plane perpendicular to that of the blade of the scapula) in Furipteridae, Natalidae, some Vespertilioninae, and Myotinae. The coracoid process curves ventromedially in Molossidae, some Vespertilionidae, and Miniopterinae. The coracoid process curves ventrolaterally in both outgroups, suggesting that the condition seen in the Eocene bats is primitive.

Character 111: *Tip of coracoid process not flared, approximately same width as coracoid shaft (0); or tip distinctly flared (1); or bifurcated (2).* The tip of the coracoid process of the scapula is blunt and approximately the same width as the shaft of the coracoid in *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, *Palaeochiropteryx*, and most extant bats. There is no evidence of a flare or bifurcation in the tip in these forms. In contrast, the tip of the coracoid process is distinctly flared (wider than the shaft) in some Emballonuridae, Phyllostomidae, Mormoopidae, Thyropteridae, Molossinae, some Vespertilioninae, and Miniopterinae. A bifurcated coracoid tip occurs in some Vespertilioninae. The tip of the coracoid process is not flared or bifurcated in the outgroups, suggesting that the condition seen in the Eocene bats is primitive. The tip of the coracoid process was broken on all skeletons of *Mystacina* available to us; *Mystacinidae* is accordingly scored “?” for this character.

Character 112: *Suprascapular process present (0); or absent (1).* The suprascapular process is a projection that extends medially and somewhat anteriorly from the anterolateral border of the scapular notch at the base of the coracoid process, just medial to the anterior edge of the glenoid fossa and just anterior to the pit for the clavicular ligament (in those forms that have this pit; see character 107 above). This process may result from ossification of part of an apparently unnamed ligament⁵ that extends between this region and the anteromedial rim of the scap-

ula, cranial to the transverse scapular ligament. In some bats (e.g., *Noctilio*), this ligament provides part of the origin for m. acromiodeltoideus (Strickler, 1978).

The suprascapular process is absent in *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. Among extant bats, the suprascapular process is similarly absent in some Pteropodidae, some Emballonuridae, Nycteridae, Megadermatidae, Rhinolophinae, some Phyllostomidae, Myzopodidae, Natalidae, Tomopeatinae, Murininae, and Kerivoulineae. In contrast, a suprascapular process is present in some Pteropodidae, some Emballonuridae, Hipposiderinae, some Phyllostomidae, Noctilionidae, Mormoopidae, Mystacinidae, Thyropteridae, Furipteridae, Antrozoidae, Molossinae, Vespertilioninae, Miniopterinae, and Myotinae. The suprascapular process is present in both outgroups, suggesting that absence of this process in the Eocene bats represents a derived condition.

Character 113: *Clavicle articulates with or lies in contact with acromion process (0); or is suspended by ligaments between acromion and coracoid processes (1); or articulates with or lies in contact with coracoid process (2).* The distal (dorsolateral) clavicle articulates with the scapula in the region between the tip of the acromion process and the base of the coracoid process. The articulation can be accomplished in several different ways, depending on whether the clavicle is associated principally with the acromion, principally with the coracoid, or is suspended between the two. Strickler (1978) indicated that differences in the claviculoscapular articulation appear to have surprisingly little effect on the mobility of the scapula with respect to rotary movements about its longitudinal axis (i.e., the axis that runs roughly from the glenoid fossa to the posteromedial corner of the scapula), but he noted that control of scapular movements about other axes has yet to be studied. Hermanson (1981) studied clavicular function in *Antrozous* and found that clavicular movements (adduction and abduction relative to the sagittal plane) were synchronous with the wingbeat cycle. He suggested that movements of the distal end of the clavicle (which describes an arcuate path in the transverse plane) permit the scapula to be abducted and adducted across

⁵ This ligament might be considered a subdivision of the transverse scapular ligament; previous descriptions of the ligaments in this area (e.g., by Vaughan, 1959; Strickler, 1978) are not clear.

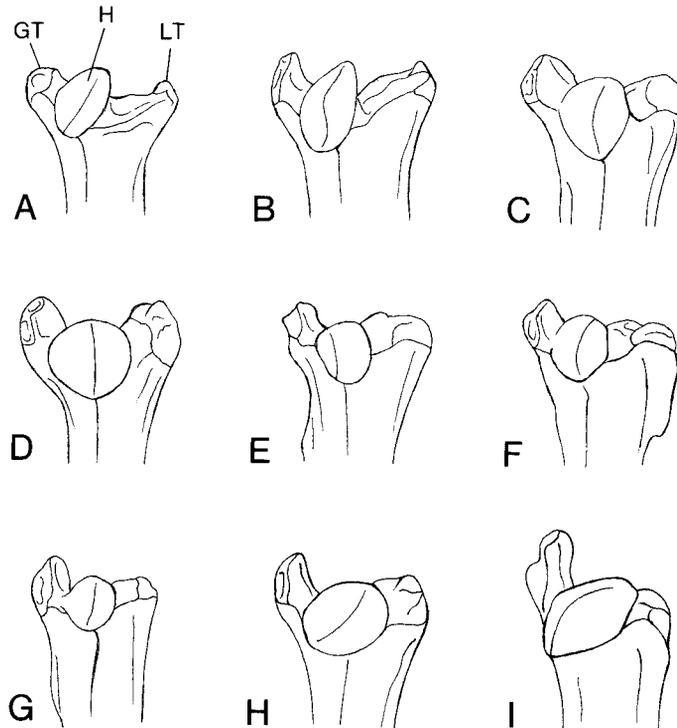


Fig. 32. Medial view of the proximal end of the left humerus in selected taxa; redrawn from Smith (1972: fig. 6). **A**, *Balantiopteryx plicata* (Emballonuridae); **B**, *Noctilio albiventris* (Noctilionidae); **C**, *Micronycteris sylvestris* (Phyllostomidae); **D**, *Desmodus rotundus* (Phyllostomidae); **E**, *Thyroptera tricolor* (Thyropteridae); **F**, *Natalus stamineus* (Natalidae); **G**, *Furipterus horrens* (Furipteridae); **H**, *Myotis grisescens* (Myotinae); **I**, *Molossus molossus* (Molossinae). GT, greater tuberosity = trochiter; H, head of humerus; LT, lesser tuberosity.

the dorsal contour of the thorax. However, this study did not address possible differences in function of the claviculoscapular joint associated with different morphologies.

Assuming little postmortem change in its position in available specimens, our observations suggest that the clavicle articulated with the acromion process of the scapula in *Icaronycteris* (figs. 22, 30). Among extant bats, a similar condition (clavicle articulates with or lies in contact with the acromion process) is seen only in Pteropodidae and Rhinopomatidae. The clavicle is suspended by ligaments (including the clavicular ligament discussed under character 107) that extend between the acromion and coracoid process in Noctilionidae, Mystacinidae, Nataloidea, Molossoidea, and Vespertilionidae. The clavicle articulates with or lies in contact with the coracoid process in Emballonuridae, Cra-

seonycteridae, Rhinolophoidea, Phyllostomidae, and Mormoopidae. The clavicle articulates with the acromion process of the scapula in both outgroups, suggesting that the condition seen in *Icaronycteris* is relatively primitive. We were unable to determine the mode of articulation of the clavicle with the scapula in *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*; these forms are therefore scored “?” for this character.

FORELIMB

Character 139: *Trochiter* does not extend to level of proximal edge of head of humerus (0); or extends just to level of proximal edge of head (1); or extends proximally well beyond level of head (2). The trochiter (= greater tuberosity) of the humerus in bats extends varying distances proximally relative

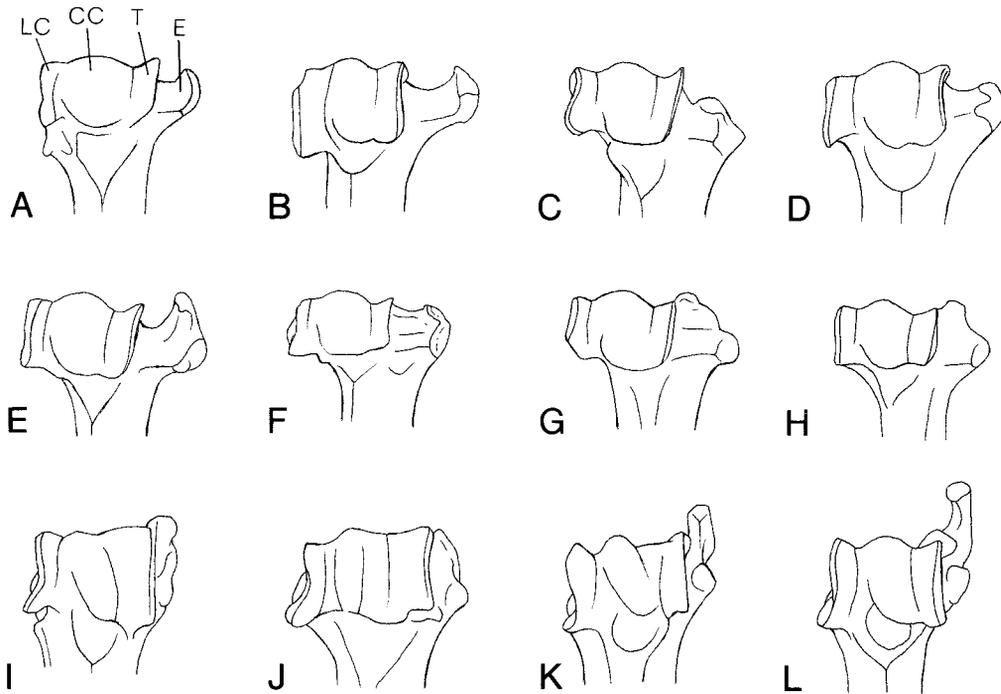


Fig. 33. Anterior view of the distal end of the left humerus in selected taxa; redrawn from Smith (1972: fig. 6). **A**, *Balantiopteryx plicata* (Emballonuridae); **B**, *Noctilio albiventris* (Noctilionidae); **C**, *Micronycteris sylvestris* (Phyllostomidae); **D**, *Desmodus rotundus* (Phyllostomidae); **E**, *Pteronotus parnellii*; **F**, *Thyroptera tricolor* (Thyropteridae); **G**, *Natalus stamineus* (Natalidae); **H**, *Furipterus horrens* (Furipteridae); **I**, *Lasiurus borealis* (Vespertilioninae); **J**, *Myotis grisescens* (Myotinae); **K**, *Tadarida brasiliensis* (Molossinae); **L**, *Molossus molossus* (Molossinae). CC, central surface of capitulum; E, epitrochlea; LC, lateral surface of capitulum; T, trochlea.

to the humeral head (fig. 32). As discussed under 98 above, the importance of the degree of proximal extension of the trochiter is related to the tendency of this structure to form a secondary articulation with the scapula during abduction of the humerus, thus facilitating a humeral locking mechanism. The distribution of trochiter morphologies is not correlated with the distribution of dorsal articular facet morphologies (see character 100); accordingly, we treat them as independent characters.

The trochiter extends proximally just to the level of the proximal edge of the head of the humerus in *Icaronycteris* (figs. 22, 30), *Archaeonycteris* (fig. 3), and *Palaechiropteryx* (fig. 2). In contrast, the trochiter extends well beyond the level of the proximal edge of the humeral head in *Hassianycteris* (fig. 4). Among extant bats, the trochiter extends just to the level of the proximal edge

of the head of the humerus in Emballonuridae, Rhinopomatidae, Nycteridae, Megadermatidae, and Noctilionidae. The trochiter extends well beyond the head of the humerus in Craseonycteridae, Rhinolophidae, and all Yangochiroptera with the exception of Noctilionidae. In contrast, the trochiter does not extend to the level of the humeral head in Pteropodidae and both outgroups. This suggests that both conditions seen among the Eocene bats are derived.

Character 140: *Head of humerus round in outline in medial view (0); or oval or elliptical (1).* The head of the humerus is round in outline when seen in medial view⁶ in *Ica-*

⁶ Determination of anatomical directions for bat limb elements is complicated by the unusual orientation of the limbs during flight. In specifying "medial view" in this character, we have followed Smith (1972) and assumed that the wing is folded and the humerus adducted.

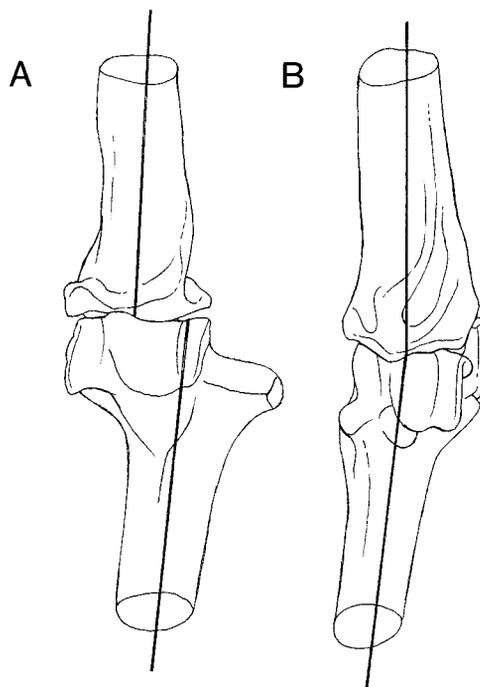


Fig. 34. Anterior view of the elbow region in **A**, *Artibeus toltecus* (Phyllostomidae) and **B**, *Molossus molossus* (Molossidae; redrawn from Smith, 1972). Note that the lateral offset of the distal articular facets in **A** places the long axes of the humerus and radius in separate but roughly parallel planes, whereas these axes lie in approximately the same plane in **B**.

ronycteris, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. A similar condition is seen in extant Pteropodidae, Rhinopomatoidea, Nycteridae, Phyllostomidae, Mystacinidae, Nataloidea, Antrozoidae, Vespertilioninae, Myotinae, Murininae, and Kerivoulineae (fig. 32). In contrast, the head of the humerus is oval or elliptical in outline in Emballonuridae, Megadermatidae, Rhinolophidae, Noctilionidae, Mormoopidae, Molossidae, and Miniopterinae. The head of the humerus is round in both outgroups, suggesting that this is the primitive condition.

Character 141: *Humerus with distal articular surfaces displaced laterally from line of shaft (0); or facets in line with shaft, not displaced laterally (1)*. Following the nomenclature used by Smith (1972) for describing humeral morphology in bats, the distal articular surfaces of the humerus include the trochlea, capitulum, and the lateral surface of capitulum (= lateral epicondyle of Hill, 1974). These articular surfaces lie adjacent to one another and are distinguished on the

basis of a series of ridges and grooves (fig. 33). The combined articular surfaces typically form a spool-shaped structure, although morphology of this structure varies considerably both among and within families of bats depending upon the relative proportions of the three component articular surfaces (Miller, 1907; Smith, 1972).

The structural unit formed by the three distal articular surfaces is laterally displaced from the line of the humeral shaft in *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. A similar arrangement is seen among extant Pteropodidae, Yinchiroptera, Phyllostomidae, some Mormoopidae, Noctilionidae, Nataloidea, Myotinae, Murininae, and Kerivoulineae (fig. 33). In each of these forms, the capitulum lies either completely or mostly lateral to the lateral edge of the humeral shaft, and the medial edge of the trochlea lies well lateral to the medial edge of the humeral shaft. This arrangement shifts the elbow joint laterally so that the long axes of the humerus and radius

move in separate but parallel planes when the joint is flexed (fig. 34A; Smith, 1972). In contrast, the distal articular surfaces of the humerus lie in line with shaft in Emballonuridae, some Mormoopidae, Mystacinidae, Molossoidea, Vespertilioninae, Miniopterinae, and Myotinae (fig. 33). The capitulum occupies variable positions in these forms, but often lies mostly or entirely medial to the lateral edge of the shaft. The medial edge of the trochlea always lies at or medial to the medial edge of the humeral shaft. As a result, the long axes of the humerus and radius lie in roughly the same plane (fig. 34B; Smith, 1972). The distal articular surfaces are displaced from the line of the shaft of the humerus in both outgroups, suggesting that the condition seen in the Eocene bats is primitive.

Character 142: *Epitrochlea broad (0); or relatively narrow (1)*. The epitrochlea (= medial process, medial epicondyle) comprises the medial portion of the distal end of the humerus adjacent to the articular facets (fig. 33). The epitrochlea is broad ($\geq 40\%$ of width of the articular facets) in *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. This condition is also seen in most extant bats. In contrast, the epitrochlea is relatively narrow ($< 25\%$ width of the articular facets) in Mystacinidae, Molossoidea, and Vespertilionidae. Morphology of the epitrochlea varies among the outgroups; the epitrochlea is broad in Scandentia and narrow in Dermoptera. Accordingly, the primitive condition for this character cannot be reconstructed a priori.

Character 144: *Sesamoid element dorsal to magnum–trapezium articulation absent (0); or present (1)*. Although wrist morphology has never been intensively surveyed across all bat families, a recent study by Cypher (1996) illustrated differences among taxa in terms of the number and location of sesamoid elements associated with tendons in the wrist. Preservation of the wrist of *Icaronycteris* in PU 18150 allowed us to score presence or absence of two of these sesamoids. No sesamoid element is present dorsal to the magnum–trapezium articulation in *Icaronycteris*. This condition is also seen in extant Pteropodidae, Hipposiderinae, Noctilionidae, Natalidae, Vespertilioninae, and

Myotinae. In contrast, a sesamoid element is present dorsal to the magnum–trapezium articulation in Emballonuridae, Nycteridae, Phyllostomidae, Mormoopidae, and Molossinae. The status of this sesamoid is unknown in the outgroups, so this character cannot be polarized a priori. The condition in *Archaeonycteris*, *Hassianycteris*, *Palaeochiropteryx*, Rhinopomatoidea, Megadermatidae, Rhinolophinae, Mystacinidae, Myzopodidae, Thyropteridae, Furipteridae, Antrozoidae, Tomopeatinae, Miniopterinae, Murinae, and Kerivoulinae is also unknown; these taxa are therefore scored “?” for this character.

Character 147: *Sesamoid element dorsal to unciform–magnum articulation absent (0); or present (1)*. No sesamoid element is present dorsal to the unciform–magnum articulation in *Icaronycteris*. This condition is also seen in extant Pteropodidae, Emballonuridae, Nycteridae, Hipposiderinae, Phyllostomidae, and Vespertilioninae. In contrast, a sesamoid element is present dorsal to the unciform–magnum articulation in Mormoopidae, Noctilionidae, Natalidae, and Molossinae. The status of this sesamoid is unknown in the outgroups, so this character cannot be polarized a priori. The condition in *Archaeonycteris*, *Hassianycteris*, *Palaeochiropteryx*, Rhinopomatoidea, Megadermatidae, Rhinolophinae, Mystacinidae, Myzopodidae, Thyropteridae, Furipteridae, Antrozoidae, Tomopeatinae, Miniopterinae, Murinae, and Kerivoulinae is also unknown; these taxa are therefore scored “?” for this character.

Character 149: *Wing digit II with ossified first phalanx (0); or first phalanx unossified or absent (1)*. Phalanges in both the manus and pes are numbered from proximal to distal. The first phalanx of each wing digit is identified by its articulation with the distal end of the corresponding metacarpal. The first phalanx in wing digit II (the “index finger”) is ossified in *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. This element is also ossified in extant Pteropodidae, Rhinopomatoidea, Megadermatidae, Noctilionoidea, Mystacinidae, Molossoidea, and Vespertilionidae. In contrast, the first phalanx of wing digit II is unossified in Emballonuridae, Nycteridae, Rhinolophidae, and Nataloidea. The first phalanx of dig-

it II is ossified in both outgroups, suggesting that the condition seen in the Eocene bats is primitive.

Character 150: *Wing digit II with ossified second phalanx (0); or second phalanx unossified or absent (1).* The second phalanx is defined by its articulation with the distal end of the first phalanx of a particular digit. The second phalanx in wing digit II is ossified in *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. Among extant bats, the second phalanx is present and ossified only in Pteropodidae and Rhinopomatidae; this element is unossified or absent in all other lineages. Digit II of the manus has an ossified second phalanx in both outgroups, suggesting that the condition seen in the Eocene bats is primitive.

Character 151: *Wing digit II with ossified third phalanx (0); or third phalanx unossified or absent (1).* The third phalanx (= ungual phalanx) is defined by its articulation with the distal end of the second phalanx, and in mammals it typically bears a claw or homologous structure (nail or hoof). The third phalanx of wing digit II is present and ossified in *Icaronycteris* and *Archaeonycteris*. In both taxa, the third phalanx of this digit clearly bore a claw. Indeed, the specific epithet "index" for the type species of *Icaronycteris* refers to presence of a claw on the index finger (digit II; Jepsen, 1966). In contrast, the third phalanx of digit II is unossified or absent in *Hassianycteris* and *Palaeochiropteryx*. Among extant bat lineages, the third phalanx is present and ossified only in Pteropodidae; it is unossified or absent in all other groups. Digit II of the manus has an ossified third phalanx in both outgroups, suggesting that the condition seen in *Icaronycteris* and *Archaeonycteris* is primitive. The state seen in *Hassianycteris* and *Palaeochiropteryx* is apparently derived.

Character 152: *Wing digit III with third phalanx completely ossified (0); or third phalanx ossified only at the base (1); or third phalanx unossified or absent (2).* The third phalanx of wing digit III is small but fully ossified in *Icaronycteris*. In contrast, the third phalanx of this digit is either unossified or absent in *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. A small but fully ossified third phalanx is found among extant

Phyllostomidae, Mormoopidae, Mystacinidae, Myzopodidae, and Thyropteridae. The third phalanx is ossified only at the base (and the distal portion of the element remains cartilaginous) in Furipteridae, Natalidae, Molossoidea, and some Vespertilionidae. The third phalanx is completely unossified or absent in Pteropodidae, Emballonuridae, Yinochiroptera, Noctilionidae, and some Vespertilionidae. The third phalanx in digit III of the manus is fully ossified in both outgroups and most other mammals, suggesting that the condition seen in *Icaronycteris* is primitive. Lack of an ossified third phalanx in *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* is relatively derived.

POSTERIOR AXIAL SKELETON AND PELVIS

Character 158: *No vertebral fusion in posterior thoracic and lumbar series (0); or at least three vertebrae fused (1).* The vertebral column of most mammals contains posterior thoracic and lumbar vertebrae as separate elements that can move relative to one another. They articulate at various hypophyseal joints, but are not fused. This is also true of the posterior thoracic and lumbar series in *Icaronycteris* (frontispiece, fig. 21), *Archaeonycteris*, *Hassianycteris* (fig. 4), and *Palaeochiropteryx* (fig. 3), all of which exhibit no evidence of vertebral fusion. Among extant bats, vertebral fusion in this area is similarly absent in Pteropodidae, Emballonuridae, Rhinopomatidae, Nycteridae, some Megadermatidae, Rhinolophidae, some Hipposiderinae, Phyllostomidae, Noctilionidae, Mystacinidae, Myzopodidae, Thyropteridae, Molossoidea, and Vespertilionidae. In contrast, at least three vertebrae are fused together in the posterior thoracic and lumbar region in Craseonycteridae, some Megadermatidae, some Hipposiderinae, Mormoopidae, Furipteridae, and Natalidae. Both outgroups lack vertebral fusion in the posterior thoracic and lumbar regions, suggesting that the condition seen in the Eocene bats is relatively primitive.

Character 159: *Sacrum terminates anterior to acetabulum (0); or extends posteriorly to at least the midpoint of the acetabulum (1).* The sacrum (as defined in this study) includes all vertebrae that articulate with the

pelvis or are fused with those that do. The posterior end of the sacrum terminates anterior to the acetabulum in *Hassianycteris*. In contrast, the sacrum extends posteriorly to at least the midpoint of the acetabulum in *Icaronycteris* (fig. 23) and *Palaeochiropteryx*.⁷ Among extant bats, the sacrum terminates anterior to the acetabulum in Nycteridae and Rhinolophidae; it extends posteriorly to at least the midpoint of the acetabulum in all other lineages. The sacrum terminates anterior to the acetabulum in both outgroups, suggesting that the condition seen in *Hassianycteris* is primitive. The condition seen in *Icaronycteris* and *Palaeochiropteryx* appears derived. We were unable to determine the extent of the sacrum in *Archaeonycteris*; this taxon is scored “?” for this character.

Character 160: *Sacral laminae narrow or absent, vertebra width (including laminae) less than or equal to three-fourths vertebral body length (0); or laminae broad, vertebra width equal to or greater than vertebral length.* Sacral laminae are thin plates of bone that extend laterally from the sacral vertebrae posterior to the iliosacral joint. These structures, which are homologous with the transverse processes of lumbar vertebrae, do not articulate with the pelvis. Instead, they typically form joints with one another that may or may not be fully fused. Gaps are frequently present between successive laminae, and lateral enclosure of such gaps may produce a series of sacral foramina between successive laminae.

The sacral laminae are broad in *Icaronycteris* (fig. 23) and *Palaeochiropteryx*. Broad sacral laminae are also present in Nycteridae, Myzopodidae, Thyropteridae, Molossoidea, and Vespertilionidae. In these forms, the width of each postischial sacral vertebra (including the sacral laminae) is subequal to or greater than the length of the

vertebral body. In contrast, the sacral laminae are narrow or absent in all other taxa, extending only a short distance laterally from the bodies of the vertebrae. Accordingly, vertebral width is less than or equal to three-fourths the length of the body of the vertebra. Among extant bats, the sacral laminae are narrow or are absent in Pteropodidae, Emballonuridae, Rhinopomatoidea, Megadermatidae, Rhinolophidae, Noctilionoidea, Mystacinidae, Furipteridae, and Natalidae. Among the outgroups, the sacral laminae are broad in Scandentia but are absent in Dermoptera. Accordingly, this character cannot be polarized a priori. Morphology of the sacral laminae in unknown in *Archaeonycteris* and *Hassianycteris*; these forms are therefore scored “?” for this character.

Character 161: *Dorsomedial edge of ascending process of ilium upturned, flares dorsally above the level of iliosacral articulation, iliac fossa large and well defined (0); or dorsomedial edge not upturned, does not extend dorsally beyond the level of the iliosacral articulation, iliac fossa not large or well defined (1).* The iliosacral articulation in mammals is formed between the ascending process of the ilium and the sacral vertebrae. The dorsomedial edge of the ascending process forms the origin for m. tensor fasciae latae, which flexes and abducts the femur (Vaughan, 1959, 1970b). M. gluteus medius (which flexes, abducts, and rotates the femur) also originates from the dorsomedial edge, although the iliac fossa on the dorsolateral surface of the ascending process forms the principal origin of this muscle (Vaughan, 1959, 1970b).

The dorsomedial edge of the ascending process of the ilium is upturned and flares dorsally above the level of the iliosacral articulation in *Icaronycteris*, *Hassianycteris*, and *Palaeochiropteryx*. Among extant bats, a dorsomedially flared ascending process is seen only in Rhinolophidae. In all taxa this flare is associated with a large, well-defined iliac fossa. In contrast, the dorsomedial edge of the ascending process is not upturned and the flare is absent in all other bats. The dorsomedial edge terminates at the level of the iliosacral articulation, and the iliac fossa is relatively small and poorly defined. The upturned edge and well-defined iliac fossa are

⁷ Our observations do not agree with those of Russell and Sigé (1970), who reported that the sacrum in *Palaeochiropteryx* was very small and included only a single vertebra. We attribute this discrepancy to an incorrect reconstruction of this region by Russell and Sigé (1970), who were working with relatively poorly preserved material. Discovery of better preserved specimens since their publication (e.g., HLMD Me 15025) demonstrate that *Palaeochiropteryx* had a long sacrum composed of multiple vertebrae.

present in Scandentia but absent in Dermoptera; accordingly, this character cannot be polarized a priori. We were unable to determine the state of the ilium in *Archaeonycteris*; this taxon is therefore scored “?” for this character.

Character 162: *Ischium with large ischial tuberosity that projects dorsally from posterior horizontal ramus (0); or ischial tuberosity small or absent, does not project dorsally beyond level of ramus (1).* The dorsal ischial tuberosity is a projection that extends dorsally and/or posteromedially from the posterior end of the ischium, originating from the “corner” of the pelvis at the junction between the horizontal and vertical rami of the ischium (Vaughan, 1959, 1970a). Two muscles may originate from the ischial tuberosity: *m. semitendinosus* and *m. semimembranosus*, both of which act to extend the femur and flex the lower leg (Vaughan, 1959, 1970b). Vaughan (1959) recognized an ischial tuberosity in all of the bats that he dissected, but noted that in some forms (e.g., *Eumops*) the ischial tuberosity is large, projects dorsally above the level of the horizontal ramus, and serves as the site of origin of both muscles. In other taxa (e.g., *Myotis*, *Macrotus*), the tuberosity is smaller, projects somewhat medially (not dorsally), and serves as the site of origin for just *m. semitendinosus*. In the latter taxa, *m. semimembranosus* originates from the lateral surface of the caudal border of the ischium (Vaughan, 1959). Our examination of skeletons from numerous families revealed a dichotomy between forms with a large, dorsally projecting ischial tuberosity and those in which the ischial tuberosity is small or absent. Although we have no new muscle data, we infer that morphology of the pelvis is correlated with differences in muscle origins as observed by Vaughan (1959).

There is no evidence of a large, dorsally projecting ischial tuberosity on the pelvis of *Icaronycteris* (fig. 23), *Hassianycteris*, and *Palaeochiropteryx*. In contrast, a large, dorsally projecting ischial tuberosity is present in *Archaeonycteris*. Among extant bats, a large dorsal ischial tuberosity is present only in *Mystacinidae* and *Molossidae*. A large dorsally projecting ischial tuberosity is present in one outgroup (Scandentia) but not in

the other (Dermoptera); accordingly, this character can not be polarized a priori.

Character 163: *Pubic spine absent (0); or straight (1); or tip of pubic spine bent sharply dorsally (2).* The pubic spine is an elongate projection from the anteroventral corner of the pubis (Vaughan, 1959; Walton and Walton, 1970; Simmons, 1994). Presence of a pubic spine is a synapomorphy of Chiroptera (Simmons, 1994).

Two muscles originate from the pubic spine in bats: *m. pectineus* from the base and lateral surface of the spine, *m. gracilis* from the entire ventrolateral surface of the spine to the tip (Vaughan, 1959, 1970). *M. pectineus* is an adductor and flexor of the femur, while *m. gracilis* is a flexor of the lower leg and an adductor of the hind limb (Vaughan, 1959, 1970b). Additionally, the pubic spine is the site of insertion of *m. psoas minor*, which originates from the lumbar vertebrae (Vaughan, 1959, 1970b). Contraction of *m. psoas minor* pulls the ventral part of the pelvis forward, thereby arching the posterior lumbar section of the vertebral column. Vaughan (1959) noted that this action may be useful in doubling up the body when the bat is grooming itself while hanging, or when pinning an insect to the uropatagium while adjusting the grip of the jaws on the prey. Action of this muscle may also help to brace the vertebral column when the bat lands, and also while the bat is flying (i.e., against the shock of the airstream hitting the uropatagium during sudden maneuvers; Vaughan, 1959).

The pubic spine is relatively straight and points anterodorsally in *Icaronycteris* (fig. 23), *Archaeonycteris*, and *Palaeochiropteryx*. Among extant bats, this condition is seen in *Pteropodidae*, *Emballonuridae*, *Rhinopomatoidea*, *Nycteridae*, and *Yangochiroptera*. In these forms, the course of the pubic spine is essentially parallel to that of the ilium, with the long axis of the spine directed at the anterior lumbar vertebrae. In contrast, the tip of the pubic spine is sharply upturned in *Megadermatidae*, *Rhinolophinae*, and *Hipposiderinae*. The tip of the pubic spine in these taxa points dorsally toward the cranial end of the ilium. In *Hipposiderinae*, a bony extension from the pubic spine contacts the anterior ilium, thereby enclosing a preaceta-

bular foramen. The pubic spine is absent in both outgroups, so the form of the pubic spine (straight or with tip upturned) cannot be polarized a priori. We could not determine the form of the pubic spine in *Hassianycteris*, so this taxon is scored “?” for this character.

Character 165: *Obturator foramen normal, rim well defined (0); or foramen partially infilled with thin, bony sheet along posteroventral rim (1).* The obturator foramen of the pelvis is enclosed dorsally and posteriorly by the rami of the ischium and anteriorly and ventrally by the pubis. In most mammals, the rim of the obturator foramen is well defined and rounded in cross section. Muscles originating around the rim of the obturator foramen include m. adductor brevis (extensor and/or adductor of femur), m. adductor magnus (extensor and rotator of femur), and m. obturator externus (extensor and adductor of femur; Vaughan, 1959, 1970b). M. obturator internus is absent in bats, probably as a result of hip modifications associated with 90° rotation of the hindlimbs (Simmons, 1994).

The obturator foramen in *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* is of the normal mammalian morphology with a well-defined rim. This is similar to the condition seen in most extant bats. In contrast, the obturator foramen is partially infilled by a thin, bony sheet along the posteroventral rim in Rhinopomatidae, Rhinolophinae, Hipposiderinae, and Thyropteridae. Such infilling is absent in both outgroups, suggesting that the condition seen in the Eocene bats is primitive.

HINDLIMB

Character 169: *Shaft of femur straight (0); or with bend that directs distal shaft dorsally (1).* Although all bats share a complex series of modifications of the hip and proximal femur that serve to rotate the hindlimbs approximately 90° from the typical mammalian condition (Simmons, 1994), the femoral shaft and distal femur remain relatively unmodified. As in most other mammals, the shaft of the femur is straight in *Icaronycteris* (frontispiece, fig. 21), *Archaeonycteris* (fig. 3), *Hassianycteris* (fig. 4), and *Palaeochiropteryx* (fig. 2). This condition is also seen in most extant bats. In some bats, however, the shaft of the femur is bent somewhat so that the distal end is directed more dorsally (the equivalent of a lateral bend if the femur were in the position typical of nonvolant mammals). In bats, which already have a femur that projects laterally from the hip, this bend serves to raise the knee joint even higher, well above the hip joint in some forms. A bend in the shaft of the femur is seen in Rhinolophoidea and some Phyllostomidae. The shaft of the femur is straight in both outgroups, indicating that the “straight” condition is primitive.

Character 170: *Fibula complete and well developed (0); or thin and threadlike (1); or absent or entirely unossified (2).* The fibula in *Icaronycteris* (frontispiece) and *Archaeonycteris* is well developed (relatively robust) and complete (ossified from knee to ankle). In contrast, the fibula in *Hassianycteris* and *Palaeochiropteryx* is relatively much thinner, almost threadlike. Among extant bats, a complete, well developed fibula is found only in Pteropodidae, some Phyllostomidae, Mystacinidae, and Molossidae. The fibula is thin, threadlike, and often only partially ossified in Emballonuridae, Rhinopomatoidea, Megadermatidae, Rhinolophidae, some Phyllostomidae, Mormoopidae, Noctilionidae, Nataloidea, Antrozoidae, and Vespertilionidae. The fibula is absent or entirely unossified in Nycteridae. Both outgroups have a complete, well developed fibula, suggesting that the condition seen in *Icaronycteris* and *Archaeonycteris* is relatively primitive. The thin, threadlike fibula seen in *Hassianycteris* and *Palaeochiropteryx* apparently represents a derived condition.

Character 171: *Calcar absent (0); or present (1).* The calcar is a bony and/or cartilaginous rod that extends from the ankle to support the trailing edge of the uropatagium. Presence of a calcar (and m. depressor ossis styliformis, which adducts the calcar toward the lower leg) is considered to be a synapomorphy of Chiroptera (Simmons, 1994, 1995). However, there is no evidence that a calcar was present in *Icaronycteris* and *Archaeonycteris*. A calcar is lacking in every known specimen, and our examination of the calcaneum suggests that no calcar facet is

present on the calcaneum of the these forms, leading us to conclude that a calcar was absent in these taxa. In contrast, a calcar is present in *Hassianycteris* and *Palaeochiropteryx*. In both taxa, the appearance of the calcar suggests that it may have been largely cartilaginous. Among extant bats, a calcar is present in most taxa; it is absent only in some Pteropodidae, Rhinopomatoidea, and some phyllostomids. Both outgroups (and all other mammals) lack a calcar, indicating that absence of the calcar is primitive. Presence of a calcar in *Hassianycteris* and *Palaeochiropteryx* represents a derived condition.

Character 172: *Digits II–V of foot with three phalanges (0); or two phalanges (1).* Digits II–V of the foot each have three phalanges in *Icaronycteris* (frontispiece, fig. 23), *Archaeonycteris* (fig. 3), *Hassianycteris* (fig. 4), and *Palaeochiropteryx* (fig. 2). This condition is also seen in most extant bats. In contrast, only two phalanges are present in digits II–V in Hipposiderinae, Myzopodidae, and Thyropteridae. Both outgroups (and most other mammals) have three phalanges in digits II–V of the foot, suggesting that the condition seen in the Eocene bats is primitive.

COMPLETENESS

One problem that plagues phylogenetic analyses that include fossil taxa is that of completeness (or lack of completeness) of available data. Numerous studies have illustrated the importance of including fossils in phylogenetic analyses, demonstrating that fossils sometimes preserve information (in the form of unique combinations of primitive and derived character states) that may be crucial to resolving relationships among extant lineages (e.g., Gauthier et al., 1988; Donoghue et al., 1989; Novacek, 1992, 1994). Fossils are also important because they frequently affect character optimizations, which in turn may affect conclusions concerning the degree of support for various monophyletic groups, taxonomic diagnoses, character independence, homoplasy, and the relative timing of various evolutionary events (Simmons, 1993a). It is also obvious that fossils must be included in any study that seeks to determine the relationships of fossils to ex-

tant groups. However, inclusion of relatively incomplete taxa—be they fossils or poorly known extant groups—can sometimes dramatically reduce the degree of phylogenetic resolution obtained by increasing the number of equally parsimonious topologies (Rowe, 1988; Simmons, 1993a, 1993c).

Completeness of a taxon may be defined as the percentage of characters for which it can be scored in a given analysis (Simmons, 1993a, 1993c). In practice, paleontologists have often sought to maximize completeness by focusing largely on osteological characters, omitting from consideration many soft-tissue or molecular characters that cannot be scored in extinct organisms (e.g., Beard, 1993). However, inclusion of fossil OTUs in an analysis with many soft-tissue characters does not necessarily lead to decreased resolution (Gauthier et al., 1988; Novacek, 1992). In some cases, inclusion of fossils can actually *increase* resolution by reducing the number of equally parsimonious trees, as was the case with Novacek's (1992) hyracoid example. When the opposite occurs and inclusion of fossils increases the number of optimal trees and decreases resolution, techniques such as Adams consensus may be used to identify relationships that remain stable in all most-parsimonious trees (Simmons, 1993a). The relative stability of topological placement of a fossil taxon in phylogenetic trees appears to depend more on the particular combination of character states that it exhibits than on its completeness. For example, in an analysis of relationships among archontan mammals, Simmons (1993a) found that one fossil taxon that was only 19% complete could be placed unambiguously relative to extant lineages, while relationships of another fossil taxon that was 53% complete could not be determined unambiguously.

In our view, the benefits of including fossils and soft tissue and molecular characters in a single analysis far outweigh the possible problems (see discussion below). Nevertheless, we calculated the percent completeness for each OTU in our data set in order to provide a basis for a posteriori considerations of the effects of completeness (table 6). Extant lineages in our data set were 62.0–100%

TABLE 6
 Statistics on Character Codings for Current Data Set

Terminal taxon	Characters scored with single state ^a	Characters scored with two or more states ^b	Characters scored “-”	Characters scored “?”	Percent completeness ^c
Scandentia	161 (77.4%)	3 (1.4%)	19 (9.1%)	25 (12.0%)	88.0%
Dermoptera	172 (82.6%)	0	18 (8.7%)	18 (8.7%)	91.3%
Pteropodidae	176 (84.6%)	26 (12.5%)	6 (2.9%)	0	100%
<i>Icaronycteris</i>	71 (34.1%)	0	3 (1.4%)	134 (64.4%)	35.6%
<i>Archaeonycteris</i>	59 (28.4%)	0	1 (0.5%)	148 (71.2%)	28.9%
<i>Hassianycteris</i>	61 (29.3%)	2 (1.0%)	1 (0.5%)	144 (69.2%)	30.8%
<i>Palaeochiropteryx</i>	75 (36.1%)	1 (0.5%)	1 (0.5%)	131 (63.0%)	37.1%
Emballonuridae	166 (79.8%)	26 (12.5%)	6 (2.9%)	10 (4.8%)	95.2%
Rhinopomatidae	185 (89.0%)	1 (0.5%)	5 (2.4%)	17 (8.1%)	91.9%
Craseonycteridae	125 (60.1%)	0	5 (2.4%)	78 (37.5%)	62.5%
Nycteridae	178 (85.6%)	6 (2.9%)	7 (3.4%)	17 (8.1%)	91.9%
Megadermatidae	183 (88.0%)	9 (4.3%)	2 (1.0%)	14 (6.7%)	93.3%
Rhinolophinae	185 (89.0%)	5 (2.4%)	5 (2.4%)	13 (6.2%)	93.8%
Hipposiderinae	170 (81.8%)	13 (6.2%)	6 (2.9%)	19 (9.1%)	90.9%
Phyllostomidae	146 (70.0%)	57 (27.6%)	5 (2.4%)	0	100%
Mormoopidae	172 (82.7%)	13 (6.2%)	5 (2.4%)	18 (8.7%)	91.3%
Noctilionidae	192 (92.3%)	0	7 (3.4%)	9 (4.3%)	95.7%
Mystacinidae	132 (63.5%)	0	6 (2.9%)	70 (33.6%)	66.4%
Myzopodidae	129 (62.0%)	0	3 (1.4%)	76 (36.6%)	63.4%
Thyropteridae	174 (83.7%)	1 (0.5%)	3 (1.4%)	30 (13.4%)	85.6%
Furipteridae	147 (70.7%)	1 (0.5%)	3 (1.4%)	57 (27.4%)	72.6%
Natalidae	181 (87.0%)	0	2 (1.0%)	25 (12.0%)	88.0%
Antrozoidae	148 (71.2%)	1 (0.5%)	3 (1.4%)	56 (26.9%)	73.1%
Tomopeatinae	125 (60.1%)	0	4 (1.9%)	79 (38.0%)	62.0%
Molossinae	182 (87.5%)	21 (10.1%)	2 (1.0%)	3 (1.4%)	98.6%
Vespertilioninae	167 (80.3%)	22 (10.6%)	3 (1.4%)	16 (7.7%)	92.3%
Miniopterinae	145 (69.7%)	0	5 (2.4%)	58 (27.9%)	72.1%
Myotinae	187 (89.9%)	9 (4.3%)	2 (1.0%)	10 (4.8%)	95.2%
Murinae	132 (63.5%)	0	4 (1.9%)	72 (34.6%)	65.4%
Kerivoulinae	145 (69.7%)	1 (0.5%)	3 (1.4%)	59 (28.4%)	71.6%
Total	4471 (71.7%)	218 (3.5%)	145 (2.3%)	1406 (22.5%)	77.5%

^a Includes only characters states 0, 1, 2, etc.; does not include characters scored as inapplicable (“-”) or missing (“?”). Percentage reflects the percent of the total characters (208) used in the analysis.

^b Includes both cases of uncertainty and taxonomic polymorphism.

^c Completeness is defined as the percentage of characters for which a taxon can be scored based on available data; it was calculated by subtracting the percentage of characters scored “?” from 100%.

complete; the fossils ranged from 28.9 to 37.1% complete.

METHODS OF PHYLOGENETIC ANALYSIS

The present study follows Simmons (1998) in adopting a character consensus (“total evidence”) approach to phylogeny reconstruction. In recent years there has been much discussion of the relative merits of character consensus versus taxonomic con-

sensus methods for resolving systematic problems (Kluge, 1989; Barrett et al., 1991, 1993; Swofford, 1991; Bull et al., 1993; de Queiroz, 1993; Eernisse and Kluge, 1993; Kluge and Wolf, 1993; Nelson, 1993; Chippendale and Weins, 1994; Hulsenbeck et al., 1994; de Queiroz et al., 1995; Farris et al., 1995; Miyamoto and Fitch, 1995). As discussed by Simmons (1993a, 1998), character congruence is the most sensible approach to the current data set because the data consist

principally of discrete-state morphological characters that cannot be reasonably partitioned. Available restriction-site data are not capable of resolving interfamilial relationships in the absence of other data (Baker et al., 1991a), hence taxonomic congruence is not a useful option.

The 208 discrete characters used in the present study (see appendix 2) were scored for phylogenetic analysis, and the resulting data matrix (appendix 3) was analyzed using PAUP version 3.1.1 (Swofford, 1993). All transformations were unordered. A heuristic search with a random-addition sequence and 1000 repetitions was used to find most-parsimonious trees. Near-most-parsimonious trees (one to six steps longer) were identified in subsequent heuristic searches using the same parameters, and a decay analysis was performed following the methods of Bremer (1988). Decay values for strongly supported clades were obtained by using constrained heuristic analyses to identify the shortest trees that did not include a particular clade. A bootstrap analysis using heuristic methods (random-addition sequence, 10 repetitions for each of 1000 bootstrap replicates) was also used to evaluate the relative support for various groupings. MacClade version 3.0 (Maddison and Maddison, 1992) was used for data entry and examination of character-state distributions.

Three complete sets of phylogenetic analyses were conducted: (1) an analysis including all characters but excluding the fossil taxa; (2) an analysis including all characters and all taxa; and (3) an analysis including all taxa but excluding those characters that could not be scored in any of the fossil forms. The first analysis was designed to provide a starting point by evaluating relationships of extant lineages in the context of the revised data matrix; this effectively represents an updated version of Simmons' (1998) analysis. Our second analysis represents the principal goal of the project, a character congruence study including both Eocene fossil genera and extant lineages. The third and final analysis was designed to evaluate the effects of soft-tissue and molecular characters on the outcome of a phylogenetic analysis including fossil forms that cannot be scored for these features.

ANALYSIS OF CHARACTER TRANSFORMATIONS

Character transformations were analyzed by mapping character-state distributions onto the shortest trees derived from the second set of phylogenetic analyses described above (i.e., those obtained using all characters and all taxa). Optimizations were calculated using both the ACTRAN (accelerated transformation optimization) and DELTRAN (delayed transformation optimization) options of PAUP version 3.1.1 (Swofford, 1993). MacClade version 3.0 (Maddison and Maddison, 1992) was used to visualize the results of character mapping.

As discussed by Simmons (1993a), two kinds of character transformations may be recognized during the optimization process: unequivocal transformations, which have only one parsimonious placement on the optimal tree(s), and equivocal transformations, which can be parsimoniously arranged in two or more ways. Both ACTRAN and DELTRAN place unequivocal transformations on a given tree in the same manner, but they treat equivocal transformations differently. ACTRAN forces transformations to the lowest possible points on the tree, and thus favors hypotheses of reversal over hypotheses of convergence. Conversely, DELTRAN forces transformations to the highest possible points on a tree, thus favoring hypotheses of convergence over reversal. DELTRAN is often favored in studies involving fossils because it places transformations at the minimal level at which they can be observed (i.e., in the face of missing data it does not conclude that derived states exist below the level at which they can be demonstrated).

In this study, we focused only on transformations that apply at and below the nodes where fossil taxa join the tree. We compared the results of ACTRAN and DELTRAN optimizations in order to identify all equally parsimonious arrangements of equivocal transformations, and interpreted our observations in the context of what is known about the function of various structures and structural complexes. Results of these analyses are presented below under "Character Evolution in Early Chiropterans."

PHYLOGENETIC RESULTS

RESULTS OF ANALYSES

Analysis 1: All characters, fossil taxa excluded (fig. 35). As noted above, this analysis was designed to provide a starting point by evaluating relationships of extant lineages in the context of the revised data matrix. This effectively represents an updated version of Simmons' (1998) analysis, and illustrates the effects of changes that we made in the data matrix (e.g., corrections, new characters, inclusion of hyoid data for Antrozoidae; see above). Analysis of the revised data set resulted in a single most parsimonious tree (661 steps; CI = 0.404, RI = 0.579) shown in figure 35.

Comparisons of the results of our Analysis 1 (fig. 35) with Simmons (1998) tree (fig. 20) reveals several topological differences, all within the yangochiropteran part of the tree. First, relationships within Nataloidea are fully resolved in our Analysis 1 tree, with Thyropteridae unambiguously placed as the sister-group of the Furipteridae + Natalidae clade. This represents a trivial change, since this topology occurred in one of the two most parsimonious trees found by Simmons (1998) and received higher bootstrap support than did any of the alternatives in that study. A potentially more significant change in our Analysis 1 tree is placement of Antrozoidae

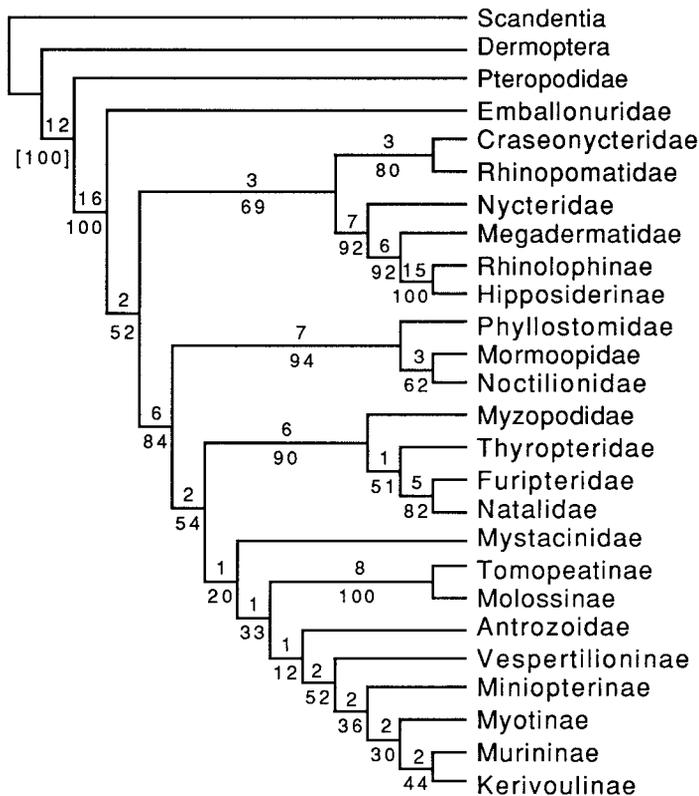


Fig. 35. Results of Analysis 1, which included all characters but omitted the fossil taxa (see text for discussion). Parsimony analysis resulted in a single most-parsimonious tree (662 steps; CI = 0.403 and RI = 0.578), which is shown here. The numbers below internal branches indicate the percentage of bootstrap replicates in which each clade appeared; numbers above the branches are decay values (the minimum number of additional steps required to collapse each clade). The bootstrap analysis was constrained to consider only trees in which Chiroptera was monophyletic; this was done because most of the characters that support bat monophyly (table 5) were omitted from this study.

as the sister-taxon of Vespertilionidae (i.e., Vespertilioninae + Miniopterinae + Myotinae + Murininae + Kerivoulinae) rather than as the sister-taxon of Molossoidea. This suggests that Molossoidea as defined by Simmons (1998) may not be monophyletic, and that Antrozoidae may form a clade with vespertilionids as traditionally thought (e.g., by Koopman, 1993, 1994). However, support for the Antrozoidae + Vespertilionidae clade was very low in Analysis 1 (bootstrap value = 12%; minimum of one additional step to collapse clade), indicating considerable uncertainty regarding this grouping. The same is also true of other clades that represent changes from Simmons (1998) topology: (1) placement of Molossoidea (Tomopeatinae + Molossinae) as the sister-group of the Antrozoidae + Vespertilionidae clade (bootstrap value = 33%; minimum of one additional step to collapse clade); and (2) placement of Mystacinidae as the sister-taxon of Molossoidea + Antrozoidae + Vespertilionidae (bootstrap value = 20%; minimum of one additional step to collapse clade). In essence, all of these changes represent rearrangements of relationships at nodes that were poorly supported in Simmons (1998) analysis and remain poorly supported in our analyses of the updated data set.

Analysis 2: All characters, all taxa (fig. 36). This analysis represents the principal goal of our project, a character-congruence study including both Eocene fossil genera and extant lineages. Encouragingly, parsimony analyses of the complete data set in Analysis 2 produced a single most-parsimonious tree (fig. 36; 681 steps; CI = 0.392, RI = 0.587). Relationships of *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* were fully resolved, and placement of each was moderately to strongly supported in the bootstrap and decay analyses (bootstrap values = 54–93%; minimum of one to six additional steps to collapse clade). These levels of support are comparable to those found for many extant clades in Analysis 2. Indeed, bootstrap values for branches associated with many extant taxa (e.g., Mystacinidae, Vespertilioninae, Miniopterinae, Myotinae, Murininae, Kerivoulinae) are much lower than those associated with the fossil branches despite the fact that the extant

lineages are represented by two to three times more data (table 6). The absence of soft-tissue and molecular character data clearly does not preclude relatively secure placement of the fossil forms in this study.

Results of our analysis indicate that *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* represent a series of consecutive sister-taxa to the microchiropteran crown group (i.e., the group comprised of all extant lineages). They do not form a paraphyletic group ancestral to both Megachiroptera and Microchiroptera (e.g., Eochiroptera sensu Van Valen, 1979), a monophyletic group within Microchiroptera (e.g., Palaeochiropterygoidea sensu Smith, 1977), or have special affinities with various extant microchiropteran superfamilies (as suggested by Smith and Storch, 1981). Of the four Eocene genera, *Palaeochiropteryx* shares the most derived traits with extant microchiropterans. *Hassianycteris* and *Archaeonycteris* are consecutive sister-taxa to the clade including *Palaeochiropteryx* and the microchiropteran crown group, and *Icaronycteris* occupies the basalmost branch in the microchiropteran part of the tree.

Comparisons of the results of Analyses 1 and 2 (figs. 35, 36) demonstrate that inclusion of *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* in the analysis produced minor changes in topology of the tree, with the changes again centered on those parts of the tree that were weakly supported in previous analyses. Specifically, inclusion of the fossils changed the position of Antrozoidae (which in Analysis 2 now forms a clade with Molossoidea, supporting monophyly of Molossoidea) and Mystacinidae (which now appears as the sister-taxon of Nataloidea + Molossoidea + Vespertilionoidea). Interestingly, all of these relationships appeared in Simmons' (1998) tree (fig. 20), although not in the results of our Analysis 1 (fig. 35).

Inclusion of the fossils affected the perceived support for many clades even when there was no effect on tree topology. This effect was most noticeable near the base of tree. Monophyly of the microchiropteran crown group (Emballonuridae + Yinochiroptera + Yangochiroptera) received only moderate support in Analysis 2 (bootstrap value

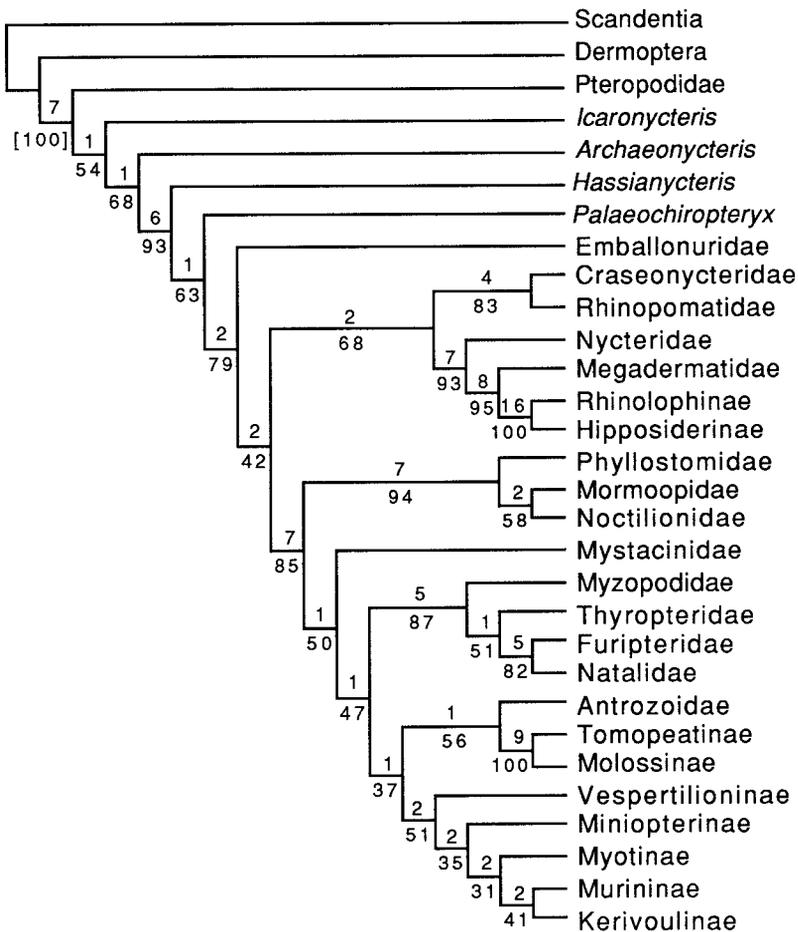


Fig. 36. Results of Analysis 2, which included all characters and all taxa (see text for discussion). Parsimony analysis resulted in a single most-parsimonious tree (680 steps; CI = 0.393; RI = 0.587), which is shown here. The numbers below internal branches are bootstrap values; numbers above the branches are decay values. The bootstrap analysis was constrained to consider only trees in which Chiroptera was monophyletic.

= 79%; minimum of two additional step to collapse clade), whereas it received extremely high support in Analysis 1 (bootstrap value = 100%; minimum of 16 additional steps to collapse clade). Clearly, many of the derived traits that diagnose extant Microchiroptera evolved in a sequential pattern over time; inclusion of the fossil taxa “spreads out” these synapomorphies over a larger part of the tree, thus reducing perceived support for any single branch. Nevertheless, monophyly of the microchiroperan crown group remains strongly supported in contrast to other hypotheses. Alternative topologies, includ-

ing those suggested by Smith and Storch (1981), appear unlikely given results of the bootstrap analysis. For example, *Hassianycteris* formed a clade with Yangochiroptera in only 6% of the bootstrap replicates. *Palaeochiropteryx* grouped with Yangochiroptera in only 5% of the bootstrap replicates, and formed a clade with some or all Vespertilionoidea in fewer than 1% of the bootstrap replicates.

As in Simmons (1998) and Analysis 1 (fig. 20, 35), results of Analysis 2 placed Emballonuridae as the sister-group of the clade containing all other extant microchiropteran lin-

eages (fig. 36). Monophyly of the latter clade (Yinochiroptera + Yangochiroptera) was only weakly supported (bootstrap value = 42%; minimum of two additional steps to collapse clade). However, alternative topologies received considerably less support. Placement of Emballonuridae within Yinochiroptera (as suggested by Koopman, 1985, 1994) was supported in only 28% of the bootstrap replicates. Emballonuridae grouped with Rhinopomatoidea in fewer than 4% of the replicates, again indicating that Emballonuroidea as traditionally recognized (i.e., including Emballonuridae + Rhinopomatidae + Craseonycteridae) is not monophyletic.

Monophyly of Yinochiroptera sensu Simmons (Rhinopomatoidea + Rhinolophoidea) was moderately supported in the current analysis (bootstrap value = 68%; minimum of two additional steps to collapse clade). Within Yinochiroptera, strong support was found for monophyly of Rhinopomatoidea (bootstrap value = 83%; minimum of four additional steps to collapse clade) and Rhinolophoidea (bootstrap value = 93%; minimum of seven additional steps to collapse clade). Relationships within Rhinolophoidea were well resolved with high bootstrap and decay values. Monophyly of Rhinolophidae (including Hipposiderinae) was very strongly supported (bootstrap value = 100%; minimum of 16 additional steps to collapse clade), as was a sister-group relationship between Megadermatidae and Rhinolophidae (bootstrap value = 95%; minimum of eight additional steps to collapse clade). Very little support was found for a Nycteridae + Rhinolophidae clade (bootstrap value = 3%) or a Nycteridae + Megadermatidae clade (bootstrap value = 2%).

Monophyly of Yangochiroptera (bootstrap value = 85%; minimum of seven additional steps to collapse clade) and Noctilionoidea (bootstrap value = 94%; minimum of seven additional steps to collapse clade) was strongly supported. Within Noctilionoidea, a sister-group relationship between Noctilionidae and Mormoopidae received weak support (bootstrap value = 58%; minimum of two additional steps to collapse clade). Substantially less support was found in the bootstrap analysis for an alternative hypothesis

grouping Mormoopidae + Phyllostomidae (bootstrap value = 19%), and the third alternative (Phyllostomidae + Noctilionidae) received no support (bootstrap value <1%). We suspect that much of the ambiguity concerning relationships among noctilionoids is a result of the high level of taxonomic polymorphism seen in Phyllostomidae. Almost 28% of the characters in this study were scored as polymorphic in Phyllostomidae (table 6), introducing considerable uncertainty with respect to polarities in this part of the tree. Better resolution of noctilionoid relationships in future studies will probably require splitting of Phyllostomidae into multiple OTUs.

As in Simmons (1998), Mystacinidae was placed as the sister-group to a clade comprising Molossoidea + Nataloidea + Vespertilionoidea (the latter sensu Simmons, 1998, not sensu Koopman, 1994) in Analysis 2. However, this grouping received only weak support (bootstrap value = 50%; minimum of one additional step to collapse clade). Alternative hypotheses that received limited support in the bootstrap analysis included placement of Mystacinidae either (1) in a clade with Noctilionoidea (bootstrap value = 38%); or (2) in a clade with Molossoidea (bootstrap value = 19%); or (3) in a clade with Molossoidea and Vespertilionoidea (bootstrap value = 19%); or (4) in a clade with Molossidae (bootstrap value = 15%); or (5) in a clade with Noctilionoidea and Nataloidea (bootstrap value = 10%). Clearly, placement of Mystacinidae remains problematic.

Weak support was found for the clade comprising Nataloidea + Molossoidea + Vespertilionoidea (bootstrap value = 47%; minimum of one additional step to collapse clade). Within this group, similarly weak support was found for a Molossoidea + Vespertilionoidea clade (bootstrap value = 37%; minimum of one additional step to collapse clade). An alternative hypothesis that received some support in the bootstrap analysis included a sister-group relationship between Nataloidea and Vespertilionoidea (bootstrap value = 31%) and a clade including Nataloidea + Vespertilionoidea + Antrozoidae (bootstrap value = 12%).

Strong support was found for monophyly

of Nataloidea (bootstrap value = 87%; minimum of five additional steps to collapse clade), and weak support was found for monophyly of Molossoidea (bootstrap value = 56%; minimum of one additional step to collapse clade). Within Nataloidea, the Neotropical taxa (Thyropteridae + Furipteridae + Natalidae) formed a weakly-supported clade (bootstrap value = 51%; minimum of one additional step to collapse clade). Within this group, Furipteridae + Natalidae formed a well-supported clade (bootstrap value = 82%; minimum of five additional steps to collapse clade). Within Molossoidea, very strong support was found for Molossidae (including Tomopeatinae; bootstrap value = 100%; minimum of nine additional steps to collapse clade).

No support was found for monophyly of Vespertilionidae as traditionally defined (i.e., including Tomopeatinae and Antrozoidae; bootstrap value <1%). Monophyly of Vespertilionidae (= Vespertilionoidea) sensu Simmons (1998), a clade including Vespertilioninae + Miniopterinae + Myotinae + Murininae + Kerivoulinae, was weakly supported (bootstrap value = 51%; minimum of two additional steps to collapse clade). Within this group, weak support was found for a Murininae + Kerivoulinae clade (bootstrap value = 41%; minimum of two additional steps to collapse clade). Myotinae appeared as the sister-group of the latter clade (bootstrap value = 31%; minimum of two additional steps to collapse clade). Miniopterinae was placed as the sister-group of the Myotinae + Murininae + Kerivoulinae clade (bootstrap value = 35%; minimum of two additional steps to collapse clade).

Several other "vespertonid" groupings received limited support in the bootstrap analyses, even though they did not appear in the most parsimonious tree. Most notably, Vespertilioninae + Myotinae formed a clade in 32% of the bootstrap replicates, indicating that monophyly of this traditional grouping cannot be ruled out. Other groupings that received weak support in the bootstrap analysis include a clade comprising Vespertilioninae + Miniopterinae + Myotinae (bootstrap value = 17%), a larger clade including Vespertilioninae + Miniopterinae + Myotinae + Kerivoulinae (bootstrap value = 16%), and

a Miniopterinae + Kerivoulinae clade (bootstrap value = 13%). Essentially no support was found for an Antrozoidae + Vespertilioninae clade (bootstrap value = 4%), an Antrozoidae + Vespertilioninae + Myotinae clade (bootstrap value <1%), or an Antrozoidae + Myotinae clade (bootstrap value <1%). In short, these results indicate that "Vespertilioninae" sensu Koopman (i.e., including myotines and antrozoinae) is not a monophyletic group. Similarly, there was little support for an Antrozoidae + Vespertilionidae grouping excluding Molossidae (bootstrap value = 8%).

Even though bootstrap and decay values associated with the molossoid and vespertonid part of the tree are low, these results indicate that support for most competing hypotheses is considerably less. The range of phylogenetic hypotheses that still appear to represent viable alternatives is thus fairly small. As with noctilionoids, it seems likely that taxonomic polymorphism in Vespertilioninae (10.6% of all characters scored as polymorphic; table 6) and Molossinae (10.1% of characters polymorphic) may be reducing tree stability. Low levels of completeness of several taxa (<75% in Antrozoidae, Tomopeatinae, Miniopterinae, Murininae, and Kerivoulinae) probably contribute to this effect.

Analysis 3: All taxa, characters limited to those that could be scored in fossil genera (fig. 37). This analysis was designed to evaluate the effects of soft-tissue and molecular characters on the outcome of a phylogenetic analysis that includes fossil forms that cannot be scored for these features. As previously noted, paleontologists interested in relationships of fossil forms to extant taxa frequently omit from their analyses any characters that cannot be scored in the fossils, thus ignoring potentially informative soft-tissue and molecular characters. What effect does this have on the outcome, both on perceived relationships of the fossils and perceived relationships among extant forms? Although ours is only a single case study, the results were striking.

Parsimony analysis of our restricted data set of 82 characters (see list under "Characters Examined in Fossil Bats" above) produced two equally parsimonious trees (306

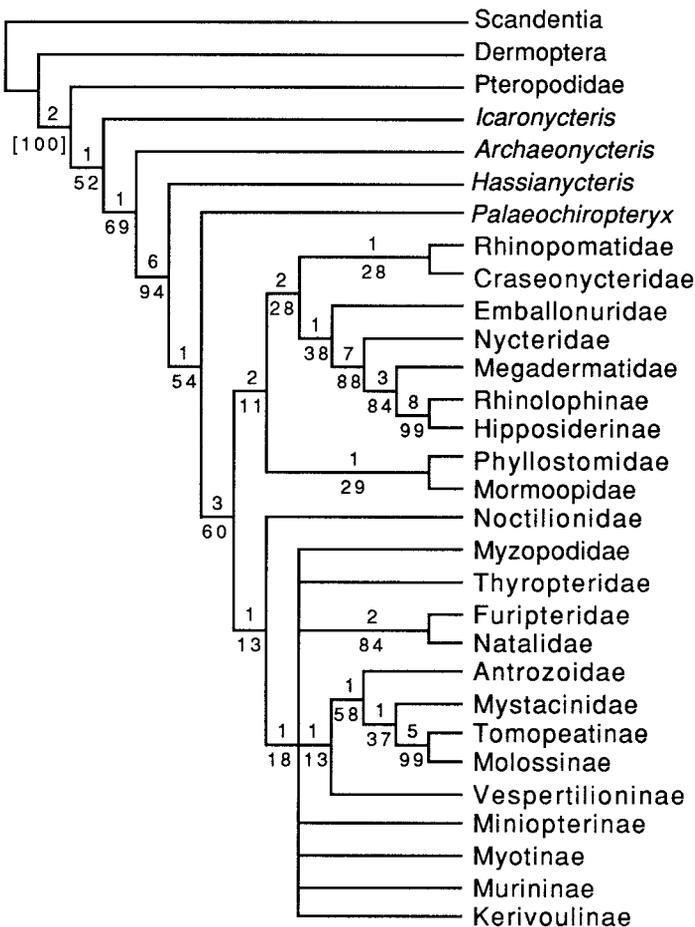


Fig. 37. Results of Analysis 3, which included all taxa but only those characters that could be scored in the fossils (see text for discussion). The tree shown is a strict consensus of eight equally most-parsimonious trees (305 steps; CI = 0.361; RI = 0.601) that resulted from parsimony analysis. The numbers below internal branches are bootstrap values; numbers above the branches are decay values. The bootstrap analysis was constrained to consider only trees in which Chiroptera was monophyletic.

steps; CI = 0.359, RI = 0.603); a strict consensus of these trees is shown in figure 37. Comparisons of this consensus tree with that derived from Analysis 2 (fig. 37) illustrate that both analyses recovered the same relationships among the fossil forms and between the fossils and the microchiropteran crown group. However, comparisons of crown-group topology in figures 36 and 37 indicate that excluding the soft-tissue and molecular characters significantly affected the perceived relationships among the extant lineages. Not only was resolution considerably reduced, but the branching pattern was

extensively rearranged. Emballonuridae, placed as the sister-group to all other microchiropterans in Analysis 2, nested within a monophyletic Yinochiroptera sensu Koopman (1994) in Analysis 3, appearing as the sister-group of Rhinolophoidea. Noctilionoidea, a clade whose monophyly was very strongly supported in Analysis 2, appeared to be polyphyletic in Analysis 3. Instead of grouping with Noctilionidae, Phyllostomidae and Mormoopidae formed a clade that was placed as the sister-group of Yinochiroptera. Resolution was considerably reduced in the yangochiropteran part of the tree, and the po-

sition of Mystacinidae was shifted to within Molossoidea.

At least one of the groupings obtained in Analysis 3 (the Phyllostomidae + Mormoopidae + Emballonuridae + Yinochiroptera clade) appears spurious based on results of Analysis 2, in which it was recovered in fewer than 1% of the bootstrap replicates. Conversely, Analysis 3 did not recover at least two important clades that were strongly supported in the analysis of the complete data set—Yangochiroptera and Nataloidea.

Topology of the hard-tissue tree is clearly not congruent with any previously proposed phylogeny for Chiroptera (e.g., Smith, 1976; Van Valen, 1979; Pierson, 1986; Novacek, 1991; Simmons, 1998), nor is it congruent with results of our analysis of the entire data set (Analysis 2). We conclude from this experiment that exclusion of soft-tissue and molecular characters resulted, at least in this case, in a biased topology that does not provide an adequate basis for inferring relationships.

SUMMARY

Results of the phylogenetic analyses described above support the hypothesis that *Palaeochiropteryx*, *Hassianycteris*, *Archaeonycteris*, and *Icaronycteris* represent a series of successively more distant sister-taxa to the clade comprised of the extant lineages of microchiropteran bats. Inclusion of these taxa significantly affected perceived relationships among extant forms, although only at nodes that were poorly supported in the analysis that included only extant lineages. Inclusion of the fossils also affected bootstrap and decay values associated with the more basal nodes of the crown group. Topology of the

microchiropteran crown group as hypothesized in our Analyses 1 and 2 is little different than that reported by Simmons (1998). The only exceptions are the suggestions that Molossoidea and Vespertilionoidea are sister-taxa (Nataloidea appeared more closely related to Vespertilionoidea in the earlier analysis), and that the Neotropical nataloids (Thyropteridae, Furippteridae, and Natalidae) form a clade.

Results of our experiment in using only characters that could be scored in the fossils (Analysis 3) argue strongly against the common practice of reducing missing data by eliminating soft-tissue and molecular characters from consideration in phylogenetic analyses including fossil organisms. In our study, which admittedly included a high ratio of extant to extinct OTUs, limiting the analysis to hard-tissue characters produced phylogenetic results that we consider fallacious. These results suggest that soft-tissue and molecular characters can be highly informative even when inclusion of such characters introduces considerable amounts of missing data (i.e., empty matrix cells) into the data set. The point at which missing data becomes a serious problem and significantly reduces resolution probably depends on the relative number of fossil taxa, the relative proportion of hard-tissue to soft-tissue and molecular characters, the degree of structure (i.e., level of congruence among characters) present within and among various data subsets, and the exact mosaic of primitive and derived character states seen in the fossils included in the analysis. In the present study, we were fortunate in that these variables combined favorably and facilitated recovery of a well-resolved, relatively well-supported phylogeny of bats.

CHARACTER EVOLUTION IN EARLY CHIROPTERANS

CHARACTER TRANSFORMATIONS ASSOCIATED WITH BASAL NODES

The phylogeny shown in figure 36 provides a framework for evaluating patterns of character transformation at the base of the chiropteran tree. Pteropodidae, *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, *Palaeochi-*

ropteryx, and the microchiropteran crown group share a variety of derived features that have previously been interpreted as synapomorphies of Chiroptera (Simmons, 1994, 1995; see table 5). Features that can be observed in the fossil forms include only about one-third of the characters listed in table 5, principally those related to the skull and

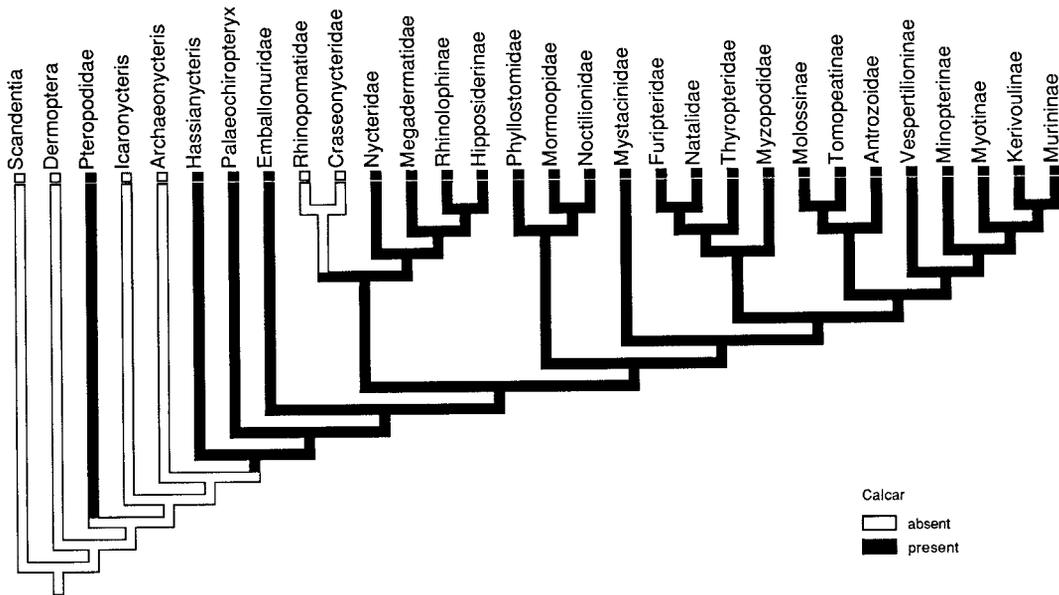


Fig. 38. Presence of the calcar (character 171) mapped on the phylogeny from figure 36. Note that a calcar apparently evolved independently in Pteropodidae and the lineage leading to extant microchiropterans. Accordingly, presence of a calcar does not appear to be a synapomorphy of Chiroptera. Loss of the calcar is presumed to have occurred independently in Rhinopomatoidea and within two terminal taxa, Pteropodidae and Phyllostomidae (loss in terminal taxa not depicted on this tree). See text for discussion.

postcranial skeleton: reduction of the jugal, modification of the elbow, absence of a supinator ridge on and entepicondylar foramen in the humerus, elongation of digits II–V of the forelimb and presence of complex carpometacarpal and intermetacarpal joints, absence of claws on digits III–V, modification of the hip joint, modification of the ankle joint, presence of a calcar, and elongation of the proximal phalanx of digit I of the foot. Virtually all of these features appear related to the evolution of powered flight and underbranch hanging behavior, both of which are presumed to have been present in the most recent common ancestor of Megachiroptera and Microchiroptera (see discussion in Simmons, 1995).

Our data do not contradict these functional hypotheses; however, our observations indicate that some modifications need to be made to Simmons' (1994, 1995) list of synapomorphies of bats. First, examination of the fossil forms and their relationships suggests that presence of a calcar (character 171) is not primitive for Chiroptera (fig. 38; see dis-

cussion below), so this feature should be removed from the list of bat synapomorphies. The principal effect of our analysis, however, has been to identify additional character states that appear to be synapomorphies of bats based on their optimizations on our optimal tree (fig. 36). These newly identified chiropteran synapomorphies (and we list only those that are unequivocal given our tree topology) include the following: (1) vomeronasal epithelial tube absent (character 7; well developed in both outgroups); (2) accessory olfactory bulb absent (character 8; present in both outgroups); (3) enlarged fenestra cochleae (character 32; small or of moderate size in both outgroups); (4) posterior laminae present on ribs (character 88; laminae absent in both outgroups); (5) two facets present in infraspinous fossa of scapula (character 103; only one facet in both outgroups); (6) sacrum terminates posterior to midpoint of acetabulum (character 159; terminates anterior to acetabulum in both outgroups); (7) baculum present (character 174; absent in both outgroups); (8) left cen-

tral lobe of liver separate from other lobes or partially fused with right central lobe (character 193; left central lobe fused with left lateral lobe in both outgroups); and (9) caecum absent (character 195; present in both outgroups). Obviously, only half of these features (characters 32, 88, 103, 159) can be scored in fossil taxa; in each case, however, available data from *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* confirm that these derived traits were present in the earliest members of the microchiropteran lineage. A revised summary of the morphological synapomorphies of Chiroptera is given in table 7.

Icaronycteris, *Archaeonycteris*, *Palaeochiropteryx*, and *Hassianycteris* were clearly well developed bats capable of powered flight (Jepsen, 1966, 1970; Habersetzer and Storch, 1987, 1989; Habersetzer et al., 1989, 1992, 1994; Norberg, 1989, 1994). By tracing character changes associated with the nodes at which these taxa branch from the tree, insight can be gained into patterns of character evolution in the lineage leading from the volant common ancestor of bats to extant microchiropterans. These taxa do not provide much information about steps in the evolution of powered flight since those changes presumably took place long before *Icaronycteris* diverged from the lineage leading to extant microchiropterans.

Icaronycteris shares a number of conditions with *Archaeonycteris*, *Hassianycteris*, *Palaeochiropteryx*, and the microchiropteran crown group that appear to be derived relative to those seen in pteropodids and the outgroups. These features include (1) presence of an elongate angular process on the lower jaw (character 22; not elongate in Pteropodidae and Dermoptera); (2) moderate enlargement of the cochlea (character 26; not enlarged in the outgroups and most Pteropodidae); (3) presence of a large orbicular apophysis on the malleus (character 35; small or absent in the outgroups and Pteropodidae); (4) a stylohyal with an expanded cranial tip (character 74; no enlargement or other modifications in Pteropodidae and Scandentia; lateral stylohyal swollen along entire length in Dermoptera); and (5) the trochiter of the humerus extends proximally to the same level as the humeral head (character 139; does

not extend to level of head in both outgroups and Pteropodidae).

Of these characters, enlargement of the orbicular apophysis, expansion of the tip of the stylohyal, and extension of the trochiter to the level of the head of the humerus are synapomorphies that unequivocally diagnose the clade comprising *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, *Palaeochiropteryx*, and the microchiropteran crown group. The change in morphology of the angular process is an equivocal transformation because an elongate angular process occurs in Scandentia. Alternative explanations for the pattern observed include (1) evolution of a short angular process in the common ancestor of Volantia, and secondary evolution of an elongate angular process in the clade containing *Icaronycteris* and extant microchiropterans; or (2) independent evolution of a short angular process in Dermoptera and Pteropodidae, implying that the elongate angular process seen in *Icaronycteris* and other members of the microchiropteran lineage is plesiomorphic.

Other equivocal transformations that may diagnose the clade comprising *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, *Palaeochiropteryx*, and the microchiropteran crown group include: (1) at least moderate enlargement of the cochlea (character 26; absent in both outgroups and most Pteropodidae); (2) presence of ventral accessory processes on cervical vertebrae 2 and 3 (character 75; absent in both outgroups and some but not all pteropodids); and (3) absence of a suprascapular process on the scapula (character 112; present in both outgroups, absent in some pteropodids). In each of these cases, the derived condition could have either evolved independently within Pteropodidae and in the lineage leading to extant microchiropterans, or it may be a synapomorphy of bats that was reversed within some Pteropodidae.

Another character transformation that occurred somewhere in the basal part of the microchiropteran tree involves a change in the type of attachment of the periotic to the basisphenoid (character 25). In the outgroups and Pteropodidae, the periotic is firmly sutured to the basisphenoid; however, the periotic is only loosely attached in *Archaeonyc-*

TABLE 7
A Revised Summary of Morphological Synapomorphies of Chiroptera

-
- 1) Deciduous dentition does not resemble adult dentition; deciduous teeth with long, sharp, recurved cusps
 - 2) Palatal process of premaxilla reduced; left and right incisive foramina fused in midsagittal plane
 - 3) Postpalatine torus absent
 - 4) Jugal reduced and jugolacrimal contact lost
 - 5) Two entotympanic elements in the floor of the middle-ear cavity: a large caudal element and a small rostral element associated with the internal carotid artery
 - 6) Tegmen tympani tapers to an elongate process that projects into the middle-ear cavity medial to the epitympanic recess
 - 7) Proximal stapedial artery enters cranial cavity medial to the tegmen tympani; ramus inferior passes anteriorly dorsal to the tegmen tympani
 - 8) Enlarged fenestra rotundum
 - 9) Vomeronasal epithelial tube absent
 - 10) Accessory olfactory bulb absent
 - 11) Posterior laminae present on ribs
 - 12) Modification of scapula: reorientation of scapular spine and modification of shape of scapular fossae; reduction in height of spine; presence of a well-developed transverse scapular ligament; presence of at least two facets in infraspinous fossa
 - 13) Modification of elbow: reduction of olecranon process and humeral articular surface on ulna; presence of ulnar patella; absence of olecranon fossa on humerus
 - 14) Absence of supinator ridge on humerus
 - 15) Absence of entepicondylar foramen in humerus
 - 16) Occipitopollicalis muscle and cephalic vein present in leading edge of propatagium
 - 17) Digits II–V of forelimb elongated with complex carpometacarpal and intermetacarpal joints, support enlarged interdigital flight membranes (patagia); digits III–V lack claws
 - 18) Modification of hip joint: 90° rotation of hindlimbs effected by reorientation of acetabulum and shaft of femur; neck of femur reduced; ischium tilted dorsolaterally; anterior pubes widely flared and pubic spine present; absence of m. obturator internus
 - 19) Sacrum terminates posterior to midpoint of acetabulum
 - 20) Absence of m. gluteus minimus
 - 21) Absence of m. sartorius
 - 22) Vastus muscle complex not differentiated
 - 23) Modification of ankle joint: reorientation of upper ankle joint facets on calcaneum and astragalus; trochlea of astragalus convex, lacks medial and lateral guiding ridges; tuber of calcaneum projects in plantolateral direction away from ankle and foot; peroneal process absent; sustentacular process of calcaneum reduced, calcaneo-astragal and sustentacular facets on calcaneum and astragalus coalesced; absence of groove on astragalus for tendon of m. flexor digitorum fibularis
 - 24) Entocuneiform proximodistally shortened, with flat, triangular distal facet
 - 25) Elongation of proximal phalanx of digit I of foot
 - 26) Embryonic disc oriented toward tubo-uterine junction at time of implantation
 - 27) Differentiation of a free, glandlike yolk sac
 - 28) Preplacenta and early chorioallantoic placenta diffuse or horseshoe-shaped, with definitive placenta reduced to a more localized discoidal structure
 - 29) Definitive chorioallantoic placenta endotheliochorial
 - 30) Baculum present
 - 31) Left central lobe of liver separate from other lobes or partially fused with right central lobe
 - 32) Caecum absent
 - 33) Cortical somatosensory representation of forelimb reverse of that in other mammals
-

teris, *Hassianycteris*, *Palaeochiropteryx*, and most members of the microchiropteran crown group. Because the type of periotic attachment could not be scored in available specimens of *Icaronycteris*, we cannot be

sure if this character transformation occurred before or after differentiation of *Icaronycteris* from the stock leading to extant microchiropterans.

The next highest node in the microchirop-

teran tree unites *Archaeonycteris* with *Hassianycteris*, *Palaeochiropteryx*, and the microchiropteran crown group. As noted above, loosening of the connection between the petrotic and basisphenoid (character 25) minimally applies at this level in the tree. Other derived characters that diagnose this clade include (1) reduction of the number of roots on P3 to two or fewer (character 19; P3 with three roots in both outgroups, Pteropodidae, and *Icaronycteris*); (2) presence of a ventral accessory process on cervical vertebra 4 (character 76; accessory process absent from C4 in both outgroups, Pteropodidae, and *Icaronycteris*); and (3) absence of ossified third phalanx in wing digit III (character 152; fully ossified third phalanx present in both outgroups and *Icaronycteris*).

Of these characters, reduction of the number of roots on P3 and presence of a ventral accessory process on C4 are synapomorphies that unequivocally diagnose the clade comprising *Archaeonycteris* and the lineage leading to the microchiropteran crown group. The absence of an ossified third phalanx on wing digit III represents an equivocal transformation because this condition also characterizes Pteropodidae. Alternative explanations for the observed pattern include (1) independent loss of ossification of this phalanx in pteropodids and the lineage leading to extant microchiropterans; or (2) loss of ossification of the third phalanx in the common ancestor of bats, and secondary acquisition of ossification of this element in *Icaronycteris*. Both hypotheses are equally parsimonious, and they also seem equally likely given the complex pattern seen elsewhere in the tree (e.g., three patterns occur within Yangochiroptera—full ossification [secondarily acquired once], ossification only at phalanx base [acquired twice], and no ossification [secondarily acquired once]).

Other character transformations that occur somewhere near the base of the microchiropteran tree (we cannot determine exactly where because of missing data) involve evolution of the phanerochlear condition (character 27), a deep, constricted stapedial fossa (character 31), presence of anterior laminae on the ribs (character 86), broad posterior laminae on the ribs (character 89), and presence of a dorsal articular facet on the

scapula (character 100). The cryptochlear condition is seen in both outgroups and Pteropodidae; the phanerochlear condition occurs in *Hassianycteris*, *Palaeochiropteryx*, and primitively in the microchiropteran crown group. The stapedial fossa in the outgroups and Pteropodidae is indistinct or shallow and broad; this contrasts sharply with the deep, constricted stapedial fossae seen in *Palaeochiropteryx* and primitively in the microchiropteran crown group. Because external cochlear morphology and form of the stapedial fossa could not be scored in available specimens of either *Icaronycteris* or *Archaeonycteris*, we cannot be sure where on the tree between Pteropodidae and *Palaeochiropteryx* the transformations to a phanerochlear condition and a deep, constricted stapedial fossa occurred. Nor can we tell if these changes were coincident or occurred at different points in the tree. Interpretive difficulties similarly occur with other character transformations as a result of missing data. Anterior laminae are absent from the ribs of both outgroups, some Pteropodidae, and *Icaronycteris*, while anterior laminae are present in *Palaeochiropteryx* and primitively within the microchiropteran crown group. Posterior laminae are narrow in Pteropodidae and *Icaronycteris*, but are broad in *Hassianycteris*, *Palaeochiropteryx*, and primitively within the microchiropteran crown group. A dorsal articular facet is absent from the scapula in the outgroups, Pteropodidae, and *Icaronycteris*; however, it is present in *Hassianycteris*, *Palaeochiropteryx*, and primitively in the microchiropteran crown group. Because the conditions of these characters in *Archaeonycteris* could not be determined, we cannot be sure if the transformations in these structures occurred before or after differentiation of *Archaeonycteris* from the lineage leading to the microchiropteran crown group.

Moving up the microchiropteran part of the tree, the next node unites *Hassianycteris*, *Palaeochiropteryx*, and the microchiropteran crown group. As noted above, presence of the phanerochlear condition (character 27), a deep, constricted stapedial fossa (character 31), anterior laminae on the ribs (character 86), broad posterior laminae on the ribs (character 89), and a dorsal articular facet on the scapula (character 100) may apply at this

level in the tree. Derived characters that unambiguously diagnose the clade comprising *Hassianycteris*, *Palaeochiropteryx*, and the microchiropteran crown group include: (1) nyctalodonty (character 21; primitive tribosphenic condition in Scandentia, *Icaronycteris*, and *Archaeonycteris*); (2) a greatly enlarged cochlea (character 26; either not enlarged or only moderately enlarged in the outgroups, Pteropodidae, *Icaronycteris* and *Archaeonycteris*); (3) distal tip of ventral process of manubrium laterally compressed (character 91; tip blunt or rounded in Dermoptera, *Icaronycteris*, and *Archaeonycteris*); (4) absence of an ossified third phalanx (claw) on wing digit II (index finger; character 151; ossified claw present in both outgroups, Pteropodidae, *Icaronycteris*, and *Archaeonycteris*); (5) fibula thin and threadlike (character 170; fibula well developed in both outgroups, Pteropodidae, *Icaronycteris*, and *Archaeonycteris*); (6) calcar present (character 171; calcar absent in both outgroups, *Icaronycteris*, and *Archaeonycteris*). Optimization of the latter character (fig. 38) is somewhat surprising given previous hypotheses (e.g., Simmons, 1994, 1995; see table 5) that presence of a calcar is a synapomorphy of Chiroptera. Our analysis suggests otherwise. A calcar seems to have been absent in the most recent common ancestor of Megachiroptera and Microchiroptera, and apparently evolved independently in Pteropodidae and in the lineage leading to extant microchiropterans.

The last clade directly involving the fossil taxa analyzed in this study is that comprising *Palaeochiropteryx* plus the microchiropteran crown group. Only a single derived character unequivocally diagnoses this clade: presence of a ventral accessory process on cervical vertebra 5 (character 77; absent in both outgroups, Pteropodidae, *Icaronycteris*, *Archaeonycteris*, and *Hassianycteris*). Two other characters minimally apply at this level, but lack of data for *Hassianycteris* and *Archaeonycteris* make it impossible to determine the point of transformation on the tree. These characters include (1) a deep, constricted stapedial fossa (character 31; fossa indistinct in both outgroups, shallow and broad in Pteropodidae), and (2) presence of anterior laminae on the ribs (character 86;

laminae absent in both outgroups, some Pteropodidae, and *Icaronycteris*).

FEATURES DIAGNOSING THE MICROCHIROPTERAN CROWN GROUP

Character transformations that appear to diagnose the microchiropteran crown group fall into two broad categories: (1) features that can be positively attributed to this particular node (by virtue of having been scored with a different state in *Hassianycteris* and more distal outgroups); and (2) derived features that minimally diagnose the crown group but could not be scored in the fossils, leaving open the possibility that they may have evolved earlier (closer to the basal node) in the tree. Transformations of the latter sort may be unambiguous synapomorphies, but it is not clear at what level they apply.

In the first category, we find that only three transformations in hard-tissue characters appear to diagnose the microchiropteran crown group: (1) free premaxilla (character 9; sutured premaxilla in both outgroups, Pteropodidae, and all four Eocene genera); (2) reduction to two lower premolars on each side of the jaw (character 20; three lower premolars in Pteropodidae and all four Eocene genera); and (3) a xiphisternum with prominent median keel (character 95; keel absent in both outgroups, Pteropodidae, *Icaronycteris*, *Archaeonycteris*, and *Palaeochiropteryx*).

In comparison to the lists of features diagnosing more inclusive clades (see above), these synapomorphies by themselves are not compelling. For example, few workers would agree that a free premaxilla is likely primitive for all extant microchiropterans (as suggested by optimization of this character on our tree; fig. 39) because yangochiropteran bats lack this complex specialization. Instead, yangochiropterans have a premaxilla that is firmly fused to the maxilla in the adult. The free premaxilla is a feature unique among mammals, and we agree that it is hard to imagine either its loss or independent origin in two different groups (which are, of course, the two most-parsimonious hypotheses given the topology of our optimal tree). Reduction from three to two lower premolars

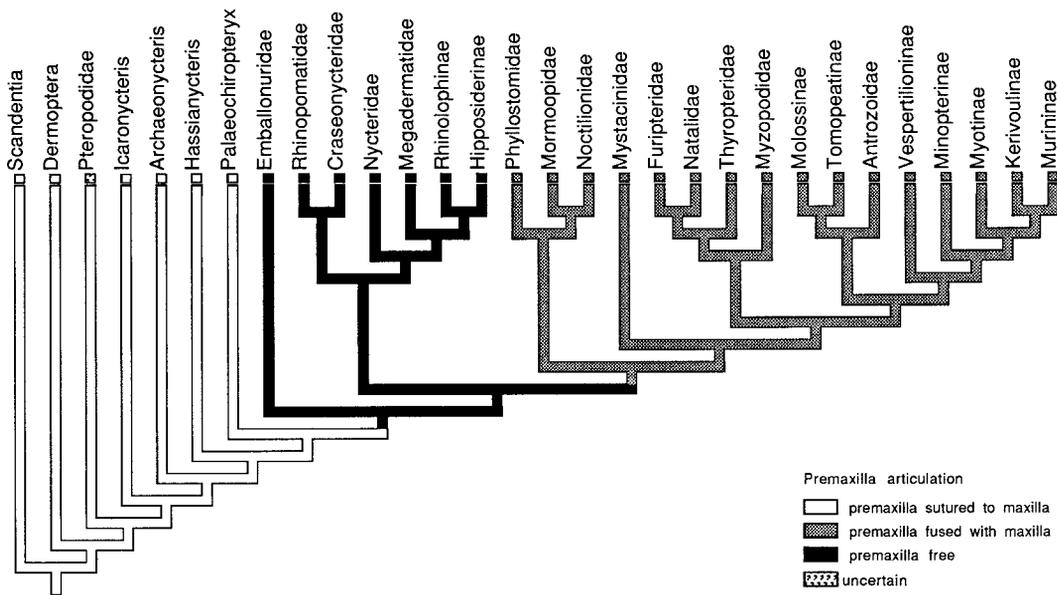


Fig. 39. Premaxilla–maxilla articulations (character 9) mapped on the phylogeny from figure 36. Presence of a free premaxilla appears to be a synapomorphy of the microchiropteran crown group (although see text for discussion). Fusion of the premaxilla to the maxilla is a synapomorphy of Yangochiroptera. The condition for Pteropodidae is depicted as “uncertain” because two conditions occur within this group: the premaxilla is sutured to the maxilla in most pteropodids, but these elements are fused in other taxa. This optimization suggests that a suture joint between the premaxilla and maxilla is primitive for Pteropodidae.

on each side is a character that is similarly troublesome, because presence of three lower premolars characterizes many groups of extant microchiropterans that nest well up within the crown group (e.g., Rhinolophidae, Mormoopidae, Nataloidea, many vespertilionids). This is also true of the xiphisternal keel. Although presence of a keel appears to diagnose the microchiropteran crown group, many lineages within that clade lack a keel on the xiphisternum (e.g., Rhinopomatidae, Hipposiderinae, some Phyllostomidae, Noctilionidae, Myzopodidae, Molossoidea, some Vespertilioninae).

Despite the relative weakness of these data, monophyly of the microchiropteran crown group is indirectly supported by a broad range of other characters that unfortunately have somewhat ambiguous distributions. These transformations minimally diagnose the microchiropteran crown group, but might have evolved earlier in the tree; we could not score them in fossil sister-taxa of the microchiropteran crown group. Such

features are numerous and include the following: (1) presence of a tragus (character 2; absent in outgroups and Pteropodidae); (2) aquaeductus cochleae small or absent (character 33; large in Dermoptera and Pteropodidae); (3) presence of sophisticated echolocation (character 36; absent in outgroups and Pteropodidae); (4) *m. styloglossus* originates from ventral surface of midpoint of stylohyal (character 58; originates from expanded tip of stylohyal and/or adjacent surface of skull in outgroups and Pteropodidae); (5) clavicle articulates with coracoid process of scapula (character 113; clavicle articulates with acromion in both outgroups, Pteropodidae, and *Icaronycteris*); (6) *m. spinotrapezius* clearly differentiated from trapezius complex (character 124; *m. spinotrapezius* not differentiated from trapezius complex in both outgroups and Pteropodidae); (7) origin of *m. acromiodeltoideus* does not include thoracic vertebra 6 (character 127; origin does include T6 in both outgroups and Pteropodidae); (8) spinal cord with angle between dorsal horns

of 0–25° (character 190; angle between dorsal horns 35–50° in both outgroups, 70–80° in Pteropodidae); and (9) inferior colliculus larger than superior colliculus (character 191; inferior colliculus significantly smaller than superior colliculus in both outgroups and Pteropodidae). One other transformation may diagnose the microchiropteran crown group, although it has been documented only in Yinochiroptera and Yangochiroptera (no data for Emballonuridae): *m. flexor digitorum profundus* does not insert on digit II of wing (character 154; muscle does insert on digit II in both outgroups and Pteropodidae). Even if these features evolved in a stepwise fashion up the tree, at least a few probably represent true synapomorphies of the microchiropteran crown group.

CHARACTER TRANSFORMATIONS AT BASAL NODES: A FUNCTIONAL PERSPECTIVE

In the previous section, we described the character transformations that seem to apply at each node in the basal part of the microchiropteran tree. An interesting pattern also emerges when these transformations are viewed from a functional perspective. Rather than changes in each organ system being concentrated at one or two nodes, we see a pattern of stepwise changes in multiple functional systems as we move up the microchiropteran tree. This suggests a complex, mosaic pattern of evolution in which several organ systems were being refined simultaneously.

Overall, the changes associated with the facial region and masticatory apparatus are relatively minor compared to those seen in other systems. In order of their appearance along the backbone of the microchiropteran tree (beginning at the base, prior to divergence of *Icaronycteris*), these transformations include (1) evolution of an elongate angular process (though this may ultimately prove to be plesiomorphic for bats), (2) reduction of the number of roots on P3, (3) evolution of nyctalodonty, and (4) reduction in the number of lower premolars and modification of the simple sutured connection between the premaxilla and maxilla.

Functional implications of these changes

remain obscure, although Slaughter (1970) noted that reduction and simplification of the premolar dentition in early bats appears correlated with shortening of the face (brachycephaly). It is possible that these trends may have been related to the need to focus the ears anteriorly and reduce interference with returning echolocation calls—the auditory equivalent of the type of facial shortening generally associated with evolution of binocular vision. Another possibility is that loss of premolars and reduction in the number of roots on the remaining teeth represent mechanisms for mass reduction. Flying animals must generate adequate lift to remain airborne, and lift requirements increase with increasing body mass (Norberg, 1985, 1986a, 1987, 1990; Rayner, 1986; Norberg and Rayner, 1987). Distribution of body mass is also important because it affects the position of the center of mass (= center of gravity), which in turn influences flight efficiency. The head is the heaviest part of the body in most vertebrates in part because of the density of the teeth. In addition to the effect that a heavy head may have on total body mass and the location of the center of mass, head mass also affect the size of neck muscles needed to support the head and resist torque (Bühler, 1992). Dental reduction in birds (most of which lack teeth entirely) is widely regarded as a specialization that increased flight efficiency because it simultaneously reduced total mass and concentrated more of the body mass near the center of gravity between the wings (e.g., Welty, 1955; Stahl, 1985; Bühler, 1992; Feduccia, 1996). Dental reduction in pterosaurs has also been noted as a possible adaptation for reducing body mass and increasing flight efficiency (e.g., Stahl, 1985; Bühler, 1992). Because bats are mammals that rely on their dentition for food processing, extreme dental reduction is rare (limited mostly to nectarivorous taxa). However, even small reductions in mass may contribute to flight efficiency.

The free premaxilla present in Emballonuridae and Yinochiroptera (and perhaps in the most recent common ancestor of extant microchiropterans; fig. 39) provides an unusual degree of mobility in the snout. Utility of this feature has not been adequately investigated, but our experience in handling

live emballonurids suggests that dorsiflexion of the snout is under voluntary control. Dorsiflexion of the snout effectively increases the gape of the mouth, which may be important in feeding and/or emission of echolocation calls. With respect to the latter, it is interesting to note that the mode of emission of echolocation calls—either through the mouth (oral emission) or through the nasal passages (nasal emission)—varies among bats that have a free premaxilla. Emballonuridae, Craseonycteridae, and perhaps Rhinopomatidae are oral emitters, while Rhinolophoidea and perhaps Rhinopomidae are nasal emitters (Pederson, 1993). Given topology of our tree (fig. 36), it appears that oral emission is primitive and nasal emission derived as suggested by Van Valen (1979) and Pederson (1993). The extent to which dorsiflexion of the snout may have played a role in the evolution of nasal emission in yinochiropteran bats has not been explored.

Free movement of the premaxilla may also be important in prey manipulation, particularly in those taxa that take large arthropod or small vertebrate prey. Fenton (personal commun.) observed a *Nycteris grandis* eating a *Nycteris thebiaca*, and noted that the former used its upper lips extensively and manipulated its prey in an almost closed-mouth fashion. The extent to which a free premaxilla may facilitate the capacity to handle large prey items has yet to be investigated.

Changes in the basicranium and ear region also appear to have evolved in a stepwise fashion. The first modifications to appear (prior to the divergence of *Icaronycteris* from the microchiropteran stem stock) included a moderately enlarged cochlea, enlarged orbicular apophysis on the malleus, and an expanded cranial tip on the stylohyal. All of these features are probably related to the evolution of echolocation. As noted earlier, presence of a large orbicular apophysis may improve the ability of the middle ear ossicles to transmit high-frequency sounds with a minimum time delay, or may play a role in the avoidance of self-deafening (see discussion under character 35 above). The fact that all known extant microchiropterans have an enlarged orbicular apophysis—and all use echolocation—leads us to suspect that

whatever the function(s) of this structure, an enlarged orbicular apophysis evolved to facilitate efficient function of the ear in echolocation. Likewise, the expanded tip on the stylohyal may represent a refinement of the system for producing echolocation calls. The microchiropteran echolocation system depends upon calls produced in the larynx, which is supported in part by muscles associated with the hyoid apparatus. The expanded tip on the stylohyal—which is firmly attached to the bulla—serves to anchor the hyoid apparatus to the skull, thus providing a stable attachment site for muscles of the throat. This attachment may be important in supporting the larynx during production of echolocation calls.

Enlargement of the cochlea (specifically the basal turn) in microchiropterans appears to be a specialization for increased sensitivity to high-frequency sounds (>20 kHz), such as the returning echoes from vocalizations used in echolocation (Henson, 1970; Novacek, 1985a, 1987, 1991; Habersetzer and Storch, 1992). In all mammals, the basal turn of the cochlea is the region where high-frequency sounds are perceived (Henson, 1970; Dallos, 1973; Bruns, 1979; Bruns et al., 1983–1984; Harris and Dallos, 1984). Enlargement of this region, which effectively lengthens the basal portion of the basilar membrane, apparently increases sensitivity to high-frequency sounds and slight frequency shifts in this range (Henson, 1970; Dallos, 1973; Bruns, 1979; Bruns et al., 1983–1984; Harris and Dallos, 1984).

In the lineage leading to extant Microchiroptera, cochlear enlargement seems to have evolved in a relatively continuous fashion that we chose to score as a series of steps (fig. 40). The primitive condition for bats was the presence of an unenlarged cochlea, one comparable in size to those seen in other mammals of similar body size. A moderately enlarged cochlea evolved prior to the divergence of *Icaronycteris*, to be followed subsequently by even greater enlargement before the divergence of *Hassianycteris*. Moderate enlargement of the cochlea does not by itself indicate that a bat could echolocate, because some nonecholocating pteropodids have a moderately enlarged cochlea (see discussion under character 26 above). However, the

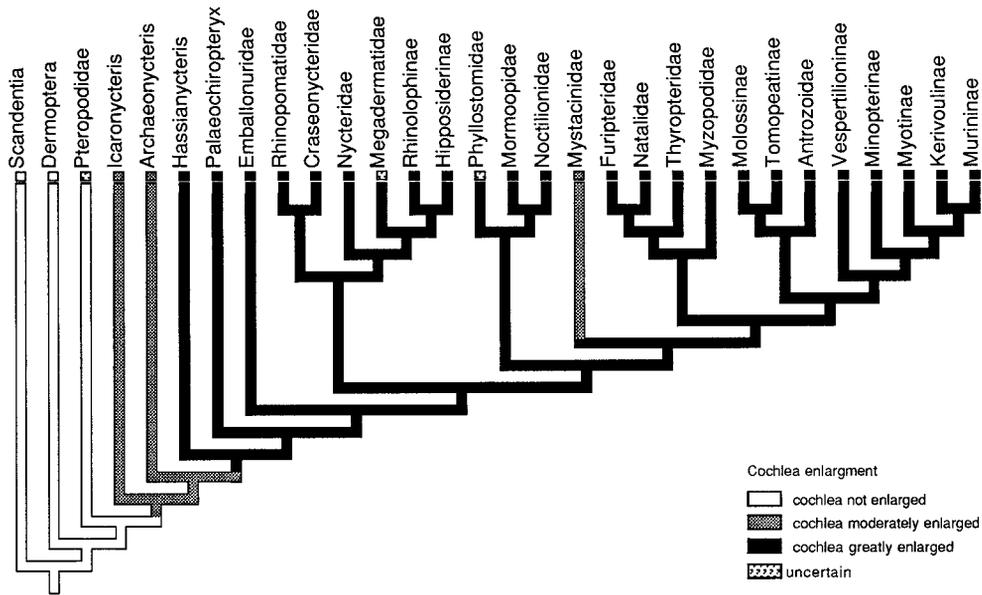


Fig. 40. Cochlear enlargement (character 26) mapped on the phylogeny from figure 36. In the lineage leading to extant microchiropterans, a “moderately enlarged” cochlea evolved prior to the divergence of *Icaronycteris*; a “greatly enlarged” cochlea evolved prior to the divergence of *Hassianycteris*. Reversions to the former condition apparently occurred independently in Mystacinidae and within Megadermatidae and Phyllostomidae (note that the latter taxa are marked as “uncertain” as a result of taxonomic polymorphism). This optimization also suggests that a moderately enlarged cochlea evolved independently within Pteropodidae (see text for discussion).

combination of a moderately enlarged cochlea, enlarged orbicular apophysis on the malleus, and an expanded cranial tip on the stylohyal are seen in extant bats *only* in forms that use echolocation. We therefore follow previous authors (e.g., Novacek, 1985a, 1987, 1991; Habersetzer and Storch, 1992) in inferring that *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* used echolocation. We agree with Pye (1968: 797), who observed that

The Eocene brought mammals mean
And bats began to sing;
Their food they found by ultrasound
And chased it on the wing.

The implications of cochlear morphology for reconstructing foraging strategies is discussed in depth below under “Foraging ecology of Eocene bats.”

Loose attachment of the periotic to the basicranium evolved prior to the divergence of *Archaeonycteris*, although we cannot determine the exact level in the phylogeny because this character could not be scored in

Icaronycteris. Based on the presumed function of this loose attachment—cochlear isolation, thought to function in reducing bone conduction of laryngeal vibrations (Henson, 1970; Van Valen, 1979)—we surmise that this feature evolved in concert with the early stages of cochlear enlargement and facilitated the evolution of echolocation.

Another transformation that took place in the microchiropteran lineage prior to the divergence of *Hassianycteris* was evolution of a phanerochlear cochlea. Unfortunately, we cannot determine the level of this transformation in the phylogenetic tree because this character could not be scored in *Icaronycteris* or *Archaeonycteris*. The phanerochlear condition was explained by Novacek (1991: 84) as “an accommodation to the problem of “packing” middle ear structures in a space constrained by the expanded cochlea.” As discussed above under character 27, this feature is probably linked to cochlear expansion, although we cannot be sure at what point the phanerochlear condition evolved relative to changes in cochlear size.

Prior to the divergence of *Palaeochiropteryx*, yet another transformation took place: evolution of a deep, constricted fossa for *m. stapedius*. Again, we cannot determine the level of this transformation in the phylogenetic tree because this character could not be scored in *Icaronycteris*, *Archaeonycteris*, or *Hassianycteris*. The function of this transformation remains somewhat obscure, although it is possible that it is in some way linked to the system for avoiding self-deafening that is used by many echolocating bats (Henson, 1964, 1965, 1966, 1967a, 1979; Jen and Suga, 1976; Fenton et al., 1995; see discussion below).

Transformations in features of the postcranial skeleton also seem to have evolved in a series of steps up the tree. The first change in the postcranium was proximal extension of the trochiter up to the level of the head of the humerus, which occurred prior to the divergence of *Icaronycteris*. Several other derived traits evolved subsequently, although we cannot be sure at what level because they could not be scored in *Archaeonycteris*. These traits include (1) presence of a dorsal articular facet on the scapula, (2) presence of anterior laminae on the ribs, and (3) presence of broad posterior laminae on the ribs. Transformations that occurred subsequent to the divergence of *Archaeonycteris* but prior to the divergence of *Hassianycteris* include (1) laterally compressed ventral process of the manubrium, (2) loss of an ossified third phalanx in digit II of the wing, (3) reduction of fibula to a thin, threadlike element, and (4) presence of a calcar.

Dividing these features by anatomical region, we see progressive changes occurring in different functional units. Modifications of the shoulder region began with enlargement of the trochiter, which preceded evolution of a dorsal articular facet on the scapula. A functional shoulder-locking mechanism, which requires a secondary articulation between the trochiter and dorsal articular facet, was clearly present by the time that *Hassianycteris* diverged from the lineage leading to extant microchiropterans. In terms of morphology, the primitive shoulder-lock apparently consisted of a trochiter that extended up to but not beyond the humeral head, and a dorsal articular facet in the form of a small

groove or oval situated on the anteromedial rim of the glenoid fossa.

In the forelimb skeleton, we see progressive reduction in the number of phalanges in digit II of the wing (the index finger) beginning after the onset of evolutionary changes in the shoulder region (fig. 41). Because the thumb is relatively small in all bats (at least in comparison to the other digits of the hand), digit II forms the leading edge of the dactylopatagium ("hand wing") near the wrist. The dactylopatagium plays an important role in both lift generation and steering during flight (Vaughan, 1959; Norberg, 1969, 1970, 1972b, 1976; Hill and Smith, 1984). Stiffness of leading edge of the dactylopatagium—particularly the section known as the dactylopatagium minus, which extends between the second and third digits—is critical to the ability of the wing to resist bending and twisting forces (Norberg, 1969, 1970, 1972b). This functional unit is also important in maintaining wing camber (Vaughan, 1959, 1970c; Norberg, 1970, 1972b, 1976).

In bats lacking the distal phalanges on digit II, a ligamentous connection runs between the end of first phalanx of digit II and the base of the second phalanx in digit III (Norberg, 1969, 1970, 1972b). This ligament is kept under continuous tension by the structure of digit III, which is bent posterodorsally due to the structure of the metacarpophalangeal joint (Norberg, 1969, 1970, 1972b). This arrangement results in a convex frame within which the dactylopatagium minus is kept stretched under tension, thus forming a unit that is stiff in the plane of the membrane (Norberg, 1969, 1970, 1972b). Photographs of flying bats show that the airstream produces little deformation of the dactylopatagium minus or its supporting elements during flight (Norberg, 1969, 1970). The tensile strength of the second digit is critical to the function of this unit, since the second digit must resist the forces placed upon the dactylopatagium minus during flight. Reduction of the number of phalanges in digit II apparently took place in a sequential fashion in bats, with complete loss of ossified phalanges evolving independently at least three times in the microchiropteran crown group (fig. 41). It seems likely that loss of phalanges served

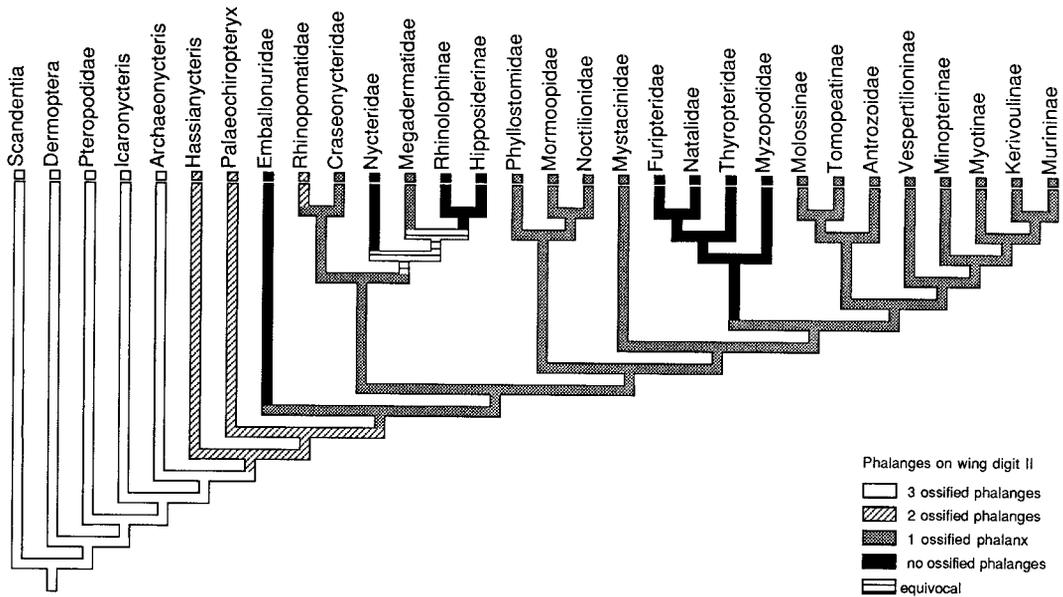


Fig. 41. Changes in the number of phalanges on wing digit II (the index finger; characters 149, 150, and 151) mapped on the phylogeny from figure 36. Presence of three ossified phalanges on digit II is primitive for bats. Reduction to two ossified phalanges occurred just prior to the divergence of *Hassianycteris* from the lineage leading to the microchiropteran crown group. The microchiropteran crown group is diagnosed by further reduction to only one ossified phalanx. Complete phalangeal reduction (no ossified phalanges on wing digit II) apparently evolved independently at least three times in the crown group—in Emballonuridae, Nataloidea, and either in the common ancestor of Rhinolophoidea or independently in Nycteridae and Rhinolophidae. Presence of two ossified phalanges in Rhinopomatidae appears to be a reversal rather than retention of the primitive condition.

to increase the tensile strength per unit mass of the distal second digit by replacing articulated phalanges (which together have a relatively low tensile strength per unit mass) with a continuous ligament that has a higher tensile strength per unit mass. Mass reduction, particularly near the distal end of the wing, contributes significantly to efficient flight performance (Swartz, 1997). Loss of the distal phalanges may represent a mechanism for distal mass reduction as constrained by the need to provide the tensile strength necessary to maintain a stiff dactylopatagium minus during flight.

Modifications in the axial skeleton in the basal part of the microchiropteran tree included evolution of anterior laminae and broad posterior laminae on the ribs. Broad posterior laminae evolved prior to the divergence of *Hassianycteris*, although we cannot be sure of the level because we could not score this character in *Archaeonycteris*. Sim-

ilarly, anterior laminae evolved at some point prior to the divergence of *Palaeochiropteryx*, although we cannot be sure of the level because we could not score this character in *Archaeonycteris* or *Hassianycteris*. In any case, these modifications are absent in *Icaronycteris*, so they must have occurred within the basal microchiropteran lineage. We expect that function of rib laminae is twofold: to stiffen the ribcage and to provide larger areas for muscle attachment. Muscle groups that originate directly from the ribcage include those of the m. serratus anterior complex, which is a critical component of the flight musculature. The posterior division of m. serratus anterior contributes to the downstroke, and the anterior division serves to anchor the medial edge of the scapula and may also help to initiate the upstroke of the wing (Vaughan, 1959, 1970b; Norberg, 1970, 1972a; Strickler, 1978; Hermanson and Altenbach, 1983, 1985).

A close association has been demonstrated between wingbeat and sound emission in microchiropterans under laboratory conditions (Schnitzler, 1968, 1970a, 1970b, 1971, 1973; Suthers et al., 1972; Schnitzler and Henson, 1980; Joerman and Schmidt, 1981; Heblich, 1986; Lancaster et al., 1992) and in free-flying bats foraging in nature (Kalko, 1994). Recent studies of flight, respiration, energy expenditure, and echolocation have indicated that while production of echolocation calls is extremely costly in resting bats, there is little additional cost for echolocation in flying bats (at least for search-phase calls; Kalko, 1994) because the same muscles that flap the wings also ventilate the lungs and produce the pulses of breath used to generate echolocation calls (Speakman et al., 1989; Rayner, 1991a, 1991b; Speakman and Racey, 1991; Speakman, 1993). A critical link in this system is *m. serratus anterior*, which ties the ribcage to the flight mechanism. The increased attachment area for this muscle complex provided by anterior and posterior laminae on the ribs—and concomitant increase in stiffness of the ribcage that we hypothesize is created by these laminae—may simultaneously increase efficiency of the flight mechanism, ventilation, and echolocation system. *M. serratus anterior* plays an important role in flight during the downstroke and early stages of the upstroke. A larger area of origin may provide for improved performance of this muscle complex in flight and may also facilitate ventilation of the lungs both by increasing the area of the connection between the flight apparatus and ribcage. Increased stiffness of the ribcage caused by presence of rib laminae could also facilitate exhaling and production of echolocation calls by increasing the force of elastic recoil of the ribcage upon relaxation of *m. serratus anterior*. We note that the echolocating bat species studied by Speakman and his colleagues (*Phyllostomus hastatus*, *Plecotus auritus*, *Pipistrellus pipistrellus*, and *Plecotus auritus*) all have some degree of development of rib laminae. It would be interesting to determine if the few microchiropterans that lack rib laminae (e.g., *Molossus molossus*) are as energy-efficient while flying and echolocating as are taxa with rib laminae. If rib laminae have been secondarily lost in these forms (as we infer

from our phylogeny), we would expect that any loss in efficiency related to ribcage structure would have been compensated for by other mechanical changes in the flight, ventilation, and echolocation systems.

Another change in the axial skeleton involved evolution of a laterally compressed ventral process on the manubrium, which appeared prior to the divergence of *Hassianycteris*. Changes in this structure, which forms a keel when laterally compressed, are likely to be functionally related to the flight muscles that originate from the manubrium, specifically *m. pectoralis*. *M. pectoralis* provides most of the power for the downstroke of the wings (Vaughan, 1959, 1970b; Strickler, 1978). More anteriorly located fibers in this complex (e.g., those originating from the manubrium rather than from the body of the sternum) draw the humerus downward and sharply forward, whereas the posterior fibers pull the humerus downward and backward (Vaughan, 1959). Modification of the ventral process of the manubrium may reflect changes in the relative size, moment arm, and functional importance of the anterior portion of *m. pectoralis*.

Moving to the hindlimbs, we find the first case in which known modifications of an anatomical region seemingly evolved in a single segment of the tree rather than in a stepwise manner. In this instance, all changes occurred after the divergence of *Archaeonycteris* and prior to the divergence of *Hassianycteris*. Two transformations occurred at this level: reduction of the fibula to a thin, threadlike element, and evolution of a calcar. The functional implications of the former are not clear. Several authors have noted fibular reduction in extant microchiropterans, and have implied that reduction of the fibula is somehow associated with lack of a need for a robust fibula in bats that habitually hang under branches and do not use typical quadrupedal locomotion (Vaughan, 1959, 1970a; Walton and Walton, 1968, 1970; Howell and Pylka, 1977; Hill and Smith, 1984). This suggests that the fibula may have been reduced by default when it was no longer needed to support compressive forces associated with quadrupedal locomotion. However, the correlation between hanging behavior and a thin fibula is not per-

fect, as pteropodids retain a relatively robust fibula. In the latter case, retention of a robust fibula may reflect the use of the hindlimbs in manipulating food, which is a behavior that is common in pteropodids (e.g., *Epomophorus*, *Rousettus*, *Dobsonia*, and *Cynopterus*; B. Fenton, personal commun.). Regardless, a more detailed evaluation of hindlimb myology and function will be needed to better assess possible causes for fibular reduction.

As noted previously, presence of a calcar was once considered to be a synapomorphy of Chiroptera (e.g., by Simmons, 1994, 1995), but it now appears that a calcar evolved independently in Pteropodidae and the microchiropteran lineage (fig. 38). Known or suspected functions of the calcar are diverse, including (1) supporting the trailing edge of the uropatagium and helping to control camber of the uropatagium during flight (which in turn may affect the amount of lift generated by the uropatagium); (2)

helping to hold the uropatagium in a cupped position to capture and hold prey during aerial hawking; (3) holding the uropatagium out of the way of the feet in species that trawl over water for prey; and (4) helping to cup the uropatagium to hold young as they are being born (Vaughan, 1959, 1970a, 1970b; Webster and Griffin, 1962; Norberg, 1976; Hill and Smith, 1984; Schnitzler et al., 1994; Kalko, 1995). Of these functions, there is little chance that the latter two (use in trawling and in parturition) were important factors in calcar evolution. Trawlers are limited to clades nested well within Microchiroptera (i.e., Noctilionidae and Vespertilionidae), and a calcar size is not sexually dimorphic. We suspect that evolution of the calcar in the microchiropteran lineage was associated with transformations in flight habits and/or foraging strategies. Correlations of calcar evolution with other postcranial modifications seem to support this hypothesis (see below for additional discussion).

EVOLUTION OF ECHOLOCATION AND FORAGING STRATEGIES

An extensive literature on the evolution of echolocation and foraging strategies in bats has developed in the decades since Griffin and Novick's influential studies (e.g., Griffin and Novick, 1955; Griffin, 1958; Novick, 1958a, 1958b, 1962, 1963a; Griffin et al., 1960) first documented the use of echolocation in microchiropterans. Numerous issues have been discussed, including (1) the timing of the origin of echolocation relative to the evolution of powered flight; (2) relationships between wing shape, echolocation call structure, and foraging behavior; and (3) costs and benefits of different flight and foraging strategies (e.g., Vaughan, 1959, 1966, 1970b; Struthsaker, 1961; Novick, 1963b, 1965, 1977; Novick and Vaisnys, 1964; Gould, 1970; Schnitzler, 1970b; Vaughan and Bateman, 1970; Fenton, 1972, 1974a, 1974b, 1980, 1982a, 1982b, 1984, 1990, 1994a, 1995; Findley et al., 1972; Gillette, 1975; Pirlot, 1977; Fiedler, 1979; Simmons et al., 1979; Pye, 1980; Schnitzler and Henson, 1980; Simmons, 1980; Simmons and Stein, 1980; Norberg, 1981, 1986a, 1986b, 1989,

1990, 1994; Bell, 1982a, 1985; Neuweiler, 1984, 1989, 1990; Barclay, 1985, 1986; Novacek, 1985a, 1987, 1991; Habersetzer, 1986; Mein and Tupinier, 1986; Scholey, 1986; Aldridge and Rautenbach, 1987; Norberg and Rayner, 1987; Schnitzler et al., 1987, 1994; Jones and Rayner, 1988, 1991; Neuweiler and Fenton, 1988; Speakman et al., 1989; Kalko and Schnitzler, 1989, 1993; Rayner, 1991b; Speakman and Racey, 1991; Speakman, 1993; Jones, 1994; Fenton et al., 1995; Kalko, 1995; Arita and Fenton, 1997). With few exceptions, these discussions have focused principally on functional correlations and have paid little attention to phylogenetic context. This has been due in part to lack of a well-corroborated phylogeny, which has hindered evolutionary interpretations of many types of data. The phylogeny proposed in the present study (fig. 36) provides an opportunity to reexamine previous hypotheses about the evolution of echolocation and foraging strategies in bats, and to draw new inferences based on examination of functional correlations in an explicitly phylogenetic

context. Because the focus of our study is relationships of the Eocene bats to extant lineages, we limit our discussion here to hypotheses relevant to the basal nodes in the tree. Evolution of echolocation call structure, wing design, and foraging strategies among and within extant lineages will be addressed elsewhere (e.g., Kalko and Simmons, ms).

TIMING OF THE ORIGIN OF FLIGHT AND ECHOLOCATION

One topic that has drawn considerable attention in recent years is the origin of flight and echolocation in bats (e.g., Padian, 1987; Norberg, 1989, 1994; Rayner, 1991b; Speakman, 1993; Fenton et al., 1995; Arita and Fenton, 1997). This has been due in part to the bat monophyly controversy (see "Relationships Among Extant Lineages of Bats" above), which promulgated the idea that flight may have evolved independently in Megachiroptera and Microchiroptera (Smith and Madkour, 1980; Hill and Smith, 1984; Pettigrew, 1986, 1991a, 1991b, 1994, 1995; Pettigrew and Jamieson, 1987; Pettigrew et al., 1989; Rayner, 1991b; Pettigrew and Kirsch, 1995). If flight evolved independently in these two groups, then it is appropriate to treat Megachiroptera and Microchiroptera separately in developing evolutionary hypotheses about the origins of flight and sophisticated echolocation. This approach superficially simplifies the problem because it eliminates the need to simultaneously explain the conditions seen in Megachiroptera (well developed flight capabilities, visual orientation in all species, use of primitive echolocation in a few species^{3, 8}) and Microchiroptera

(well developed flight capabilities, orientation by sophisticated echolocation in all species).

Considering the origin of flight and echolocation in Microchiroptera, three theories have recently emerged: the "tandem evolution" theory (Speakman, 1993), the "flight first" theory (Norberg, 1989, 1994), and the "echolocation first" theory (Hill and Smith, 1984; Fenton et al., 1995). Speakman's (1993) hypothesis that flight and echolocation evolved simultaneously in Microchiroptera is based on the observed functional link between flight, ventilation, and echolocation in extant microchiropterans (Speakman et al., 1989; Speakman and Racey, 1991). This theory suggests that microchiropterans evolved from small nocturnal insectivores that may have used ultrasound for intraspecific communication, and were thus able to "capitalize on the opportunity to develop in tandem with flight a sophisticated echolocation system, since this would require no major redirection in its sensory specialization" (Speakman, 1993: 56). The details of just how and why flight and sophisticated echolocation evolved have not been explored under this scenario, although a link between predation and echolocation has been suggested (Speakman, 1993). Speakman (1993: 58) noted that an alternative model where flight evolved first and was followed much later by the evolution of echolocation "seems improbable," but he did not present any arguments in support of this position.

The flight-first (Norberg, 1989, 1994) and echolocation-first (Hill and Smith, 1984; Fenton et al., 1995) theories apparently agree that microchiropterans probably arose from gliding, nocturnal insectivores that used a primitive form of echolocation with short, broadband (i.e., frequency modulated) clicks to help in orientation. The flight-first theory proposes that the next step involved the evolution of powered flight to improve mobility in the arboreal milieu and reduce the amount of time and energy required for foraging (Norberg, 1994). At this stage, these animals would have been able to fly, but still lacked the ability to capture airborne prey because they were not maneuverable enough (Norberg, 1989, 1994). Sophisticated echolocation—which could be used for detecting,

⁸ Echolocation is thought to be used by only a very few megachiropteran bats: *Rousettus aegypticus*, *R. amplicaudatus*, *R. leschenaulti*, and perhaps *Eonycteris spelaea* (Möhres and Kulzer, 1956; Griffin et al., 1958; Novick, 1958b; Gould, 1988; Kingdon, 1974; Sales and Pye, 1974; Roberts, 1975; Hebert, 1986). In *Rousettus*, echolocation signals are produced by clicking the tongue (Möhres and Kulzer, 1956; Kulzer, 1958, 1960; Novick, 1958b; Kingdon, 1974; Sales and Pye, 1974; Roberts, 1975). *Eonycteris* produces signals that may be used in echolocation by slapping the tips of the wings together during flight (Gould, 1988). Both *Rousettus* and *Eonycteris* apparently use echolocation only in situations where there is little or no ambient light (e.g., in the back of a cave or in a dark room); tongue-clicks and wing-slaps cease when light levels are increased (Kingdon, 1974; Gould, 1988).

tracking, and evaluating airborne prey—is hypothesized to have evolved only after powered flight (Norberg, 1989, 1994; Arita and Fenton, 1997). Contra Speakman (1993), Arita and Fenton (1997) noted that the flight first hypothesis is supported by the mechanical coupling of flight and echolocation in extant microchiropterans (Speakman et al., 1989; Rayner, 1991a, 1991b; Speakman and Racey, 1991; Speakman, 1993), which suggests that laryngeal echolocation may be cost-effective only when linked to a well developed flight and ventilation system.

An alternative to this hypothesis is the echolocation-first theory proposed by Fenton et al. (1995). They suggested that the ability to use echolocation to detect, track, and assess airborne prey evolved in the gliding ancestors of microchiropterans as a result of selection for stronger signals to increase the effective range of echolocation (Fenton et al., 1995; Arita and Fenton, 1997). The echolocation-first theory argues that gliding “pre-bats” hunted from perches using echolocation to detect, track, and assess airborne prey in the subcanopy, and that powered flight evolved later to increase maneuverability and simplify returning to the hunting perch (Fenton et al., 1995; Arita and Fenton, 1997). The latter scenario was first suggested by Hill and Smith (1984), although they did not provide any details.

Arita and Fenton (1997: 56) reviewed the flight-first and echolocation-first theories and concluded that “both theories are coherent with current knowledge on echolocation and flight.” They failed to observe, however, that only one—the flight-first theory—is realistically compatible with bat monophyly. As discussed above under “Relationships Among Extant Lineages of Bats,” chiropteran monophyly is now supported by an enormous body of evidence, and it indeed represents one of the most strongly supported hypotheses in all of higher-level mammalian systematics (Lockett, 1980a, 1993; Wible and Novacek, 1988; Kovtun, 1989; Adkins and Honeycutt, 1991, 1993, 1994; Mindell et al., 1991; Thewissen and Babcock, 1991, 1993; Ammerman and Hillis, 1992; Bailey et al., 1992; Kay et al., 1992; Novacek, 1992, 1994; Stanhope et al., 1992, 1993, 1996; Beard, 1993; Honeycutt and Adkins, 1993;

Knight and Mindell, 1993; Simmons, 1993a, 1994, 1995; Wible and Martin, 1993; Simmons and Quinn, 1994; Kirsch et al., 1995; Allard et al., 1996; Hutcheon and Kirsch, 1996; Kirsch, 1996; Miyamoto, 1996; Porter et al., 1996). Given that bats are monophyletic, it seems clear that powered flight evolved only once in mammals, and that the most recent common ancestor of Megachiroptera and Microchiroptera was a flying mammal—a bat (Simmons, 1994, 1995).

Speakman (1993) suggested that bats could be monophyletic but derived from a nonflying most recent common ancestor. We reject this hypothesis because it is highly unparsimonious. By our tally, supposing that flight evolved independently in the two suborders requires the independent evolution of more than a dozen derived traits and character complexes of the postcranial musculoskeletal and nervous systems (table 7), a scenario that we consider to be extremely unlikely. There is no compelling evidence that these traits are not homologous in Megachiroptera and Microchiroptera, and we are not convinced by Speakman’s (1993) suggestion that flight and echolocation must have evolved in tandem in Microchiroptera. Flight can clearly evolve in the absence of echolocation, as demonstrated by the existence of Megachiroptera and birds. Accordingly, we accept—because these represent the best supported hypotheses given all the data available—that bats are monophyletic and flight arose prior to the split between megachiropterans and microchiropterans.

Given these inferences, it seems clear that the origin of sophisticated echolocation must have occurred after the origin of flight as proposed by Norberg (1989, 1994). Sophisticated echolocation is unknown in Megachiroptera, so it is unlikely that this system evolved earlier than in the basal microchiropteran lineage. According to Fenton et al. (1995) and Arita and Fenton (1997), if bats are monophyletic and flight arose only once, then the echolocation first theory could be adjusted to fit. Fenton et al. (1995: 230) suggested that

In this case, echolocation was lost early in the Megachiroptera and reappeared [later] on in the genus *Rousettus*. The echolocation signals in *Rousettus* are tongue clicks, not vocalizations, supporting the po-

sition that echolocation per se is not a common feature of the Chiroptera.

We agree completely with the latter observation, but fail to see how this is consistent with the echolocation-first theory. In our view, the fact that known megachiropteran echolocators use systems different from that seen in Microchiroptera (see footnote 8) provides additional evidence that the most recent common ancestor of extant bats did *not* use echolocation. Because this ancestor was presumably a flying mammal, it follows that echolocation did not evolve first, but rather powered flight did. Hill and Smith (1984) and Rayner (1991b) observed that the obvious benefits of echolocation for nocturnal orientation and obstacle detection are so great that it seems highly unlikely that megachiropterans would have lost such an adaptation only to redevelop it in another form. The success and broad distribution of *Rousettus*, as well as the continued use of echolocation by frugivorous and nectarivorous microchiropterans (i.e., phyllostomids), indicate that echolocation can be advantageous even for phytophagous forms (Hill and Smith, 1984; Rayner, 1991b; Speakman, 1993). We agree with these authors, and see no reason to postulate a loss and reevolution of echolocation in the megachiropteran lineage, especially since a more parsimonious explanation is available—that flight evolved in a common ancestor of all bats and sophisticated echolocation arose later, early in the microchiropteran lineage.

The primitive types of echolocation seen in *Rousettus* and *Eonycteris* apparently evolved independently of one another and of echolocation in Microchiroptera. This interpretation is supported by the most recent phylogenies of Megachiroptera derived from morphological data, DNA hybridization data, and 12S rRNA-valine tRNA mitochondrial gene sequences (Springer et al., 1995; Hollar and Springer, 1997). *Rousettus* and *Eonycteris* do not form a clade to the exclusion of other megachiropterans in any trees, and neither occupies a basal position within Megachiroptera (Springer et al., 1995; Hollar and Springer, 1997). Accordingly, the most parsimonious interpretation is that orientation using tongue-click echolocation (*Rousettus*),

wing-slap echolocation (*Eonycteris*), and laryngeal echolocation (Microchiroptera) originated as independent evolutionary events after the divergence of Megachiroptera and Microchiroptera.

The flight-first theory as articulated by Norberg (1989, 1994) is not entirely compatible with the current phylogenetic evidence because it suggests that the gliding ancestors of bats used a primitive form of laryngeal echolocation (short broadband vocal clicks) to help with orientation in their nocturnal, arboreal habitat. Again, our difficulties with this idea stem from the absence of such echolocation in Megachiroptera as well as the absence of any evidence that echolocation predated the evolution of flight in the lineage leading to bats. Many authors (e.g., Jepsen, 1970; Fenton, 1974b; Hill and Smith, 1984; Padian, 1987; Norberg, 1989, 1994; Speakman et al., 1989; Speakman, 1993; Altringham, 1996) have suggested that a primitive form of echolocation is probably plesiomorphic for bats because this sort of echolocation appears today among small nocturnal mammals, including many lipotyphlan insectivores (e.g., *Sorex*, *Blarina*, *Hemicentetes*, *Echinops*, *Microgale*, *Centetes*; Gould et al., 1964; Gould, 1965; Sales and Pye, 1974; Buchler, 1976; Tomasi, 1979; Foreman and Malmquist, 1988) and at least one rodent (*Rattus*; Rosenzweig et al., 1955; Chase, 1980; Henson and Schnitzler, 1980). Although many workers have assumed that bats evolved from some branch of what we now recognize as Insectivora (e.g., Jepsen, 1970; Hill and Smith, 1984; Kovtun, 1989), recent phylogenetic studies of interordinal relationships of mammals have not generally supported a close relationship between bats and lipotyphlan insectivores, nor between bats and other small nocturnal mammals such as rodents (Wible and Novacek, 1988; Bailey et al., 1992; Novacek, 1992, 1994; Stanhope et al., 1992, 1993, 1996; Adkins and Honeycutt, 1993, 1994; Simmons, 1993a, 1994, 1995; Szalay and Lucas, 1993; Wible, 1993; Simmons and Quinn, 1994; Vrana, 1994; Al-lard et al., 1996; Miyamoto, 1996; Porter et al., 1996). The fact that some living insectivores and rodents use a primitive form of echolocation is thus only slightly more relevant to our understanding of bat evolution

than is the observation that some birds (e.g., oilbirds [*Steatornis*] and cave swiftlets [*Collocalia*, *Aerodramus*]) also use echolocation (Griffin, 1953; Novick, 1959; Medway, 1959, 1967; Cranbrook and Medway, 1965; Griffin and Suthers, 1970; Fenton, 1975; Henson and Schnitzler, 1980). These cases illustrate that a limited form of echolocation can (and has) evolved more than once, and that such systems may be employed effectively by small nocturnal mammals and volant organisms. These examples also provide some insight into how such echolocation systems work. However, in the absence of a sister-group relationship between one of these taxa and Chiroptera, they provide no evidence concerning the abilities of the earliest bats.

VISION AND THE EVOLUTION OF ECHOLOCAION

Presently, there are essentially two competing hypotheses regarding the relationships of bats to other mammalian lineages: (1) the "Archonta" hypothesis, which supports the idea that bats, dermopterans, primates, and treeshrews are closely related (i.e., they all belong to a monophyletic group Archonta); and (2) the "non-Archonta" hypothesis, which places bats well outside the primate-dermoptera clade as the sister-group to one or more other eutherian orders (e.g., Artiodactyla, Carnivora). Broadly speaking, the former hypothesis is strongly supported by morphological and some molecular evidence, while the majority of the molecular evidence supports alternatives that we have lumped under the latter hypothesis (see discussion under "Outgroups"). Although the identity of the sister-group of bats has not been satisfactorily resolved, the possibility that bats may belong to a monophyletic Archonta raises the interesting possibility that presence of a well developed visual system is primitive for bats, having been inherited from their archontan ancestors (Greenwald, 1990, 1991; Baker et al., 1991b; Simmons et al., 1991). If so, the well developed visual orientation system of Megachiroptera (which strongly resembles that of tree shrews, primates, and dermopterans; Pettigrew et al., 1989) would represent a retention of the ancestral condi-

tion, while the echolocation system of microchiropterans would represent a major adaptive shift from a vision-based to an auditory-based system (Greenwald, 1990, 1991; Simmons et al., 1991). This alternative was discussed and dismissed by Pettigrew et al. (1989: the "blind cave bat" hypothesis⁹), but

⁹ Pettigrew et al. (1989: 548) described this hypothesis as follows:

Suppose that all early bats had the primate features that we have described in the living megabats, but that the microbats lost these features subsequently, perhaps as they passed through an evolutionary bottleneck involving the cavernicolous niche. We have called this the "blind cave bat" scenario in reference to the ease with which some cavernicolous vertebrates appear to be able to "lose" visual capabilities."

One of the principal arguments that Pettigrew et al. (1989) used in dismissing bat monophyly and the "blind cave bat" scenario was based on an incorrect interpretation of the fossil record. They argued that the known ages of the earliest fossils referred to Microchiroptera (Early Eocene) and Megachiroptera (Middle Oligocene) at the time of that publication) refuted the idea that these groups might be sister taxa—and precluded the possibility that visual specializations might have predated echolocation—because "the origin of microbats was earlier than that of megabats, by at least 20 Ma" (Pettigrew et al. 1989: 549). A similar argument was presented by Rayner (1991b). Unfortunately, these arguments were based on flawed reasoning. Paleontologists clearly recognize that the earliest appearance in the fossil record provides only a *minimum* age for any given lineage, not an indication of its actual time of origin (Schaeffer et al., 1972; Novacek and Norell, 1982; Baker et al., 1991b; Norell, 1992; Norell and Novacek, 1992a, 1992b; Huelsenbeck, 1994; Padian et al., 1994; Smith, 1994; Flynn, 1996; Novacek, 1996; Benton and Hitchin, 1997). Although each lineage of a pair of sister-taxa must be the same age since they originated in a single speciation event, it is rare that sister-taxa appear simultaneously in the fossil record (Norell, 1992; Huelsenbeck, 1994; Padian et al., 1994; Smith, 1994; Benton and Hitchin, 1997). Typically, one taxon of a pair of sister-taxa has a longer record than the other due to the stochastic nature of fossil preservation and discovery, or to differences in ecology or distribution that affect the chances of preservation and recovery of fossils (Norell, 1992). Information from phylogenies is now routinely used to reconstruct "ghost lineages," those parts of evolutionary lineages that must have existed but for which we have no fossils presently (Norell, 1992; Padian et al., 1994; Smith, 1994; Flynn, 1996; Novacek, 1996). A good fit between stratigraphic occurrence and cladistic

clearly deserves further discussion in light of the strong evidence that now supports bat monophyly.

Even if bats are not related to archontan mammals, we suspect that the first bats relied on vision for nocturnal orientation and obstacle detection. Vision is clearly of central importance in Megachiroptera, but is also used by microchiropterans under many conditions. Microchiropterans use vision for obstacle avoidance (Bradbury and Nottebohm, 1969; Chase and Suthers, 1969), and many use vision for predator surveillance at the roost site (Suthers, 1970, 1978; Suthers and Wallis, 1970; Vaughan, 1970c; Bradbury and Emmons, 1974). Vision has been shown to play a role in escape responses (e.g., in choosing an escape route when threatened) in representatives of several microchiropteran families (Davis and Barbour, 1965; Chase, 1981), and it may be crucial for long-distance homing (Davis, 1966; Mueller, 1966, 1968; Williams et al., 1966; Williams and Williams, 1967, 1970; Suthers, 1970; Childs and Buchler, 1981).

rank (relative time of splitting) is seen in some groups of mammals, mostly large-bodied hervivorous forms (Norell and Novacek, 1992a, 1992b; Novacek, 1996). For smaller bodied forms (e.g., primates and rodents), the fit is poor at best; much of the history of these groups is not adequately preserved in the fossil record, so long ghost lineages are necessary to explain temporal patterns (Norell and Novacek, 1992a, 1992b; Novacek, 1996). This is most likely also true of bats, most of which are small and live in habitats that are not conducive to fossil preservation (e.g., tropical rainforests). Given bat monophyly, Microchiroptera and Megachiroptera must be equally old, dating to at least the Early Eocene. In turn, their sister-taxon (e.g., Dermoptera) must be at least slightly older. Support for this hypothesis does not require that we have a complete chronicle of these lineages preserved in the fossil record. However, we do expect that continued discoveries of fossils might fill in the gaps and decrease the lengths of ghost lineages that must be postulated. This is just what has happened in the case of bats. Since the publication of Pettigrew et al. (1989) and Rayner (1991b), new fossil discoveries in Thailand have brought the earliest known records of the relevant groups into closer agreement: the fossil record of Megachiroptera and Dermoptera now extends back to the Late Eocene (Ducrocq et al., 1992, 1993), considerably reducing the length of ghost lineages that must be postulated given the phylogeny supported in the current study.

Suthers and Wallis (1970: 1170–1171) studied eye morphology in six microchiropterans (*Phyllostomus hastatus*, *Anoura geoffroyi*, *Carollia perspicillata*, *Desmodus rotundus*, *Myotis sodalis*, and *Pipistrellus subflavus*) and concluded that

The eyes of these echolocating bats appear in some ways to be well adapted for nocturnal vision. The most salient of these adaptations are the very large corneas and the presence of relatively densely packed rod retinæ. In these respects the Microchiroptera studied compare favorably with other non-echolocating nocturnal mammals and contrast sharply with diurnal mammals such as Man.

The optical properties of microchiropteran eyes suggest that vision is used for detecting objects beyond the relatively short range of echolocation (Suthers and Wallis, 1970; Chase, 1972; Suthers, 1978; Fenton, 1985; Pettigrew et al., 1988). Microchiropterans reduce the frequency of repetition of echolocation calls with increasing light levels, and may ultimately cease call production when there is adequate light for orientation by vision (Bell, 1982b; Fenton, 1985). At least some gleaning microchiropterans (e.g., *Macrotus californicus*) apparently use vision to locate their prey (Bell, 1985). However, aerial prey capture apparently requires echolocation in most or all microchiropterans.¹⁰ Microchiropteran bats are routinely heard to make feeding buzzes (terminal phase echolocation calls), even when foraging in high-light situations (Pettigrew, 1988; Rydell, 1992). In general, it seems that echolocation is probably superior to vision for obtaining information about fast-moving insect-sized prey, while vision is more useful than echolocation for long-range obstacle avoidance.

Although visual acuity is modest in micro-

¹⁰ Pettigrew (1988) reported that *Craseonycteris* uses vision for aerial prey capture, often omitting the terminal phase feeding buzz when there is adequate light to see their prey. However, these observations must be viewed with caution, as the echolocation calls of *Craseonycteris* are high in frequency and the feeding buzz may have been present but not detected (B. Fenton, personal commun.; E. Kalko, personal commun.). Factors such as directionality of the echolocation call and the microphone, distance between the bat and the microphone, and frequency sensitivity of the microphone may significantly affect the results of recording sessions, particularly under field conditions (E. Kalko, personal commun.).

chiropterans, in many species it is comparable to that of nocturnal muroid rodents (e.g., *Rattus*, *Peromyscus*) and marsupials (e.g., *Didelphis*; Suthers, 1966; Rahmann, 1967; Suthers et al., 1969; Chase, 1972; Manske and Schmidt, 1976; Bell, 1982b; Fenton, 1985; Bell and Fenton, 1986; Pettigrew, 1988; Pettigrew et al., 1988). In both Microchiroptera and Megachiroptera, visual acuity deteriorates with decreasing light levels more slowly than in humans, so bats can usually see better than humans in dim light; thresholds are similar to those reported for owls (Neuweiler, 1967; Suthers, 1970; Manske and Schmidt, 1976; Fenton, 1985; Bell and Fenton, 1986). We surmise that the earliest bats had at least the same visual capabilities as nocturnal rodents and marsupials, and may have been much better equipped (i.e., if they possessed the derived visual systems seen in primates, dermopterans, and megachiropterans; for a summary see Pettigrew et al., 1989). Reliance on the visual system alone for orientation probably precluded aerial insectivory and flight within cluttered environments (e.g., within dense vegetation and many subcanopy habitats). Nevertheless, these early bats would have benefited from many of the advantages of powered flight—rapid, energy-efficient transportation over relatively long distances and an increased foraging radius (Smith, 1977; Norberg, 1986a, 1989, 1994; Rayner, 1986; Scholey, 1986; Norberg and Rayner, 1987; Thomas, 1987), as well as easy avoidance of predators (Pomeroy, 1990).

This hypothesis raises the linked questions of how and why one fully functional orientation system (vision-based orientation) would be exchanged during evolution for another (echolocation). While such a transformation is admittedly unlikely if one postulates a simple one-step process, it makes considerably more sense when viewed as a multistep process that allowed the microchiropteran lineage to successfully invade an enormous yet empty set of ecological niches for nocturnal aerial insectivores. In a rarely cited paper on the evolution of feeding strategies in bats, Gillette (1975) argued that major adaptive shifts might have evolved through what he termed “duality”—a period during which both the primitive and derived

behaviors were present simultaneously. In the case of a transformation from visual orientation to echolocation, we suggest that the early microchiropteran lineage passed through a period during which they oriented principally using vision, but also used echolocation to provide supplementary information about their surroundings. This possibility was first suggested by Pettigrew (1988: 649), although in the context of bat diphyly:

I . . . think it unlikely that sonar would have been sufficiently developed in the first microbat to enable much useful guidance toward an airborne insect. The short range of ultrasound pulses makes it unlikely that it was an echo from an insect that first enticed our early microbat off its branch, as does the required neural processing which seems unlikely to have been sufficiently sophisticated on the first try. Vision seems a more likely candidate to provide the appropriate resolution and range, just as it does in many living microbats today. The primary role of sonar would then have been in the detection of obstacles, particularly in the cave roost where there is no alternative sensory channel and where three other flying vertebrates have sought shelter, independently inventing sonar on each occasion (swiftlets, oilbirds and rousette megabats). If this is correct, then the use of sonar for insect capture occurred as a modification of the avoidance system after flight was achieved.

Indeed, adequate vision may have been a necessary prerequisite for the evolution of echolocation in bats. The sensory range of echolocation is relatively short (e.g., Suthers, 1970, 1978; Griffin, 1971; Fenton, 1980, 1982a, 1984, 1994a; Kick, 1982; Lawrence and Simmons, 1982), and quickly moving, flying organisms may require more information about distant obstacles than can be obtained from echolocation alone (Suthers and Wallis, 1970; Chase, 1972; Fenton, 1985; Pettigrew et al., 1988). This may be especially true in the warm, moist air of the tropics, where atmospheric attenuation of ultrasonic frequencies is greatest (Griffin, 1971; Suthers, 1978; Lawrence and Simmons, 1982). Particularly when orienting over long distances (e.g., when commuting to and from foraging areas), vision appears to be crucial for obstacle avoidance and landmark recognition (Davis, 1966; Mueller, 1966, 1968; Williams et al., 1966; Williams and Williams, 1967, 1970; Suthers, 1970). We find it hard to imagine how echolocation—which is essentially a short-range sensory system—could have evolved in a group

of flying organisms in the absence of vision for longer-range obstacle detection.

Speakman (1993) argued that an early bat which relied on a combination of vision and echolocation would be a "sensory generalist" that might be at a selective disadvantage compared with sensory specialists that used either vision or echolocation. This hypothesis was offered as a possible explanation for the absence of echolocation in Megachiroptera, but might also apply to the earliest microchiropterans. However, we do not find this hypothesis compelling, at least as an argument against a transformation from vision to echolocation as the primary sensory system in early Microchiroptera. Early members of the microchiropteran lineage would have faced no competition from sensory specialists in echolocation, because specialized aerial echolocators—their descendants—had not yet evolved. Rather than being at a selective disadvantage when compared with vision specialists (i.e., megachiropterans), we have every reason to believe that early microchiropterans would have immediately gained several advantages when they first began to evolve echolocation, including an increased ability to detect obstacles at short range (particularly in low-light situations) and an increased ability to utilize caves as roosting places.

Previous authors have suggested that the primitive echolocation system within Microchiroptera may have consisted of short broadband or multiharmonic clicks produced in the larynx (Pye, 1980; Simmons, 1980; Simmons and Stein, 1980; Fenton, 1984; Norberg, 1994; Fenton et al., 1995; Arita and Fenton, 1997). Such a system probably evolved from vocalizations used for other purposes, most likely intraspecific communication (Fenton, 1984, 1985; Novacek, 1985a). This hypothesis is supported by observations that some extant microchiropterans use echolocation calls simultaneously for orientation and communication, while others have distinct calls that are apparently used only in a social context (Möhres, 1967a, 1967b; Habersetzer, 1981; Miller and Degan, 1981; Brown et al., 1983; Fenton, 1984, 1985, 1994b; Guppy et al., 1985). Megachiropteran bats use short broadband or multiharmonic FM calls in a variety of social sit-

uations, including female contact, precopulation, and hostile male–male interactions (Nelson, 1964; Fenton, 1985). Similar calls are sometimes used by microchiropteran bats, often in comparable social situations (e.g., hostile interactions between males; Porter, 1979; Fenton, 1985). Young bats of many species (both megachiropterans and microchiropterans) apparently use similar calls when they are isolated from their mothers (Fenton, 1985). Together, these observations suggest that broadband or multiharmonic clicks or buzzes were present in the vocal repertoire of the earliest bats, and thus were available as a behavioral substrate from which echolocation calls could evolve.

Early members of the microchiropteran lineage, flying and using vision as well as a primitive echolocation system such as described above, would have had access to many habitats and food sources but would have been poorly equipped to fly in cluttered spaces or capture flying insects (Norberg, 1994). Perfection of echolocation for detecting, tracking, and assessing airborne prey would have increased the foraging options open to these bats, especially given the absence of competition (Fenton, 1974a, 1974b, 1980, 1982a, 1984, 1994a; Norberg, 1994; Speakman, 1995). Nocturnal flying insects offer an abundant food supply, so much so that there is little evidence that prey abundance is a limiting resource for most microchiropteran aerial insectivores,¹¹ at least

¹¹ Possible exceptions to this general pattern may include aerial insectivores that summer in high latitude habitats, where the nights are very short and peak aerial insect availability occurs before it gets dark (Rydell, 1992; Speakman, 1995). It has recently been shown that some bats living under these conditions frequently fail to meet their energy requirements, instead using torpor to balance their daily energy budgets (Kunz, 1980; Kurta et al., 1987, 1989; Speakman and Racey, 1987; Audet and Fenton, 1988). Speakman (1995) suggested that it is nocturnality (and lack of adequate prey resources at night) that forces the use of torpor in these animals. Although this may be true, we suggest that it is the availability of torpor that has permitted these species to expand their summer ranges beyond the limit of most other bats. In tropical and subtropical environments (where most insectivorous microchiroptans live), nights are longer and prey densities are generally high, thus prey availability is probably not a limiting factor under normal conditions (e.g., Fenton et al., in press).

those in tropical and subtropical habitats (Fenton, 1980; Fenton et al., in press). The potential advantages of evolving adaptations to exploit nocturnal flying insects as a food source are obvious.

Fenton et al. (1995) noted that transformation to the sophisticated echolocation system used by extant microchiropterans to detect, track, and evaluate flying insects required production of longer, stronger (high-intensity) tonal signals and concomitant evolution of a system to avoid self-deafening. Among extant bats, two such systems are known: separation of the pulse and echo in time (the "low-duty-cycle" approach), and separation of the pulse and echo in frequency rather than time (the "high-duty-cycle" approach; Fenton, 1994a, 1995; Fenton et al., 1995). Low-duty-cycle echolocation involves short signal pulses with relatively long gaps between them; high-duty-cycle echolocation involves longer pulses and shorter gaps, with pulses longer than the gaps between them (Fenton, 1994a, 1995; Fenton et al., 1995). Low-duty-cycle bats prevent self-deafening by freezing movement of the middle-ear ossicles through contraction of the middle-ear muscles during pulse emission and by reducing auditory sensitivity in the inner ear through changes in the sensory cells along the basilar membrane (Henson, 1964, 1965, 1966, 1967a, 1967b, 1970; Jen and Suga, 1976). Returning echoes are received in the gaps between pulse emissions, when the middle-ear muscles relax and auditory sensitivity is maximized. High-duty-cycle bats produce long constant frequency (CF) echolocation signals that overlap with returning echoes. These bats utilize the Doppler effect, which shifts the frequency of returning echoes to a frequency different from that of the original pulses (Schnitzler, 1970b, 1973, 1987; Schuller et al., 1975; Schuller and Pollack, 1976; Schuller, 1977; Neuweiler et al., 1980; Schnitzler and Henson, 1980; Simmons and Stein, 1980; Emde and Schnitzler, 1986, 1990; Neuweiler, 1989, 1990; Grinnell, 1995). Self-deafening is reduced because the emitted pulse is dominated by frequencies outside the acoustic fovea (zone of maximum hearing sensitivity), while both the external and inner ears are sharply tuned to the frequencies of the re-

turning echoes (Schuller and Pollack, 1976; Bruns, 1979; Neuweiler et al., 1980; Schnitzler and Henson, 1980; Vater et al., 1985; Emde and Schnitzler, 1986, 1990; Schnitzler, 1987; Vater, 1987; Neuweiler, 1990; Obrist et al., 1993; Fenton, 1994a; Fenton et al., 1995).

Most extant microchiropterans are low-duty-cycle echolocators; high-duty-cycle echolocation is used only by rhinolophines, hipposiderines, and one mormoopid (*Pteronotus parnellii*; Novick, 1958a, 1962, 1963a, 1963b, 1977; Novick and Vaisnys, 1964; Schnitzler, 1970b, 1973, 1987; Fenton, 1974a, 1974b, 1980, 1982a, 1982b, 1984, 1990, 1994a, 1995; Schuller et al., 1975; Schuller and Pollack, 1976; Schuller, 1977; Neuweiler et al., 1980; Schnitzler and Henson, 1980; Simmons and Stein, 1980; Fenton and Bell, 1981; Neuweiler, 1984, 1989, 1990; Neuweiler and Fenton, 1988; Kalko and Schnitzler, 1989, 1993; Lancaster et al., 1992; Surlykke et al., 1993; Fenton et al., 1995; Grinnell, 1995). It seems clear that low-duty-cycle echolocation is primitive for extant Microchiroptera based on optimization of echolocation strategies on our phylogenetic tree (fig. 36). Optimization indicates that the high-duty-cycle approach evolved twice, once in the lineage leading to Rhinolophidae and once within the genus *Pteronotus*. This confirms previous hypotheses (e.g., Pye, 1980; Simmons, 1980; Simmons and Stein, 1980; Fenton et al., 1995) that suggested independent origins for the use of long CF signals and Doppler compensation in these two groups.

The transformation from primitive to sophisticated low-duty-cycle laryngeal echolocation likely took place in several stages (Fenton, 1984), probably facilitated by the mechanical coupling of flight and ventilation discussed previously (Speakman et al., 1989; Rayner, 1991b; Speakman and Racey, 1991; Speakman, 1993). If there was indeed "no cost of echolocation for bats in flight" (Speakman and Racey, 1991: 421), or (more realistically) a relatively low cost, it is easy to imagine how this system might have evolved quickly. However, refinement of this system—and increased reliance on aerial insectivory—apparently brought with it an im-

portant series of evolutionary constraints, including limitations on body size and reproduction (Barclay and Brigham, 1991; Barclay, 1994, 1995; Jones, 1994; Arita and Fenton, 1997).

Maximum body size may be limited in microchiropteran aerial insectivores for the several reasons, including (1) the small size of available prey (McNab, 1969; Black, 1974); (2) the metabolic requirements for sustained flight, particularly at night when thermal gliding and soaring are not possible (Rayner, 1981); (3) the mechanics of flight and aerial prey capture (Norberg, 1986a, 1994; Norberg and Rayner, 1987); (4) the effective range of echolocation calls (relatively short) and the concomitant need to be maneuverable and agile enough to catch small prey at short range (Barclay and Brigham, 1991); and (5) the coupling of flight and echolocation, which may limit the ability of large bats (which have lower wing-beat frequencies and thus lower call-repetition rates) to detect small flying prey (Jones, 1994, although see Heller, 1995). As a probable result of these constraints, microchiropteran aerial insectivores are typically very small (<30 g adult body weight), with only four extant species weighing more than 100 g¹² (McNab, 1969; Black, 1974; Fenton and Fleming, 1976; Krazanowski, 1977; Barclay and Brigham, 1991; Arita and Fenton, 1997). Within this size range, most larger aerial insectivores seem to be limited to relatively large insect prey (e.g., moths and large beetles; Vaughan, 1977), while smaller bats can exploit either large or small prey (Barclay and Brigham, 1991; Arita and Fenton, 1997).

Returning to the problem of explaining the evolution of sophisticated echolocation—specifically our hypothesis that this form of orientation replaced a vision-based system in microchiropteran bats—we note that small body size may have precluded the retention of derived structures of the visual system (such as those seen in Primates, Dermoptera, and Megachiroptera) once neural modifications associated with echolocation began to evolve. In a review article on encephalization

in vertebrates, Harvey and Krebs (1990: 145) noted that

If overall size [of the brain] is constrained . . . it may well be that specialized enlargement of one region has to be associated with reduction in size of another In other words, there may be trade-offs in the evolutionary specialization of the brain.

Cooper et al. (1993a: 340) similarly concluded that

. . . non-visual systems may “compete” with neurons of the visual system for available metabolites Although the use of the expression competition to describe these evolutionary events is somewhat unexplicit, the relative expansion of one cerebral structure, restrained within the confines of a braincase of limited volume, may depend upon concomitant decrease elsewhere, notwithstanding the problem of maintaining the most efficient and adaptive neuronal populations.

Small body size places limitations on the size of neuron populations and may constrain the metabolic energy available for brain functions (Martin, 1981; Armstrong, 1983; Williams and Herrup, 1988; Deacon, 1990a, 1990b; Cooper et al., 1993a). Neurons have high energy requirements; the brain can consume up to 20% of circulating oxygen and glucose even though the brain constitutes only a small fraction of total body weight (Kety and Schmidt, 1948; Martin, 1981; Armstrong, 1983; Williams and Herrup, 1988; Cooper et al., 1993a). Reviewing relationships between body size, brain size, and metabolic rates in small mammals, Cooper et al. (1993a: 339) summarized their findings as follows:

These arguments emphasize the conclusion that in small animals, such as moles and bats, the fraction of metabolism devoted to neurons is great and bioenergetic limits become critical. Supplying the brain with sufficient oxygen is a challenge to the body for survival. Superfluous neurons . . . are thus strongly selected against and their reduction can contribute to the animal's fitness by improving metabolic efficiency (Ricklefs and Marks, 1984).

In the early evolution of microchiropteran bats, it may not have been efficient or feasible to retain derived complex structures in the visual system (e.g., laminated dorsal lateral geniculate nucleus, large superior colliculus; Sanderson, 1986; Pettigrew et al., 1989) and simultaneously provide the neurons and metabolic energy necessary for processing increasingly complex auditory information

¹² *Taphozous peli* (Emballonuridae), *Hipposideros commersoni* (Rhinolophidae), *Scotophilus nigrita* (Vespertilionidae), and *Cheiromeles torquatus* (Molossididae).

(e.g., in a large inferior colliculus; Aitkin, 1986; Casseday and Pollak, 1988; Pollack and Casseday, 1988; Pollak and Park, 1995). From a dual orientation system employing both vision and limited echolocation, we surmise that the auditory system of microchiropteran bats simply "outcompeted" the visual system for the resources available.

Evolutionary reduction in brain centers responsible for processing visual information could have occurred through a variety of ontogenetic changes, including truncation of development of visual centers at increasingly early stages. This hypothesis is supported by observed similarities between the relatively simple adult dorsal lateral geniculate nucleus (dLGN) in microchiropteran bats (Pettigrew et al., 1989) and early developmental stages of the dLGN in *Tupaia* (Casagrande and Brunso-Bechtold, 1985). If development of the dLGN in *Tupaia* was arrested at an early stage, the adult dLGN would resemble that of a microchiropteran bat—and eight of the derived traits defined by Pettigrew et al. (1989: 512) would be reversed as the result of a single ontogenetic change. The same would presumably hold true for the dLGN of megachiropteran bats, which is similar to that of *Tupaia* in most respects (Pettigrew et al., 1989).

Another mechanism that might contribute to reduction in visual centers in the brain is changes in the magnitude of neuron death during early development. Neuron death is a normal part of brain development in many vertebrates, including all mammals (Finlay et al., 1987; Williams and Herrup, 1988). Not surprisingly, the magnitude of neuron death within homologous neuron populations varies phylogenetically (Finlay et al., 1987; Williams and Herrup, 1988). For example, normal development includes no death of retinal ganglion cells in fish and amphibians (Wilson, 1971; Easter et al., 1981), but 40% of retinal ganglion cells normally die in chickens (Rager, 1980), 60–70% die in rats and primates (Rakic and Riley, 1983; Crespo et al., 1985; Provis et al., 1985), and 80% die in cats (Williams et al., 1986). Neuron death is known to be a normal part of development of the dLGN in primates (Williams and Rakic, 1988) and has been shown to change the proportion of contralateral (crossed) versus ipsilateral (uncrossed) retinal projections in

cats (Jacobs et al., 1984). Evolutionary changes in taxon-specific rates of neuron death in components of the visual system during development may thus affect the size and interconnections of visual centers in adults. As auditory information became increasingly important to early members of the microchiropteran lineage, we suspect that brain centers involved in processing visual information were reduced and/or simplified through developmental changes such as these.

The hypothesized evolutionary reduction of the visual system in microchiropteran bats is not a unique event; similar transformations are postulated to have occurred independently in other mammalian groups that depend little on vision, including moles (Johnson, 1954; Lund and Lund, 1965, 1966; Suthers and Bradford, 1980; Kudo et al., 1988, 1991), mole rats (Bronchti et al., 1991; Cooper et al., 1993a, 1993b), and odontocete whales (Jacobs et al., 1975; Sanderson, 1986; Deacon, 1990b). In this context, it is interesting to note that odontocetes are the only other group of mammals known to use sophisticated echolocation comparable to that of microchiropterans (e.g., Norris et al., 1961; Norris, 1968; Purves and Pilleri, 1983; Pilleri, 1983, 1990). Extensive reversals in the visual system are also commonly accepted as explanations for the morphology of blind snakes, gymnophionan amphibians, and blind cave populations of fishes (e.g., Wilkens, 1971; Halpern, 1973; Repérant et al., 1987; Voneida and Sligar, 1976; Clairambault et al., 1980; Fritzsche et al., 1985; Himstedt and Manteuffel, 1985). Similar evolutionary reductions have taken place in other sensory systems in some mammals, such as reduction of the olfactory system in whales (Oelschläger and Buhl, 1985; Oelschläger, 1989) and the vomeronasal system in catarrhine primates (Meredith, 1991). As noted above, these sorts of changes appear to represent modifications for efficient use of cellular and metabolic resources. When a system is no longer of critical importance, regression or reduction—which may be interpreted as reversal in a phylogenetic context—takes place to avoid wasting cells and metabolic energy that may be better spent elsewhere (Cooper et al., 1993a).

The evolution of flight and echolocation

required modifications of many anatomical and behavioral systems, and this process undoubtedly took place in several stages. To summarize, we hypothesize that flight evolved first, prior to the divergence of Megachiroptera and Microchiroptera. The first bats most likely used vision for orientation and obstacle detection in their arboreal/aerial environment. The evolution of flight was later followed by the origin of low-duty-cycle echolocation in basal members of the microchiropteran lineage. This system, which was probably derived from vocalizations originally used for intraspecific communication, was most likely simple at first, permitting orientation and detection of obstacles but not detection or tracking of airborne prey. However, due to the mechanical coupling of ventilation and flight, energy costs of echolocation to flying bats were low, and the benefits of aerial insectivory quickly led to development of a more sophisticated low-duty-cycle echolocation system capable of detecting, tracking, and assessing airborne prey. The need for an increasingly derived auditory system, combined with limits on body size imposed by the mechanics of flight, echolocation, and prey capture, may have resulted in reduction and simplification of the visual system as echolocation became increasingly important.

The theory presented above is consistent with (and is indeed based on) bat monophyly and the phylogeny proposed in the current study. When considered in a phylogenetic context, the Eocene fossil bats *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* are not informative about the origin of flight (which preceded diversification of the entire microchiropteran lineage), but they do provide some information concerning early steps in the acquisition of sophisticated echolocation. As noted above, some of the earliest morphological transformations in the lineage leading to extant Microchiroptera (those that took place before the divergence of *Icaronycteris*) included changes in features associated with the production of echolocation calls (enlargement of the cranial tip of the stylohyal), transmission of sounds through the middle ear (enlargement of the orbicular apophysis), and some fine-tuning of the inner ear (initial enlarge-

ment of the basal turn of the cochlea). Loosening of the attachment of the periotic to the basicranium evolved at this level or just subsequently (prior to the divergence of *Archaeonycteris*). It is interesting to note that all of these modifications occurred before achievement of what we described as “great enlargement of the cochlea” (i.e., to the size range of most extant microchiropterans), which evolved somewhat later, just prior to the divergence of *Hassianycteris* (fig. 40). Postcranial modifications that may have increased efficiency of the ventilation system (e.g., increased breadth of posterior laminae on the ribs) evolved in the microchiropteran lineage sometime between the divergence of *Icaronycteris* and the divergence of *Palaeochiropteryx*. Other derived features potentially related to the echolocation system also evolved at some point in the early microchiropteran lineage. These include a phanerochlear cochlea (probably associated in some fashion with cochlear expansion) and a deep, constricted fossa for m. stapedius (perhaps related to the system for avoidance of self-deafening). The former was minimally present before the divergence of *Hassianycteris*, the latter before the divergence of *Palaeochiropteryx*. As noted above, missing data for cochlear ossification in *Icaronycteris* and *Archaeonycteris* and for stapedial fossa form in *Archaeonycteris* and *Hassianycteris* make it impossible to exactly place these transformations in the phylogenetic tree.

Even given uncertainty about the relative timing of some transformations, our observations confirm the hypothesis that sophisticated echolocation evolved in a stepwise fashion in the early microchiropteran lineage. However, evolutionary changes in this system certainly did not cease with the origin of the microchiropteran crown group. Considerable cochlear size variation exists among living clades of Microchiroptera, with most extant microchiropterans (and all high-duty-cycle echolocators) having a cochlea even larger than those seen in *Palaeochiropteryx* and *Hassianycteris* (Haberstezer and Storch, 1992). Reduction in cochlear size (back to the “moderately enlarged” condition) has apparently occurred in some lineages—in Mystacinidae, within Phyllostomidae, and within Megadermatidae (Fig. 40). Significant

changes (some associated with cochlear enlargement) have also occurred in some lineages with respect to (1) length, width, and thickness of the basilar membrane, (2) length and height of the spiral ligament, (3) total number of cochlear neurons, (4) size and distributions of hair cell populations, (5) size and pattern of fluid spaces in the cochlea, and (6) form of the frequency map and "acoustic fovea" (Pye, 1966a, 1966b, 1967; Henson, 1970; Bruns, 1979; Bruns et al., 1981, 1983–1984; Burda and Ulehlova, 1983; Rübtsamen et al., 1988; Neuweiler, 1990). Most or all of these changes may reflect modifications of the auditory system associated with different echolocation and foraging strategies (Bruns et al., 1981, 1983–1984; Rübtsamen et al., 1988; Neuweiler, 1990).

FORAGING ECOLOGY OF EOCENE BATS

One aspect of morphology and ecology not mentioned in the preceding discussion is the relationship between wing shape and foraging ecology. There is an extensive literature on this topic (e.g., Revilliod, 1916; Betz, 1958; Vaughan, 1959, 1966; Struthsaker, 1961; Hartman, 1963; Farney and Fleharty, 1969; Fenton, 1972; Findley et al., 1972; Kopka, 1973; Lawlor, 1973; Pirlot, 1977; Smith and Starrett, 1979; Norberg, 1981, 1986a, 1986b, 1987, 1994; Findley and Wilson, 1982; Findley and Black, 1983; Aldridge, 1986; Baagøe, 1987), with many recent contributions integrating data on echolocation call structure as well (e.g., Simmons et al., 1979; Neuweiler, 1984, 1989, 1990; Habersetzer, 1986; Aldridge and Rautenbach, 1987; Norberg and Rayner, 1987; Neuweiler and Fenton, 1988; Norberg, 1989, 1990, 1994; Fenton, 1990; Arita and Fenton, 1997). One outcome of this research has been identification of a series of features of wing design that affect flight performance and are correlated with foraging strategies. Among the most important measures of these are wing loading, aspect ratio, and a variety of wing tip indices designed to measure the size and shape of the dactylopatagium (e.g., Findley et al., 1972; Norberg and Rayner, 1987).

Wing loading (= body weight/wing area) provides a measure of the relative size of the

wings and of the minimum weight per unit area that the wings must support during flight (Findley et al., 1972; Norberg and Rayner, 1987; Arita and Fenton, 1997). Increased wing loading requires greater flight speeds to generate enough lift to remain airborne; flight speed is proportional to the square root of wing loading (Findley et al., 1972; Norberg and Rayner, 1987). High wing loading is typical of fast fliers; slow-flying, more maneuverable animals usually have lower wing loading, with either lower body weight and/or increased wing area (Findley et al., 1972; Norberg and Rayner, 1987).

Aspect ratio (= wing span²/wing area; Norberg and Rayner, 1987) describes the overall shape of the wings by quantifying their length relative to their chord (Findley et al., 1972; Norberg and Rayner, 1987; Arita and Fenton, 1997). For any given body weight and wing loading, high aspect ratio wings are subject to less drag and thus facilitate greater flight speeds than do lower aspect ratio wings (Findley et al., 1972). However, high aspect ratio wings also generate less lift than do low aspect ratio wings, and thus bats with high aspect ratio wings may require greater wingbeat frequencies and airspeeds to remain airborne (Findley et al., 1972). Some bats with very high aspect ratio wings (e.g., *Molossus*, *Eumops*) cannot generate enough lift to become airborne from a flat surface (personal obs.), and thus usually drop from their elevated roosts to build up enough speed and lift to initiate flight (Vaughan, 1959). Low aspect ratio wings generate considerable drag at higher speeds, but maximize lift at low speeds (Findley et al., 1972).

A variety of different measures of the relative size and shape of the wing tip have been proposed, including the tip index (Findley et al., 1972), alpha angle (Smith and Starrett, 1979), tip length ratio (Norberg and Rayner, 1987), tip area ratio (Norberg and Rayner, 1987), and tip shape index (Norberg and Rayner, 1987). All of these quantify various aspects of the relative size and shape of the dactylopatagium (that portion of the wing distal to digit V), which provides much of the propulsion generated by the wing during flight (Findley et al., 1972).

The most comprehensive study of wing

design and foraging strategies in bats was that of Norberg and Rayner (1987), who summarized morphometric and behavioral data for more than 250 bat species. In addition to the ratios mentioned above, they also considered total body weight (mass), wingspan, and wing area. They interpreted these data in the context of mechanical and aerodynamic models for different modes of flight. Norberg and Rayner (1987: 337) summarized their results as follows:

Some adaptive trends in bat wing morphology are clear from this analysis. Insectivores hunt in a range of different ways, which are reflected in their morphology. Bats hawking high-flying insects have small, pointed wings which give good agility, high flight speeds and low cost of transport. Bats hunting for insects among vegetation, and perhaps gleaning, have very short and rounded wingtips, and often relatively short, broad wings, giving good maneuverability at low flight speeds. Many insectivorous species forage by 'flycatching' (perching while seeking prey) and have somewhat similar morphology to gleaners. Insectivorous species foraging in more open habitats usually have slightly longer wings, and hence lower cost of transport. Piscivores forage over open stretches of water, and have very long wings giving low flight power and cost of transport, and usually long, rounded tips for control and stability in flight. Carnivores must carry heavy loads, and thus have relatively large wing areas; their foraging strategies consist of perching, hunting and gleaning, and wing structure is similar to that of insectivorous species with similar behavior. Perching and hovering nectarivores both have a relatively small wing area; this surprising result may result from environmental pressure for short wingspan or from the advantage of high speed during commuting flight; the large wingtips of these bats are valuable for lift generation in slow flight.

Habersetzer and Storch (1987, 1989) and Habersetzer et al. (1994) capitalized on the observed relationships between wing form and flight behavior in extant bats to reconstruct the possible habits of *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. Habersetzer and Storch (1987) estimated wing loading, aspect ratio, and tip index for a series of fossil specimens, and compared these values with similar data from an extant bat fauna from tropical India (i.e., Habersetzer, 1986). They concluded that *Icaronycteris* and *Archaeonycteris* have a relatively high wing loading and low aspect ratio (Habersetzer and Storch, 1987, 1989; Habersetzer et al., 1994). Based on comparisons with extant forms, they found that *Ica-*

ronycteris and *Archaeonycteris* have wings that resemble those of large rhinolophoids or the mean of vespertilionids (Habersetzer and Storch, 1987, 1989). Concerning the combination of low aspect ratio and high wing loading, Habersetzer and Storch (1989: 216) noted that "this parameter combination is most likely for unspecialized flight characteristics as can be found within the majority of the vespertilionids (e.g., *Myotis myotis*)."

In contrast, *Palaeochiropteryx* was found to have a somewhat more specialized wing morphology (Habersetzer and Storch, 1987, 1989; Habersetzer et al., 1994). *Palaeochiropteryx tupaiodon* was characterized as having very low aspect ratio and very low wing loading, while both values were somewhat higher in *P. spegeli* (Habersetzer and Storch, 1987, 1989). On the basis of these values, both taxa were found to be very similar to extant rhinolophine and hipposiderine species (Habersetzer and Storch, 1987; Habersetzer et al., 1994). This similarity led Habersetzer and Storch (1987, 1989) and Habersetzer et al. (1994) to conclude that *Palaeochiropteryx* was characterized by slow, highly maneuverable flight close to the ground. In the case of *P. tupaiodon*, aerial capabilities may have included flight close to and even within foliage with potentially long-lasting hovering phases, as is seen today in *Hipposideros bicolor*, a species with a comparable combination of aspect ratio and wing loading values (Habersetzer and Storch, 1987, 1989; Habersetzer et al., 1994). Wing parameters of *Palaeochiropteryx spiegali* more closely resemble those of *Hipposideros speoris*, a form that hunts near obstacles but always stays in open airspace, never flying amongst foliage (Habersetzer and Storch, 1987, 1989; Habersetzer et al., 1994).

Habersetzer and Storch (1987) found that both species of *Hassianycteris* are characterized by a high aspect ratio and high wing loading. On the basis of comparisons with Habersetzer's (1986) data from Indian bats, Habersetzer and Storch (1987, 1989) and Habersetzer et al. (1994) observed that *Hassianycteris* species are even more specialized than high-flying tropical vespertilionids and rhinopomatids, instead showing a greater resemblance to extant high-flying molossid and emballonurids. As a result, they con-

cluded that *Hassianycteris messelensis* and *H. magna* “can be considered to be distinctly adapted to flight in free spaces” (Habersetzer et al., 1994: 238).

Habersetzer and Storch (1987, 1989) and Habersetzer et al. (1994) noted that all four Eocene genera are characterized by a short wing tip and a small dactylopatagium that accounts for only about 37% of the entire wing area. Among extant bats, they noted that this morphology is seen in rhinolophoids. Habersetzer et al. (1994) concluded that the Messel bats had succeeded in occupying a diverse set of ecological niches by evolving variations of the rhinolophoid wing type, and suggested that this wing type (i.e. low aspect ratio with short wing tip) represents the primitive wing form for bats.

To further investigate the correlations described above, Habersetzer and Storch (1989) used multivariate methods developed by Norberg and Rayner (1987) to remove the effects of size (the first principal component), resulting in a plot of normalized wing loading (second principal component) versus normalized aspect ratio (third principal component). Although they used Norberg and Rayner’s (1987) method, Habersetzer and Storch (1989) did not use their data, but instead compared the fossil forms to Habersetzer’s (1986) reference fauna (with known flight and foraging habits) from tropical India. Habersetzer et al. (1989) interpreted the results of this multivariate analysis as supporting their previous conclusions about the flight behavior of the fossil bats (see above). However, *Icaronycteris*, *Archaeonycteris trigonodon*, and *Palaeochiropteryx tupaiodon* appeared to have very similar wing parameters based on the size-normalized analysis (at least in our judgment). This was not explicitly discussed by Habersetzer et al. (1989); however, they cautioned that their comparisons might be biased by the fact that they calculated body weight of the fossil forms using a measure of wingspan, which introduced circularity into the analysis and might have resulted in the observed clustering.

Norberg (1989) reanalyzed wing morphology of the Eocene fossil forms in the context of the much larger data set collected by Norberg and Rayner (1987). Norberg (1989) suggested that the estimates of body mass

calculated by Habersetzer and Storch (1987) may have been too high for several reasons (e.g., use of wingspan length regression equations, straight rather than curved wingtips in the fossil reconstructions). Using revised wing reconstructions (fig. 42) and revised estimates of body weight based on regression equations for radius length against total mass in recent bats, Norberg (1989) recalculated wing loading and aspect ratio for each of the fossil species, and additionally calculated wingtip length ratio, wingtip area ratio, and wingtip shape index for each taxon. Comparisons with recent bats (figs. 43, 44; data from Norberg and Rayner, 1987) led Norberg (1989: 204–205) to the following conclusions regarding *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*:

Based on my reconstructions, the ancient bats examined here . . . had low aspect ratio and high or average wing loading . . . (that is, high or average wing loadings in relation to body size), as compared with recent bats. This indicates that they had expensive and average to fast flight. Their wingtips were extremely short and with fairly large area, which are adaptations for maneuverable flight. Wingtip length ratios T_1 (handwing length/armwing length) are all between 0.93 and 1.09 $T_1 < 1$ is rather unusual among modern bats.

The wing shape of the fossil species are similar to several recent pteropodids and phyllostomids and some rhinolophids (*Rhinolophus hipposideros* and *R. ferrumequinum*) and vespertilionids (*Barbastella barbastellus*, *Lasiurus borealis*, *Rhogeessa tumida* and some *Myotis*, *Eptesicus* and *Pipistrellus* species). *Palaeochiropteryx* and *Hassianycteris* were also similar to *Rhinopoma hardwickei* . . . , both in wing shape and with their extremely short wingtips. Rhinopomatids are found mainly in deserts and steppes. They have been noted to forage for insects in open country as well as in open spaces around tree canopies, and their flight has been described as swift, fast and undulating (alternating flutters and glides)(see Norberg & Rayner 1987 for references) . . . *Hassianycteris messelensis* and *H. magna* had higher wing loadings and slightly higher aspect ratio than the other fossil species, and were thus faster fliers. They had though much lower aspect ratio than molossids and emballonurids. They may have been foraging in rather open spaces, like rhinopomatids, or along vegetation like noctules and lasiurines. The other ancient bats included here have lower aspect ratio and lower wing loading. Because their short wings and low aspect ratio these ancient bats probably foraged or lived among vegetation (which was also suggested by Habersetzer & Storch 1987) and may have been perch hunters.

Perch hunting—making short flights out to

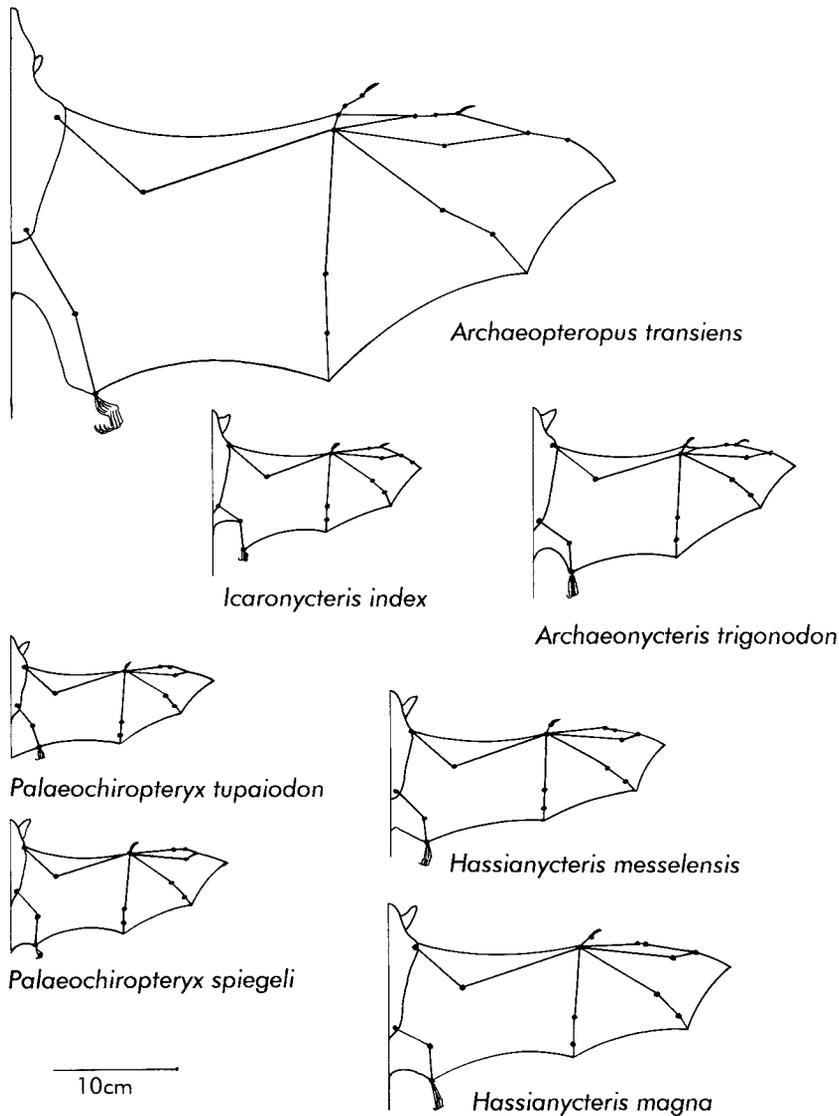


Fig. 42. Reconstructions of wing shapes of fossil bats; redrawn from Norberg (1989: fig. 3). Norberg (1989) modified reconstructions published by Habsersetzer and Storch (1987) by adding curved wingtips such as those seen in extant bats, changing the angles between the phalanges of the fourth digit in *Archaeopteropus*, and changing the angles between the third, fourth, and fifth digits in most species.

capture prey detected from a fixed perch—is widely regarded as a behavior that reduces the energy required for successful foraging (Norberg and Rayner, 1987; Fenton, 1990; Fenton et al., 1990; Norberg, 1994). Extant bats that forage near or within vegetation may use perches because their short, low aspect ratio wings make flight relatively expensive (Norberg and Rayner, 1987; Nor-

berg, 1994). Because flights to capture prey are infrequent and of short duration, less energy is apparently spent than would be required by sustained hawking (Norberg and Rayner, 1987; Fenton, 1990; Fenton et al., 1990; Norberg, 1994). Another possible advantage of perch hunting is that it may broaden the available prey spectrum by facilitating the capture and handling of larger

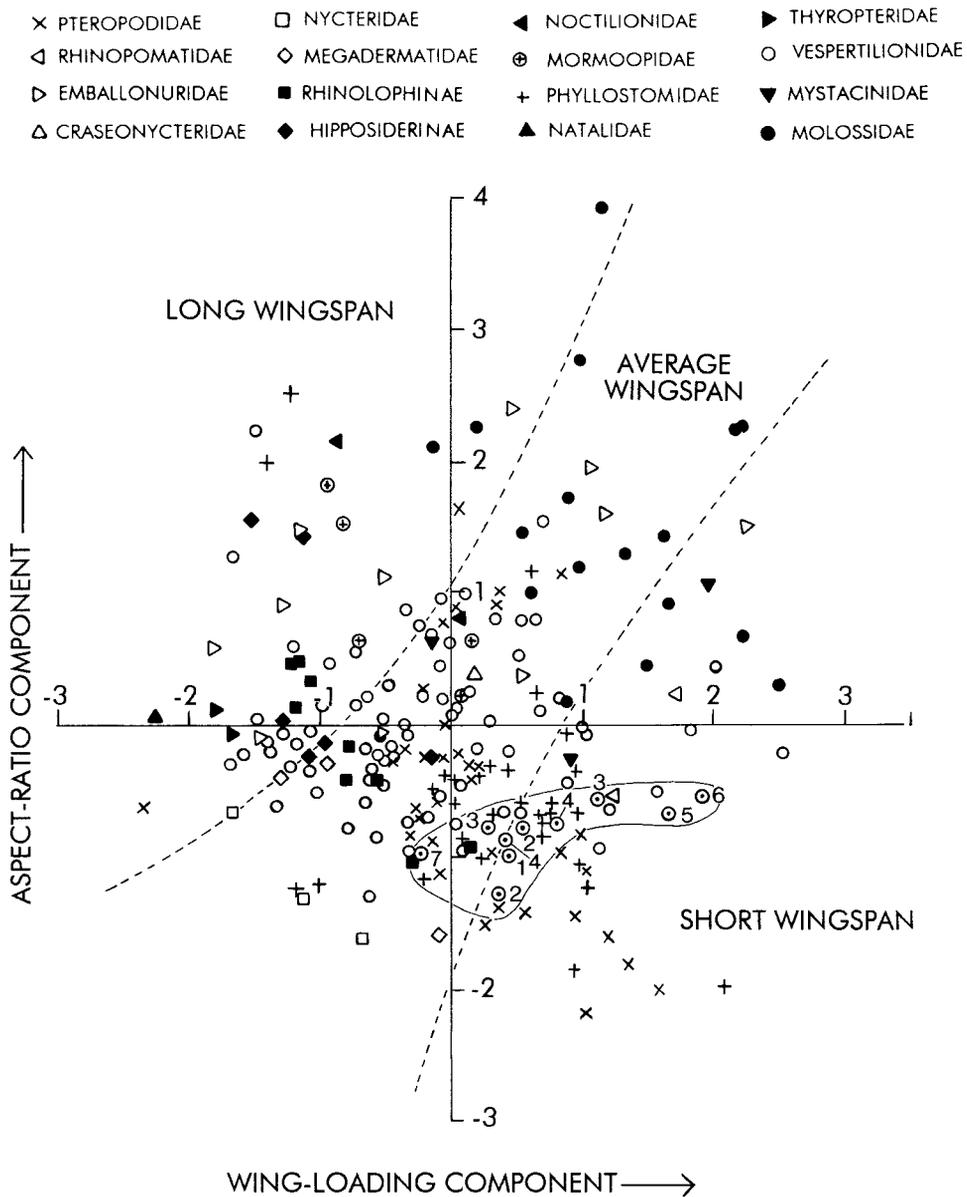


Fig. 43. Comparative wing morphology described using principal components analysis; redrawn from Norberg (1989: fig. 3). This diagram is a scatter plot of the second and third principal components of wing morphology, which were identified by Norberg and Rayner (1987) as measures of wing loading and aspect ratio. The wing loading (WL) and aspect ratio (AR) components were obtained using the following exponential equations: $e^{WL} = 3.77 \times 10^{-3} M^{3.02} b^{-2.08} S^{-3.71}$ and $e^{AR} = 1.81 \times 10^{-5} M^{-1.47} b^{14.6} S^{-5.12}$, where M = mass in grams, b = wingspan, and S = wing area (Norberg, 1989). Points representing fossil bats are circled and identified by number as follows: 1, *Icaronycteris index*; 2, *Archaeonycteris trigonodon*; 3, *Palaeochiropteryx tupaiodon*; 4, *Palaeochiropteryx spiegelii*; 5, *Hassianycteris messelensis*; 6, *Hassianycteris magna*; 7, *Archaeopteropus transiens*. The data used to construct this plot were provided in Norberg and Rayner (1987; extant bats except *Pteronotus parnellii*) and Norberg (1989; fossil bats and *Pteronotus parnellii*).

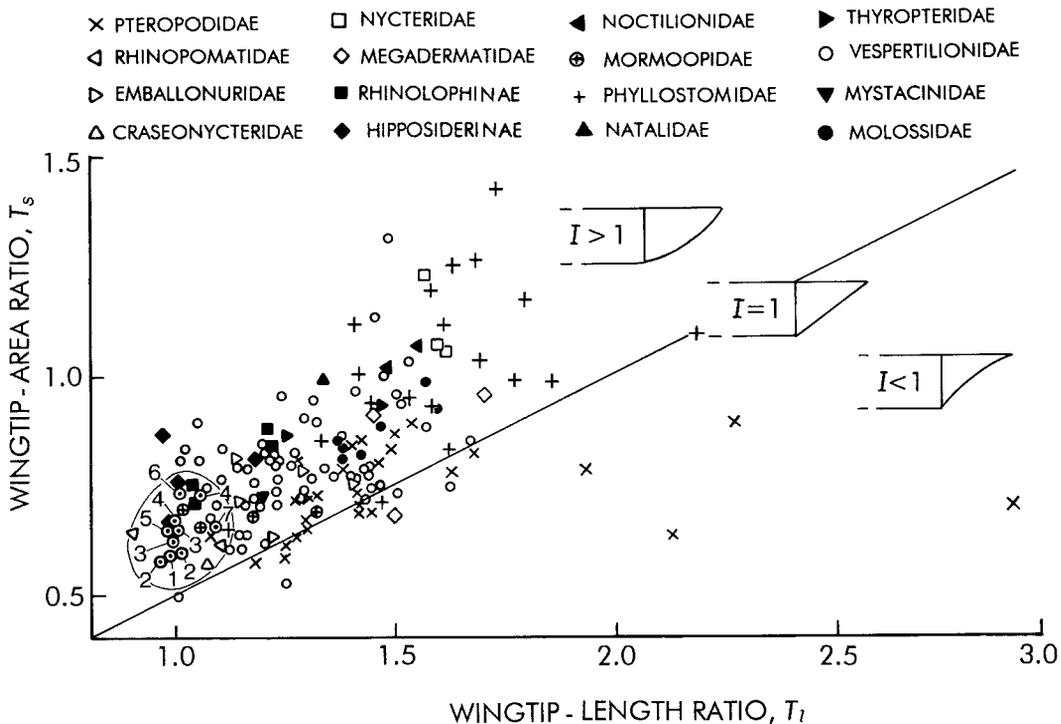


Fig. 44. Comparisons of size and shape of the wingtip as described by plotting wingtip length ratio T_l (length of handwing/length of arm wing) versus wingtip area ratio T_s (handwing area/armwing area); redrawn from Norberg (1989: fig. 4). Wingtip index I equals $T_s/(T_l - T_s)$, where $I < 1$ indicates pointed wingtips and $I > 1$ indicates rounded wingtips. Points representing fossil bats are circled and identified by number as follows: 1, *Icaronycteris index*; 2, *Archaeonycteris trigonodon*; 3, *Palaeochiropteryx tupaiodon*; 4, *Palaeochiropteryx spiegelii*; 5, *Hassianycteris messelensis*; 6, *Hassianycteris magna*; 7, *Archaeopteropus transiens*. Data on which this graph was based were provided in Norberg and Rayner (1987; extant bats) and Norberg (1989; fossil bats).

prey (Vaughan and Vaughan, 1986; Norberg and Rayner, 1987; Fenton, 1989, 1990). Examples of bats that use perches to forage for flying prey ("flycatching" or "sally foraging" bats) include megadermatids (e.g., *Laviana frons*, *Megaderma spasma*), nycterids (e.g., *Nycteris grandis*, *Nycteris thebaica*), some rhinolophids (e.g., *Rhinolophus hildebrandti*, *Rhinolophus rouxi*, *Hipposideros commersoni*), and some vespertilionids (e.g., *Nyctophilus bifax* and juvenile *Myotis lucifugus*) (Vaughan, 1977; Buchler, 1980; Fenton, 1982b, 1990; Fenton and Rautenbach, 1986; Vaughan and Vaughan, 1986; Neuweiler et al., 1987; Norberg and Rayner, 1987; Tyrell, 1988; Fenton et al., 1990). Other perch hunters take nonflying prey that they glean from the ground or vegetation (e.g., most megadermatids, some nycterids, and

probably some phyllostomids; Vaughan, 1976; Sazima, 1978; Fiedler, 1979; Fenton et al., 1983, 1990; Tidemann et al., 1985; Norberg and Rayner, 1987; Fenton, 1990; Norberg, 1994). Most megadermatids and nycterids that glean prey from surfaces also engage in flycatching (Vaughan, 1976; Fenton et al., 1983, 1990; Norberg and Rayner, 1987), demonstrating that these are not mutually exclusive habits.

Many (perhaps all) extant perch-hunting bats switch between perch hunting and continuous flight when searching for prey (e.g., *Rhinolophus hildebrandti*, *R. rouxi*, *Nycteris grandis*, *N. thebaica*, *Megaderma lyra*, *Macroderma gigas*; Tidemann et al., 1985; Fenton and Rautenbach, 1986; Neuweiler et al., 1987; Audet et al., 1988; Fenton et al., 1987, 1990; Fenton, 1990). In at least some cases

(e.g., *Nycteris grandis* in Zimbabwe), allocation of time between these two foraging strategies may reflect prey availability, with more time being spent on hunting from continuous flight when prey is relatively scarce (Fenton, 1990; Fenton et al., 1990). Although Norberg and Rayner (1987) treated perch hunting as a foraging strategy distinct from continuous aerial hawking, and categorized species as using either one or the other approach, Fenton (1990) argued that data now available preclude regarding perch hunting and continuous aerial hawking as mutually exclusive foraging strategies. Even if *Icaronycteris*, *Archaeonycteris*, and/or *Palaeochiropteryx* hunted from perches, they may also have foraged from continuous flight under some circumstances.

Hill and Smith (1984) suggested that perch hunting may be the primitive foraging strategy for microchiropteran bats. This hypothesis clearly makes sense in terms of energy efficiency. Observations of perch hunting by juvenile *Myotis lucifugus* additionally suggest that this form of hunting requires less elaborate flight maneuvers than those used by adults during continuous aerial hawking (Buchler, 1980). Perch hunting by juvenile *Myotis* may also have the effect of removing these bats from group-foraging situations, thus minimizing distractions, reducing the need for complex evasive behaviors, and simplifying the analysis of information from returning echoes (Buchler, 1980). As such, perch hunting appears to be less demanding than full-time aerial hawking in terms of the flight and echolocation skills required for successful prey capture (Buchler, 1980).

In the context of our theories about the evolution of flight and echolocation, perch hunting represents a possible intermediate between foraging strategies characteristic of arboreal mammals (e.g., scansorial foraging while clinging to surfaces) and full-time aerial hawking. The demands of perch hunting are probably more complex than those of scansorial foraging even when passive cues are used to locate prey because the hunter must simultaneously fly and keep track of the prey while approaching it. However, perch hunting is apparently less complex (in terms of required flight maneuvers and neural processing) and probably requires lower energy

expenditures than aerial hawking. The evolutionary transition to full-time aerial hawking may have mirrored the ontogenetic transformations seen today in bats like *Myotis lucifugus*:

... the bats progress from: (1) first flights and landing attempts, during which the moving bat is probably most attentive to large, stationary objects, through (2) ... a short 'flycatcher' period during which the bat is initially fixed and the target is in motion, to (3) the most complex stage of integration involving both a continually moving signal source [the bat] and moving target. (Buchler, 1980: 216)

Critical factors in this transformation appear to be degree of development of echolocation abilities and the integration of echolocation and flight behavior during foraging. Norberg (1989) considered correlations among wing morphologies and echolocation call structure, again building on the work of Norberg and Rayner (1987) to reconstruct the possible behaviors of the Eocene fossil bats. Norberg (1989: 209) found that

... modern bats with similar wing design to the fossil species *Hassianycteris messelensis* and *H. magna* have echolocation calls for long-range detection in open spaces (CF + narrowband FM), which occur for example in rhinopomatids, or calls which include both steep and shallow FM sweeps, which occur in species that hawk fast relatively close to obstacles (such as *Lasiurus borealis*, *L. cinereus*, and *Nyctalus noctula*). The predicted fast foraging flight in *H. messelensis* and *H. magna* indicates that they used echolocation calls of similar structure.

The smaller size, lower wing loading, low aspect ratio and short wings of *Icaronycteris*, *Archaeonycteris* and *Palaeochiropteryx* suggest that they foraged more close to, or among, vegetation. They should therefore have benefitted most from echolocation calls for short-range detection.

Extant bats with similar aspect ratio and wing-loading parameters to *Icaronycteris*, *Archaeonycteris*, and *Palaeochiropteryx* use either long CF echolocation calls (e.g., *Rhinolophus hipposideros*, *Rhinolophus ferrumequinum*) or broadband FM calls (e.g., *Pipistrellus kuhlii*, *Pipistrellus hesperus*, *Myotis volans*, *Myotis yumanensis*, *Micronycteris megalotis*; Norberg, 1989). Use of long CF calls (high-duty-cycle echolocation) is associated with greater cochlear enlargement than is seen in any of the Eocene fossils; therefore, it seems unlikely that any of the Eocene taxa used such a system (Habersetzer and Storch, 1989, 1992). This suggests that *Ica-*

ronycteris, *Archaeonycteris*, and *Palaeochiropteryx* probably used broadband FM calls, which are useful for target texture discrimination, range finding, and short-range detection among clutter (Simmons et al., 1975; Norberg, 1989).

There is a great deal of variation in call structure among extant bats that use broadband FM calls, with calls being either short or long, steep or shallow, concave up or concave down, etc. (e.g., Simmons et al., 1975, 1980; Fenton and Bell, 1979, 1981; Simmons, 1980; Simmons and Stein, 1980; Fenton et al., 1983; Barclay, 1985). High-intensity calls of varying durations and forms are used by aerial insectivores. Surface gleaners typically use very short (<2 msec), low-intensity multiharmonic calls that are apparently well-suited for fine texture discrimination of targets on a surface by either temporal cues or spectral differences in the echoes (Möhres and Kulzer, 1957; Möhres and Neuweiler, 1966; Möhres, 1967b; Simmons et al., 1974; Simmons, 1979; Simmons and Stein, 1980; Barclay et al., 1981; Habersetzer and Vogler, 1983; Guppy et al., 1985; Norberg and Rayner, 1987; Suthers and Wenstrup, 1987; Schmidt, 1988; Norberg, 1989; Audet, 1990; Faure and Barclay, 1992; Faure et al., 1993). These short, low-intensity calls may minimize echoes from clutter while simultaneously minimizing the chances of alerting possible prey (Barclay et al., 1981; Habersetzer and Vogler, 1983; Fullard, 1987; Roverud, 1987; Fenton, 1990; Kober and Schnitzler, 1990; Faure et al., 1993). In some cases, calls may be "switched off" to facilitate passive prey localization by vision or by listening for sounds produced by the prey (e.g., *Megaderma lyra*, *Antrozous pallidus*, *Macrotus californicus*; Fiedler, 1979; Bell, 1982a, 1992b, 1985).

Prey-generated sounds used by bats include mating calls (e.g., of frogs and katydids), rustling noises, and the sounds of insects landing on or crashing into vegetation (Fiedler, 1979; Tuttle and Ryan, 1981; Guppy and Coles, 1983; Ryan and Tuttle, 1983, 1987; Fenton, 1984, 1990, 1994a; Belwood and Morris, 1987; Tyrell, 1988; E. Kalko, personal commun.). In some instances (e.g., some phyllostomids), the bat uses these noises to identify the area in which the prey is

located, not the exact position of the prey; this area is then engulfed with the wing membranes and the prey is located by touch or other cues (E. Kalko, personal commun.). Olfaction may be used by some bats (e.g., *Myotis myotis*, *Mystacina tuberculata*) for detecting prey under leaf litter, in tree holes, and in other concealed locations (Kolb, 1961; B. Lloyd, personal commun.). Passive prey localization—with or without accompanying echolocation calls—is apparently used by various nycterids, megadermatids, phyllostomids, mystacinids, antrozoids, and vespertilionids (Kolb, 1959, 1961; Fiedler, 1979; Barclay et al., 1981; Tuttle and Ryan, 1981; Bell, 1982a, 1982b, 1985; Guppy and Coles, 1983; Ryan and Tuttle, 1983, 1987; Fenton, 1984, 1990, 1994a; Bell and Fenton, 1986; Norberg and Rayner, 1987; Belwood and Morris, 1987; Schmidt et al., 1988; Tyrell, 1988; Norberg, 1989; B. Lloyd, personal commun.). At least one of these species, the gleaner phyllostomid *Micronycteris megalotis*, has wing parameters similar to those of the Eocene fossil bats (Norberg and Rayner, 1987; Norberg, 1989).

Cochlear size and structure provide another source of data useful for evaluating hypotheses about echolocation behavior. Habersetzer and Storch (1992) found correlations between relative cochlear size (width of the second half of the basal turn plotted against basicranial width; see character 26 above) and the echolocation strategies adopted by various taxa. Bats that use long CF calls emitted at high duty cycles (e.g., rhinolophines) are typically characterized by exceptionally large cochleae (Habersetzer and Storch, 1992). Most bats that use broadband FM calls and forage by continuous aerial hawking (e.g., *Rhinopoma*) have somewhat smaller cochleae, but still fall well above the lower limits of cochlear size in microchiropterans (Habersetzer and Storch, 1992). Microchiropterans with the smallest cochleae (those that fall near or within the zone of overlap between Microchiroptera and Megachiroptera) include forms that use broadband FM echolocation calls but are not typical aerial insectivores (Habersetzer and Storch, 1992). This group includes several phyllostomids (e.g., *Phyllostomus hastatus*, *Trachops cirrhosus*, *Leptonycteris nivalis*,

Carollia perspicillata, *Desmodus rotundus*), megadermatids (e.g., *Megaderma spasma*, *Megaderma lyra*), and nycterids (e.g., *Nycteris grandis*). Several of these hunt from perches much of the time (see above); as far as is known, all use calls of short duration and often low intensity, and many apparently use cues other than echolocation to locate their food (Fiedler, 1979; Tuttle and Ryan, 1981; Fenton, 1984, 1990, 1994a; Bell and Fenton, 1986; Norberg and Rayner, 1987; Ryan and Tuttle, 1987; Tyrell, 1988; Norberg, 1989).

Habersetzer and Storch (1992) compared values for cochlear width and basicranial width in six species of Messel bats to those obtained from extant forms (see discussion under character 26 above) and used the results to infer possible echolocation strategies for the fossil bats. They found that *Hassianycteris* and *Palaeochiropteryx* resemble taxa at the lower end of the range of variation for typical continuous aerial hawkers (fig. 29). Other aspects of cochlear structure explored by Habersetzer and Storch (1989) and Habersetzer et al. (1994) included (1) the relative size of the cross-sectional area of the bony cochlear canal above the spiral laminae, (2) the degree of development of the secondary spiral lamina, and (3) the distance between the primary and secondary spiral laminae in the basal turn (this dimension provides an approximate measure of the width of the basilar membrane). On the basis of comparisons with extant forms and consideration of body sizes, Habersetzer and Storch (1992) proposed echolocation calls within a frequency band of 30–90 kHz for *Palaeochiropteryx*, and intense sound frequencies below 30 kHz for *Hassianycteris*.

In comparison to *Palaeochiropteryx* and *Hassianycteris*, species of *Archaeonycteris* have distinctly smaller cochleae, falling within the zone of overlap between Microchiroptera and Megachiroptera (fig. 29). These forms had basal cochlear widths well below the range typical for obligate aerial insectivores. Instead, they most closely resembled perch hunting/aerial hawking megadermatids and the phyllostomid gleaner *Trachops* (Habersetzer and Storch, 1992). On this basis, Habersetzer and Storch (1992: 466) proposed that *Archaeonycteris* echolocated

using “rather short, multiharmonic pulses.” Based on our examinations of *Icaronycteris* and estimates of cochlear size (see discussion under character 26 above), we suspect that *Icaronycteris* had echolocation capabilities and calls similar to those of *Archaeonycteris*.

Another source of information regarding the foraging habits of Eocene bats is analysis of fossilized stomach contents. No such data are available for *Icaronycteris*, but Richter and Storch (1980) and Habersetzer et al. (1992, 1994) reported the results of analyses of stomach contents of *Palaeochiropteryx tupaiondon*, *P. spiegelii*, *Archaeonycteris trigonodon*, *Hassianycteris messelensis*, and *H. magna*. The most recent summary was provided by Habersetzer et al. (1994), who reported on stomach contents of a larger series of specimens (33 individuals) than were available in previous studies.

Habersetzer et al. (1994) concluded that the two species of *Palaeochiropteryx* (*P. tupaiondon*, represented by 20 specimens, and *P. spiegelii*, 5 specimens) show little or no difference in their diet. Stomach contents included thick layers of scales, hairs, and cuticle fragments similar to those known from primitive Microlepidoptera (e.g., Micropterigidae, Hepialidae, and Eriocraniidae), Trichoptera, and scale-bearing Diptera (e.g., Culicidae; Habersetzer et al., 1994). In one case, details of scale ultrastructure permitted unambiguous identification of the prey as a micropterigid microlepidopteran (Habersetzer et al., 1994). Microlepidopterans such as these are all small moths that are weak night fliers; Trichoptera (caddis flies) are similar in size and flight habits (Habersetzer et al., 1992). Caddis flies are active at night, and at the time of hatching they often swarm in large numbers just above the water surface at the edges of lakes and streams (Habersetzer et al., 1992). Thick cuticles, such as are characteristic of coleopterans (beetles) and blattoids (cockroaches and their kin), are rare in the gut contents of both species of *Palaeochiropteryx* (Habersetzer et al., 1994). These results suggest that *Palaeochiropteryx tupaiondon* and *P. spiegelii* may have fed mainly on small, scale-bearing insects with weak exoskeletons that tend to fly close to the ground or water surface (Habersetzer et al., 1992, 1994). These bats must have been

capable of detecting, tracking, and capturing flying insects on the wing; it is very hard to imagine how so many individuals could have filled their stomachs with tiny moths and caddis flies if they were not expert aerial hawkers. This conclusion is consistent with the presumed flight styles of *Palaeochiropteryx* as reconstructed from wing parameters (Habersetzer et al., 1992, 1994).

The fossilized stomach contents of *Hassianycteris messelensis* (seven specimens) and *H. magna* (one specimen) similarly includes chitinous scales, hairs, and cuticle fragments, but the proportions of these items are markedly different from those seen in *Palaeochiropteryx* (Habersetzer et al., 1992, 1994). Habersetzer et al. (1994: 246) noted that

Whereas in *Palaeochiropteryx* thick layers of closely packed scales clearly prevail, in *Hassianycteris* scales are generally rare, which means that scale-bearing insects are not the predominant prey. Moreover, most scales found in *Hassianycteris* show a different and more elaborate ultrastructure This type of scale is not restricted to higher evolved Lepidoptera, yet it is comparatively rare in primitive moths. So its predominance in the gut contents makes it at least probable that *Hassianycteris* mainly preyed on Macrolepidoptera There are still more general differences in the diet of both genera. Whereas in *Palaeochiropteryx* most cuticulae are thin and hairy, but with an otherwise smooth surface, in *Hassianycteris* thick cuticulae with strongly sculptured surface prevail (Richter and Storch, 1980; Richter, 1987). Cuticulae of a similar design are known from many Messel insects (e.g., Coleoptera and Blatto[ide]a).

Inclusion of coleopteran prey in the diet would be consistent with the massive dentition and deep mandible seen in *Hassianycteris* (fig. 24). The dentition and jaw structure of *Hassianycteris* resemble that seen in many extant molossids, particularly those thought to feed regularly on hard-shelled beetles (Freeman, 1979, 1981). Scales referable to Trichoptera and Microlepidoptera are very rare or even lacking in stomachs of *Hassianycteris*, suggesting that these bats did not hunt close to the ground, but instead hunted larger prey in relatively open spaces (Habersetzer et al., 1994). No obvious differences were detected between the stomach contents of *H. messelensis* and *H. magna*, although the latter is known from only a single specimen (Habersetzer et al., 1994).

Little information is available about stomach contents of *Archaeonycteris*; apparently

only two specimens of *A. trigonodon* have thus far been investigated (Habersetzer et al., 1992). The gut contents of these specimens consist predominantly of thick chitin fragments, among which are some with iridescent structural colors such as those seen in Messel coleopterans (e.g., Lutz, 1992). Fragments referable to scale-bearing insects (e.g., lepidopterans, Tricoptera) are completely absent in *A. trigonodon* (Habersetzer et al., 1992). This suggests that *Archaeonycteris* may have been a beetle specialist.

In summary, much can be inferred about the ecology of Eocene bats (particularly those from Messel) based on their morphology and stomach contents. Given the flight and echolocation habits suggested for *Hassianycteris* by Habersetzer and Storch (1987, 1989, 1992), Norberg (1989), and Habersetzer et al. (1992, 1994), it seems very likely that members of this genus foraged by continuous aerial hawking comparable to that seen today in many microchiropterans (e.g., *Rhinopoma*, some *Lasiurus*). *Palaeochiropteryx* was probably also capable of continuous aerial hawking; indeed, the abundance of this taxon at Messel (and analyses of stomach contents) suggests that these bats were hawking insects over ancient Lake Messel at the time of their death. Most extant bats that forage by continuous aerial hawking use the uropatagium for catching flying insects (Vaughan, 1959, 1970a, 1970b; Webster and Griffin, 1962; Norberg, 1976; Hill and Smith, 1984; Schnitzler et al., 1994; Kalko, 1995). Both *Hassianycteris* and *Palaeochiropteryx* have a well developed calcar, suggesting the presence of a large uropatagium appropriate for aerial insect capture.

Wing morphology, body size, cochlear morphology, dental morphology, and stomach contents indicate that *Hassianycteris* probably foraged by hawking insects (perhaps mostly beetles and cockroaches) while in fast flight well above the ground in forest gaps and above the canopy. Echolocation calls were probably intense, of relatively low frequency (<30 kHz), and may have been either narrowband FM signals or calls that included both steep and shallow FM sweeps. In contrast, *Palaeochiropteryx* may have foraged close to the ground and vegetation, probably hunting from perches as well as hawking in-

sects while in slow flight. *Palaeochiropteryx* apparently specialized in preying on small-scaled insects (i.e., small moths and caddis flies), and its echolocation calls were most likely broadband calls of moderate to high frequency (30–90 kHz). There is no evidence that any of the Messl bats used high-duty-cycle CF echolocation.

Wing morphology of *Icaronycteris* and *Archaeonycteris* suggests that these taxa probably foraged close to the ground and close to vegetation, as did *Palaeochiropteryx* (Habersetzer and Storch, 1987, 1989, 1992; Norberg, 1989; and Habersetzer et al., 1992, 1994). However, presence of only moderate enlargement of the cochlea—together with absence of a calcar—suggests that these forms may have been perch hunters that specialized in gleaning their prey from surfaces rather than catching it on the wing. *Archaeonycteris* may have been a beetle specialist; we have no record of the preferred prey of *Icaronycteris*. Echolocation calls in both taxa were probably short (≤ 2 msec) broadband FM signals of moderate to high frequency (30–90 kHz) or short, multiharmonic calls. In either case, these echolocation calls may have been of low intensity, and may have been “turned off” at times to facilitate location of prey by passive means (e.g., listening for prey-generated sounds or looking for prey movements). It is unlikely that *Icaronycteris* and *Archaeonycteris* used echolocation for detection, tracking, or evaluation of prey. Echolocation was probably used only for orientation and obstacle detection, while prey detection and tracking were accomplished by passive means.

EVOLUTION OF FORAGING STRATEGIES: A PHYLOGENETIC PERSPECTIVE

The phylogeny generated in our study (fig. 36) provides a framework for interpreting the morphological data and behavioral inferences presented above. Given the topology of this tree, we suggest that the earliest members of the microchiropteran lineage (forms currently unknown from fossils) probably used vision for orientation and obstacle detection in their arboreal/aerial environment, and probably foraged by gleaning insects and

perhaps some fruits and other edible items from foliage, bark, and perhaps the ground. Location of potential food items was probably accomplished by a combination of vision and listening for prey-generated sounds. Like *Archaeopteropus*, *Icaronycteris*, *Archaeonycteris*, and *Palaeochiropteryx*, these bats probably had low aspect ratio wings, moderate wing loading, and relatively large wing tips, all of which suggest that they habitually flew close to the ground and near vegetation.

Low-duty-cycle echolocation evolved subsequently, probably from communication calls that incidentally produced informative echoes. As we suggested earlier, this system was probably simple at first, permitting only orientation and obstacle avoidance but not detection, tracking, or evaluation of airborne prey. Basicranial modifications presumed to be associated with increased efficacy of echolocation began prior to the divergence of *Icaronycteris* from the microchiropteran lineage. However, wing morphology, a moderately enlarged cochlea, and absence of a calcar in this taxon suggest to us that *Icaronycteris* was a perch-hunting gleaner rather than a predator on aerial insects. This foraging strategy would have had the advantage of being relatively energy-efficient while at the same time requiring only moderate auditory data-processing capabilities to successfully sort the information from returning echoes. Echolocation calls were most likely short (≤ 2 msec) broadband FM signals or multiharmonic calls, probably of relatively low intensity. These calls may have been “turned off” at times to facilitate passive prey localization. Indeed, prey detection, tracking, and evaluation were probably not done with echolocation, but rather by vision or listening for prey-generated sounds. Passive acoustic cues may have been particularly important if these bats were strictly nocturnal. In essence, the only major change in foraging method at this level would have been the addition of echolocation as a tool for orientation and obstacle detection. The basic foraging strategy—gleaning from a perch—would have been the same as seen in the nonecholocating chiropteran ancestors of *Icaronycteris*.

The derived morphological transformations that diagnose the node linking *Archaeo-*

nycteris with *Hassianycteris*, *Palaeochiropteryx*, and the microchiropteran crown group (e.g., reduction of the number of roots on P3, presence of a ventral accessory process on C4, absence of an ossified third phalanx on wing digit III) are relatively small changes that do not indicate any major shifts in foraging ecology. This pattern suggests to us that *Archaeonycteris* retained much the same foraging strategy as *Icaronycteris*. *Archaeonycteris* and *Icaronycteris* share a similar wing morphology, moderately enlarged cochlea, and lack of a calcar, features we interpret as indicating that these bats foraged by gleaning prey that were detected from a perch using passive means rather than echolocation.

The next node as one moves up the tree—that which links *Hassianycteris* with *Palaeochiropteryx* and the microchiropteran crown group—is associated with a much more extensive suite of morphological changes (see discussion above under “Character Transformations at Basal Nodes”). Most notable among these are: (1) a greatly enlarged cochlea, (2) a dorsal articular facet on the scapula (although this may have evolved earlier), (3) a laterally compressed ventral process on the manubrium of the sternum, (4) increased development of rib laminae (this may have evolved somewhat earlier), (5) a threadlike fibula, and (6) presence of a calcar. Taken together, these features suggest that a major shift in foraging strategy occurred in the microchiropteran lineage just prior to the divergence of *Hassianycteris*: the evolution of aerial hawking. This behavior involves using echolocation to detect, track, and assess prey, and the use of the uropatagium (supported and controlled by a calcar) to capture prey on the wing. Changes in the postcranial skeleton, particularly the pectoral girdle, suggest that some “fine tuning” of the flight mechanism may have accompanied the behavioral change to aerial hawking. This seems reasonable given the demands of aerial foraging behavior, particularly if these bats occasionally foraged in group situations (e.g., when caddis flies were hatching along the shore of Lake Messel) where complex capture and evasive maneuvers may have been required.

Interestingly, the morphological and behavioral changes associated with the evolu-

tion of aerial hawking do not seem to have been correlated with any appreciable modifications in wing shape or wing loading (based on the results of Norberg, 1989; see figs. 43, 44). Similarities in aspect ratio, wing tip indices, and wing loading in *Palaeochiropteryx*, *Archaeonycteris*, *Icaronycteris*, and *Archaeopteropus* lead us to conclude that the body size and wing form of *Palaeochiropteryx* is plesiomorphic, and that this morphology was present in the most recent common ancestor of *Palaeochiropteryx* and *Hassianycteris*. Accordingly, the body size and wing morphology seen in *Hassianycteris* (discussed below) are autapomorphic features.

Like *Icaronycteris* and *Archaeonycteris*, *Palaeochiropteryx* had low aspect ratio wings, moderate wing loading, and relatively large wing tips, all of which indicate that these bats habitually flew close to the ground and near vegetation. However, the greatly enlarged cochlea and well developed calcar suggest that *Palaeochiropteryx* was fully capable of aerial hawking. This hypothesis is consistent with the analyses of stomach contents and taphonomy of *Palaeochiropteryx* at Lake Messel. Echolocation signals used by *Palaeochiropteryx* were probably short- to moderate-length broadband FM calls.

As pointed out by Fenton (1990) and Fenton et al. (1990), many extant bats that hunt from perches also hawk insects in continuous flight, with allocation of time between these two foraging strategies reflecting prey availability. Given that gleaning from a perch probably represents the primitive foraging strategy for the microchiropteran lineage, we suspect that *Palaeochiropteryx* may have used a combination of perch hunting (including flycatching) and slow aerial hawking to capture its prey, much like modern nycterids. This would be consistent with cochlear size in *Palaeochiropteryx* (as estimated by Habersetzer and Storch, 1992; fig. 29), which places this genus just at the lower end of the range of variation seen among forms that are continuous aerial hawkers (e.g., most vespertilionids) and at the upper end of the range of variation in extant perch-hunting forms that use low-duty-cycle echolocation (e.g., nycterids and megadermatids).

The transition from gleaning stationary

prey detected by passive means (vision or listening for prey-generated sounds) to aerial hawking using echolocation to detect and track prey must have been a complex process that involved intermediate steps. It seems unlikely that echolocation was used for detecting stationary prey during this transition, because detection of hard targets resting on hard or irregular backgrounds is one of the more difficult tasks faced by echolocators (Simmons et al., 1980; Fenton, 1990, 1994a, 1995). Instead, we hypothesize that bats that regularly foraged by gleaning stationary prey (detected by passive means) increasingly came to hunt moving insects, perhaps leaping after prey that had been startled by movements or attacks by the bat. At this point, echolocation (which they were already using for orientation and obstacle avoidance) could provide more information about prey location and movement than could be obtained by passive means. To fully exploit this form of data collection, the animals would have had to increase signal strength in order to maximize range and provide the necessary time to track and evaluate targets. However, environmental clutter (which produces many distracting echoes) would have presented a major impediment to the evolution of effective flycatching behavior. It therefore seems likely that flycatching using echolocation to detect and track prey probably evolved in bats that frequented forest gaps and the edges of forests along lakes and rivers, places where vegetation (with potential perches) lies adjacent to relatively clutter-free open spaces. Once flycatching from perches was well established, it is easy to imagine a progressive transition to spending more time on the wing, ultimately leading to the evolution of taxa that relied exclusively on foraging by continuous aerial hawking. It is not clear when bats began to use the uropatagium for prey capture, but evolution of the calcar apparently preceded or was coincident with the evolution of aerial hawking.

Our hypothesis that the evolutionary transition from gleaning (using passive prey detection) to aerial hawking (using echolocation) took place in habitats associated with forest gaps or forest edges along bodies of water cannot be tested given the sparse fossil record of bats. However, it is interesting to

note that all four of the fossil bats considered here (*Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*) have been collected from lake deposits that are presumed to have been surrounded by subtropical or tropical forests at the time of deposition (MacGinitie, 1969; Grande, 1980; Schaarschmidt, 1992). The excellent preservation of many of the bat fossils found at Messel and Fossil Basin indicates that these animals were not transported far after death, suggesting that they may have foraged around the edges and over the lakes in which they were ultimately preserved.

Species of *Hassianycteris* are larger in many dimensions than most of the other Eocene bats, and analyses of wing morphology by Norberg (1989) indicated that *Hassianycteris* was characterized by significantly higher wing loading than were *Palaeochiropteryx*, *Archaeonycteris*, or *Icaronycteris*. Indeed, *Hassianycteris* apparently had a higher wing loading than most extant bats (fig. 43). These observations, taken together with a reasonably high aspect ratio, a greatly enlarged cochlea, and presence of a calcar, suggest that *Hassianycteris* foraged by fast aerial hawking, most likely well above the ground in forest gaps or above the canopy. *Hassianycteris* thus represents another shift in foraging strategy, away from combined perch hunting and aerial hawking near the ground or vegetation to a fast-flying, continuous aerial hawking foraging strategy similar to that seen in extant rhinopomatids and some vespertilionids. As noted above, however, this shift apparently occurred after the lineage leading to *Hassianycteris* diverged from the lineage leading to the microchiropteran crown group.

Continuing to move up the phylogenetic tree, we find that the clade comprising *Palaeochiropteryx* plus the microchiropteran crown group is diagnosed by only one unambiguous synapomorphy, the presence of a ventral accessory process on C5. This feature is not indicative of any change in foraging habits, but rather a continuation of neck modifications associated with roosting behavior (see discussion under character 77). Transformations that diagnose the microchiropteran crown group (e.g., modification of the premaxilla articulation, reduction in the

number of lower premolars) indicate changes in the masticatory apparatus, but no major behavioral shifts.

In summary, we propose that foraging behavior in the microchiropteran lineage evolved in a series of steps: (1) gleaning food objects during short flights from a perch using vision for orientation and obstacle detection; prey detection by passive means, including vision and/or listening for prey-generated sounds (no known examples in fossil record); (2) gleaning stationary prey from a perch using echolocation and vision for orientation and obstacle detection; prey detection by passive means (*Icaronycteris*; *Archaeonycteris*); (3) perch hunting for both stationary and flying prey using echolocation and vision for orientation and obstacle detection; prey detection and tracking using echolocation for flying prey and passive means for stationary prey (no known example, although *Icaronycteris* and/or *Archaeonycteris* may have done this at times); (4) combined perch hunting and continuous aerial hawking using echolocation and vision for orientation and obstacle detection; prey detection and tracking using echolocation for flying prey and passive means for stationary prey; calcar-supported uropatagium used for prey capture (common ancestor of *Hassianycteris* and *Palaeochiropteryx*; retained in *Palaeochiropteryx*); and (5) exclusive reliance on continuous aerial hawking using echolocation and vision for orientation and obstacle detection; prey detection and tracking using echolocation (*Hassianycteris*; common ancestor of microchiropteran crown group). Given the topology of the tree we derived earlier (fig. 36), it seems most likely that the latter foraging strategy—reliance on continuous aerial hawking—was primitive for the microchiropteran crown group. This is consistent with optimization of foraging strategies both within the microchiropteran crown group and among the fossil stem group forms.

The conclusion that aerial hawking is the primitive foraging strategy for the microchiropteran crown group suggests that gleaning, passive prey detection, and perch hunting among extant taxa represent secondarily derived specializations rather than retentions of primitive habits. If so, topology of our tree

(fig. 36) indicates that passive prey detection evolved independently at least five or six times—in phyllostomids, mystacinids, antrozoids, vespertilionids, and either independently in nycterids and megadermatids or in the common ancestor of Rhinolophidae. Similarly, gleaning must have evolved independently at least four times within Microchiroptera—in phyllostomids, antrozoids, vespertilionids, and rhinolophoids. Perch hunting apparently evolved at least three times—in phyllostomids, vespertilionids, and rhinolophoids. Although passive prey detection, gleaning, and perch hunting are linked in some taxa (e.g., most megadermatids and nycterids), they are decoupled in other forms. For example, *Mystacina* apparently uses passive prey detection but does not glean or hunt from perches; instead, it approaches its prey “on foot” (B. Lloyd, personal commun.). Rhinolophids sometimes hunt from perches and glean, but apparently do not use passive cues to detect their prey (Norberg and Rayner, 1987). *Lavia frons* hunts from perches but apparently does not glean or use passive prey detection (Vaughan and Vaughan, 1986). These observations suggest that passive prey detection, gleaning, and perch hunting evolved in different ways in different microchiropteran lineages.

The relative timing of the evolutionary and behavioral changes in the lineage leading to extant Microchiroptera can be estimated from the fossil record. Taxa representing stages 2, 4, and 5 as defined above were apparently present simultaneously at Messel, suggesting that evolutionary transformations in foraging strategies may have occurred very rapidly in early members of the microchiropteran lineage. This was probably facilitated by the mechanical coupling of ventilation and flight, which meant that the energy costs of echolocation to flying bats were low, particularly in comparison to the energetic benefits of aerial hawking for insects in the absence of any competitors.

The evolution of continuous aerial hawking may have been the “key innovation” (sensu Liem, 1973) responsible for the burst of diversification in microchiropteran bats that occurred in the Eocene. Fossils referable to six major extant lineages are known from Middle–Late Eocene deposits (table 1): (1)

Emballonuridae, (2) Megadermatidae, (3) Hipposiderinae, (4) Rhinolophinae, (5) Nataloidea, and (6) Molossinae. Reconstruction of ghost lineages following the methods of Norell (1992) leads to the conclusion that many more extant lineages were minimally present by the end of the Eocene, including (7) Rhinopomatoidea, (8) Nycteridae, (9)

Noctilionoidea, (10) Mystacinidae, (11) Antrozoidae, (12) Tomopeatinae, and (13) Vespertilionidae. All of these must have diverged during the Eocene given the Eocene ages of their sister-taxa. It thus appears that *Icaronycteris* and the Messel bats provide an unprecedented view of the steps leading up to a major adaptive radiation of mammals.

CLASSIFICATION OF EOCENE BATS

The phylogenetic results of this study indicate that many groupings of Eocene taxa previously recognized in formal classifications (e.g., Eochiroptera, Palaeochiropterygoidea, Archaeonycterididae [including *Icaronycteris*]) are not monophyletic. Beginning at the lowest taxonomic level, it seems most appropriate to place each of the four genera considered in this study in its own monophyletic family¹³: *Icaronycteris* in Icaronycteridae

dae Jepsen, 1966; *Archaeonycteris* in Archaeonycteridae Revilliod, 1917b; *Hassiancycteris* in Hassiancycteridae Habersetzer and Storch, 1987; and *Palaeochiropteryx* in Palaeochiropterygidae Revilliod, 1917b. This arrangement preserves monophyly of higher taxonomic groups and serves to highlight the morphological and presumed behavioral differences among genera.

¹³ There is considerable disagreement in the literature concerning the formation of family-group names based on generic names ending in -nycteris. The family name in common usage for extant *Nycteris* is Nycteridae (Koopman and Jones, 1970; Hill and Smith, 1984; Koopman, 1984, 1993, 1994). Revilliod (1917b) used a similar formation when he named Archaeonycteridae, as did Jepsen (1966) when he named Icaronycteridae. However, Russel and Sigé (1970) argued that the proper formation of family-group names from -nycteris required the spelling -nycterididae. They thus changed the spelling of Archaeonycteridae to Archaeonycterididae. Some authors have followed this usage (e.g., Habersetzer and Storch, 1987, 1989; Habersetzer et al., 1992, 1994), but many have continued to use Archaeonycteridae (e.g., Hill and Smith, 1984; Hand et al., 1994; McKenna and Bell, 1997). Habersetzer and Storch (1987) followed Russel and Sigé's (1970) usage when they named Hassiancycterididae, and subsequent authors have used this spelling (e.g., Habersetzer et al., 1992; McKenna and Bell, 1997).

As we view them, Icaronycteridae, Archaeonycteridae, and Hassiancycteridae each currently contain only the nominate genus. The situation is slightly more complex in the case of Palaeochiropterygidae. Two additional genera, *Cecilionycteris* and *Matthesia*, have been referred to Palaeochiropterygidae by previous authors based on dental features (e.g., Sigé and Russell, 1980; Hill and Smith, 1984; Beard et al., 1992). In the absence of additional data, we provisionally accept this assessment, although we note that discovery of more complete material may ultimately demonstrate that Palaeochiropterygidae as thus defined (including *Palaeochiropteryx*, *Cecilionycteris*, and *Matthesia*) is a paraphyletic assemblage.

Despite Russell and Sigé's (1970) argument about the nature of the greek root of -nycteris, we think that it is counterproductive to spell some family-group names in one fashion and others differently. Because Nycteridae is widely accepted as the spelling of the family-group name based on *Nycteris*, we argue that all family-group names based on genera ending in -nycteris should be spelled in the same fashion. Accordingly, we recognize the Icaronycteridae, Archaeonycteridae, and Hassiancycteridae as the most appropriate spellings for family-group names based on *Icaronycteris*, *Archaeonycteris*, and *Hassiancycteris*.

Ageina, which is known only from dental fragments, has been referred variously to "family uncertain" (Russell et al., 1973), Palaeochiropterygoidea (Smith, 1977; Smith and Storch, 1981), Eochiroptera (Sigé and Legendre, 1983), Archaeonycteridae (Hill and Smith, 1984), and possibly Natalidae sensu Van Valen (Beard et al., 1992). We consider the assessment of Beard et al. (1992), which is based on the most recent evidence (including comparisons with the new taxon *Honrovits*), to represent the best current working hypothesis. Accordingly, we follow suggestions made by Beard et al.

(1992) and refer both *Ageina* and *Honrovits* to *Nataloidea incertae sedis*.

Australonycteris, which is also poorly known, was placed in Microchiroptera, family incertae sedis by Hand et al. (1994). They noted that this form has a dentition similar to that of *Archaeonycteris* (at least in terms of the absence of derived traits), although the petrosal referred to *Australonycteris* appears relatively more derived and is somewhat vesperilionoid-like (Hand et al., 1994). These and other observations suggest to us that *Australonycteris* probably fits in the tree somewhere between *Archaeonycteris* and the microchiropteran crown group. Given this hypothesis, any decision about how to classify *Australonycteris* requires consideration of broader issues surrounding the classification of stem-group forms.

The principal nomenclatural problem faced in this study concerns higher-level classification of the Eocene groups that fall outside the microchiropteran crown group—in other words, where to put Icaronycteridae, Archaeonycteridae, Hassiancyteridae, and Palaeochiropterygidae. Debates have raged in the systematic literature for decades concerning the relative pros and cons of different approaches to defining and naming taxonomic groups (e.g., Ghiselin, 1966, 1984; Nelson, 1972, 1974; Bock, 1974; Duncan and Estabrook, 1976; Estabrook, 1978, 1986; Jefferies, 1979; Wiley, 1979, 1981; Duncan, 1980; Phillips, 1984; Rowe, 1987, 1988; Gauthier et al., 1988; Heywood, 1988; de Quieroz and Gauthier, 1990, 1992, 1994; Minelli, 1991; Lucas, 1992; Meier and Richter, 1992; Lucas and Luo, 1993; Wyss and Flynn, 1993; Bryant, 1994, 1996; de Queiroz, 1994; Smith, 1994; Wyss and Meng, 1996; McKenna and Bell, 1997). Four principal issues have been debated: (1) whether taxa should be recognized on the basis of shared characters (i.e., diagnoses) or defined phylogenetically (i.e., on the basis of their relationships); (2) whether all named groups above the species level must be monophyletic (some workers have argued that convex paraphyletic groups may be usefully employed in classifications); (3) the pros and cons of recognizing formal ranks (e.g., “order,” “family”) in classifications; and (4) the relative merits of node-based, crown-clade-restricted, stem-based,

stem-modified node-based, and other types of phylogenetic definitions. We concur with most recent authors in concluding that phylogenetic definitions are essential and that all named taxa should be monophyletic (or at least potentially monophyletic). We consider issues related to rank to be of secondary importance compared with the definition of taxa (see discussion below). The central issue, in our opinion, is the method(s) used to define the limits of taxa, particularly those to which we may apply well-known taxonomic names (e.g., Microchiroptera).

Given the phylogenetic relationships hypothesized here, three general options for defining Microchiroptera seem appropriate. Using a node-based definition that emphasizes the importance of the extant crown group (i.e., a crown-clade-restricted definition), we might define Microchiroptera as the clade stemming from the most recent common ancestor of Emballonuridae and Yangochiroptera. If defined this way, Yinochiroptera would be included within Microchiroptera regardless of whether Emballonuridae falls outside Yinochiroptera (as suggested by this study) or inside Yinochiroptera (as suggested by Koopman, 1985, 1994). A less explicit crown-clade definition might define Microchiroptera as the clade stemming from the most recent common ancestor of all extant bats that use sophisticated echolocation. When defined either way, Microchiroptera would be equivalent to the microchiropteran crown group as discussed earlier, and would therefore exclude Palaeochiropterygidae, Hassiancyteridae, Archaeonycteridae, and Icaronycteridae. The main advantages of these definitions are that they are congruent with general usage of the name Microchiroptera by most biologists, and that they can be expected to remain relatively stable (e.g., discovery of new fossils will not affect the limits of Microchiroptera; fossil species would either fall inside or outside this clade). The latter option (defining Microchiroptera as the clade stemming from the most recent common ancestor of all extant echolocating bats) depends on persistence of extant forms, and thus might be considered potentially unstable because major extinctions could affect group contents in the future (see discussion of this problem in Lucas [1992] and Lucas and Luo

[1993]). However, we consider this to be of minor importance in the case of bats since the basal lineages (e.g., Emballonuridae, Yinochiroptera, and Yangochiroptera) are all speciose.

The principal disadvantage of using a crown-clade-restricted definition is that it effectively excludes some Eocene taxa from Microchiroptera simply because they are extinct. Given their morphology, relationships, and presumed ecologies (see above), it is likely that *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* would be considered microchiropterans were they alive today. Without a formal name linking these forms to extant Microchiroptera, considerable phylogenetic (and inferred behavioral and ecological) information would be lost from any classification scheme.

An alternative node-based definition of Microchiroptera could include the Eocene groups (Icaronycteridae, Archaeonycteridae, Hassianycteridae, and Palaeochiropterygidae) in Microchiroptera if the latter was defined as the clade stemming from the most recent common ancestor of Icaronycteridae and Yangochiroptera (or some other extant clade). Advantages of this definition include concurrence with current usage as applied by most paleontologists (e.g., Habersetzer and Storch, 1987, 1988, 1992; Novacek, 1987, 1991; Carroll, 1988; Storch and Habersetzer, 1988; Hand et al., 1994; McKenna and Bell, 1997), and congruence of this definition with ideas about the "key character" of Microchiroptera—sophisticated laryngeal echolocation, which we infer was present in *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx*. However, this definition leaves us without a formal name for the microchiropteran crown group, which is the clade of central interest to most biologists. Moreover, this definition might prove problematic if additional bat fossils are found that fall outside the Icaronycteridae + Yangochiroptera clade, yet stem from the branch leading to Microchiroptera rather than that leading to Megachiroptera.

This problem raises yet another possibility, namely a stem-based approach. Microchiroptera might be defined as all chiropterans sharing a more recent common ancestor with Yangochiroptera than with Pteropodidae.

This definition would eliminate the problem of classifying future stem-group fossils, but still leaves us without a formal name for the microchiropteran crown group. Such a definition is also problematic because it blurs the distinction between Megachiroptera and Microchiroptera. Sophisticated laryngeal echolocation, the single trait most often associated with living microchiropterans, was apparently absent in the most recent common ancestor of Megachiroptera and Microchiroptera. This implies that echolocation was also absent in the very earliest members of the microchiropteran stem group. Use of a stem-group definition for Microchiroptera would thus force us to include nonecholocating relatives of extant microchiropterans in Microchiroptera, a solution that many workers would not find acceptable.

Still another issue involves what names (if any) should be applied to nodes along the backbone of the tree below the microchiropteran crown group. For example, there are considerable morphological (and inferred ecological) differences between the basal branches (e.g., Icaronycteridae and Archaeonycteridae) and the more derived clade including Hassianycteridae, Palaeochiropterygidae, and the microchiropteran crown group. Monophyly of the latter clade is well supported, and a formal name for this group would draw attention to its existence and facilitate discussion of this group, objectives that we consider desirable. Although providing names for every node in a tree is excessive, some previously unnamed clades do, in our view, require formal recognition.

Keeping all of these issues in mind, we propose a new higher-level classification for bats (table 8) that combines both node-based and stem-based definitions in a way that we think maximizes both utility and stability. This solution is similar to that proposed by Wyss and Meng (1996) for gliriform mammals (rodents, lagomorphs, and their extinct relatives). In our classification, we apply stem-based names to the two principal branches of the chiropteran tree. Microchiropteramorpha is defined as all chiropterans sharing a more recent common ancestor with Microchiroptera than with Megachiroptera; Megachiropteramorpha is defined as all chiropterans sharing a more recent common ancestor with Megachiroptera than

TABLE 8

A Higher-level Classification of Bats Including Selected Fossil Genera Discussed in the Text^a

Order Chiroptera
Megachiropteramorpha, new taxon
† <i>Archaeopteropus</i>
Suborder Megachiroptera
Family Pteropodidae
Microchiropteramorpha, new taxon
† <i>Australonycteris</i>
†Family Icaronycteridae
† <i>Icaronycteris</i>
†Family Archaeonycteridae
† <i>Archaeonycteris</i>
Microchiropteraformes, new taxon
† <i>Eppsinycteris</i>
†Family Palaeochiropterygidae
† <i>Palaeochiropteryx</i> , † <i>Matthesia</i> , † <i>Cecilonycteris</i>
†Family Hassiancyteridae
† <i>Hassiancycteris</i>
Suborder Microchiroptera
† <i>Vampyravus</i>
Superfamily Emballonuroidea
Family Emballonuridae
Subfamily Taphozoinae
† <i>Vespertiliavus</i>
Subfamily Emballonurinae
Infraorder Yinochiroptera
Superfamily Rhinopomatoidea
Family Craseonycteridae
Family Rhinopomatidae
Superfamily rhinolophoidea
Family Nycteridae
Family Megadermatidae
† <i>Necromantis</i>
Family Rhinolophidae
† <i>Vaylatsia</i>
Subfamily Rhinolophinae
Subfamily Hipposiderinae
† <i>Hipposideros</i> (<i>Pseudorhinolophus</i>),
† <i>Palaeophyllophora</i> , † <i>Paraphyllophora</i>
Infraorder Yangochiroptera
†Family Philididae
† <i>Philisis</i> , † <i>Dizzya</i>
Family Mystacinidae
Superfamily Noctilionoidea
Family Phyllostomidae
Family Moromoopidae
Family Noctilionidae
Superfamily Nataloidea
† <i>Honrovits</i>
† <i>Aegina</i>
† <i>Stehlinia</i>
† <i>Chadronycteris</i>
Family Myzopodidae
Family Furipteridae

TABLE 8—(Continued)

Family Thyropteridae
Family Natalidae
Superfamily Molossoidea
Family Antrozoidae
Family Molossidae
Subfamily Tomopeatinae
Subfamily Molossinae
† <i>Wallia</i> , † <i>Cuvierimops</i>
Superfamily Vespertilionoidea
Family Vespertilionidae
Subfamily Vespertilioninae
Subfamily Miniopterinae
Subfamily Myotinae
Subfamily Murininae
Subfamily Kerivoulinae

^a See text for a discussion of classification below the level of subfamily. Genera that are not placed in a specific family or subfamily are considered incertae sedis within the next higher-level taxon listed above (e.g., *Stehlinia*, which is listed under superfamily Nataloidea without reference to family or subfamily, is considered incertae sedis within Nataloidea).

with Microchiroptera. As so defined, Microchiropteramorpha includes Icaronycteridae, Archaeonycteridae, Hassiancyteridae, Palaeochiropterygidae, and Microchiroptera, as well as a number of poorly known fossil forms (e.g., *Australonycteris*) that are more closely related to extant Microchiroptera than to Megachiroptera.

Within Microchiropteramorpha, Microchiropteraformes is defined as the clade stemming from the most recent common ancestor of Hassiancyteridae, Palaeochiropterygidae, and Microchiroptera; this is a node-based definition. Any fossil forms that nest within these groups or fall between them on the tree would be placed in Microchiropteraformes. *Australonycteris* may someday be shown to belong to this group, but for now it must be considered Microchiropteramorpha incertae sedis.

Finally, we define (and thereby restrict) Microchiroptera to the clade stemming from the most recent common ancestor of Emballonuridae and Yangochiroptera. This node-based, crown-group-restricted definition equates Microchiroptera with what we have thus far in this paper called the “microchiropteran crown group”—the smallest clade that comprises all of the extant lineages of

microchiropteran bats. As noted above, the advantages of this definition of Microchiroptera are that it is congruent with general usage of the name by biologists, and it provides stability because future fossil discoveries or extinctions will not affect the limits of this taxon. The principal disadvantage of this definition—exclusion of the Eocene fossil taxa largely because they are extinct—is mitigated by our recognition of Microchiroptera-morpha and Microchiropteraformes, which focuses attention on the microchiropteran affinities of these taxa without squeezing them into Microchiroptera itself.

This system of classification, which recognizes two named groups more inclusive than Microchiroptera and less inclusive than Chiroptera, presents problems from the point of view of ranks, since no ranks are recognized to exist between order and suborder. This sort of problem has haunted systematists for decades, most particularly since the advent of cladistic methods for phylogenetic analysis. Some workers have advocated elimination of all ranks in favor of a simple hierarchical system (e.g., de Queiroz and Gauthier, 1992), while others have maintained fully ranked classifications despite methodological problems that arise from too many names and too few ranks (e.g., McKenna, 1975; Wilson and Reeder, 1993; McKenna and Bell, 1997). We adopt an intermediate position. While recognizing that formal ranks are extremely useful for communication, arrangement of systematic collections, and other bookkeeping chores (e.g., bibliographic projects), we also think that the formal ranks available (even the relatively large number recognized by McKenna and Bell, 1997) cannot suffice to describe the complex hierarchies now being recovered from phylogenetic analyses. Accordingly, we choose to recognize both ranked and unranked names. We retain ranks for many taxonomic names, particularly those that apply principally to extant taxa and are in broad use in the neontological literature (e.g., Order Chiroptera, Suborder Microchiroptera, Family Phyllostomidae). For other clade names, particularly those that we anticipate will be used principally for discussions of fossils (e.g., Microchiroptera-morpha, Microchiropteraformes), we do not propose formal ranks.

This compromise allows the formal recognition of names for clades at numerous levels in the tree, while at the same time promoting stability by retaining most familiar names at familiar ranks (e.g., Microchiroptera does not have to be reduced to the rank of superfamily to accommodate recognition of more inclusive taxa within Chiroptera). Although this approach will probably be criticized by adherents to both the “no rank” and “always rank” schools of classification, we think that it is the only reasonable solution for the taxonomic problems presented by Chiroptera.

To avoid proliferation of redundant names, we currently limit the use of traditional infraordinal and superfamilial rank names to within Microchiroptera. We follow Simmons (1998) in recognizing seven monophyletic superfamilies and two infraorders within Microchiroptera. All of these taxa are recognized on the basis of node-based definitions. The superfamilies we recognize are Emballonuroidea (Emballonuridae), Rhinopomatoidea (Rhinopomatidae + Craseofoxyteridae), Rhinolophoidea (Nycteridae + Megadermatidae + Rhinolophidae), Noctilionoidea (Noctilionidae + Mormoopidae + Phyllostomidae), Nataloidea (Myzopodidae + Thyropteridae + Furipteridae + Natalidae), Molossoidea (Antrozoidae + Molossidae), and Vespertilionoidea (Vespertilionidae). Yin-chiroptera contains Rhinopomatoidea + Rhinolophoidea; Yangochiroptera contains Mystacinidae + Noctilionoidea + Nataloidea + Molossoidea + Vespertilionoidea. Not all families are referred to superfamily-level taxa (e.g., Mystacinidae is left incertae sedis in Yangochiroptera), and not all superfamilies are referred to infraorders (e.g., Emballonuroidea) because we see no purpose in providing redundant names. The reason that we recognize two monotypic superfamilies (Emballonuroidea and Vespertilionoidea) is that we anticipate that future workers may subdivide these groups into multiple families as phylogenetic resolution increases in these parts of the tree.

Classification of most of the remaining Eocene taxa is relatively straightforward given what is known about these forms and the classification proposed above. Following the conclusions of previous authors (see the Introduction), we place *Vespertiliavus* in Em-

ballonuridae: Taphozoinae, and refer *Necromantis* to Megadermatidae (table 8). Similarly, we follow the consensus that *Hipposideros* (*Pseudorhinolophus*), *Palaeophyllophora*, and *Paraphyllophora* should be classified as Rhinolophidae: Hipposiderinae. Rather than placing *Vaylatsia* in Hipposiderinae as did Sigé (1990), we follow McKenna and Bell (1997) and refer *Vaylatsia* to Rhinolophidae incertae sedis, although we note that this taxon may subsequently be shown to represent a basal member of Rhinolophinae (see discussion in Hand and Kirsch, 1998).

As noted by Simmons (1998), recognition of Hipposiderinae and Rhinolophinae as subfamily-level taxa (rather than as distinct families) is preferred because it facilitates discussion of the larger clade comprising these taxa (i.e., Rhinolophidae). We do not agree with McKenna and Bell (1997) that the name Hipposiderinae should be replaced with Rhinonycterinae. Although Rhinonycterinae (= Rhinonycterina Gray, 1866) has priority over Hipposiderinae Flower and Lydekker, 1891 as a family-group name, no author other than Gray (1866) used the former name until it was resurrected by McKenna and Bell (1997). Miller (1907) used the name Hipposideridae for this group in his influential monograph on the families and genera of bats because *Hipposideros* Gray, 1831 has priority over *Rhinonycteris* Gray, 1866 (= *Rhinonycteris* Gray, 1847). All subsequent authors have followed Miller's (1907) usage of Hipposideridae/-inae, and we think that little would be gained by replacing it with an unknown name. Resolution of this problem will require a petition to the International Commission on Zoological Nomenclature; meanwhile, we retain Hipposiderinae for the sake of stability.

Although we agree with Hooker (1996) that *Eppsinycteris* is a bat, we do not agree that it should be referred to Emballonuridae. Hooker (1996) listed two synapomorphies linking *Eppsinycteris* to emballonurids: progressive mesial elongation of the trigonid from m3 to m1, and bilobation of p4. We find neither of these to be convincing evidence of emballonurid affinities. Published photographs of *Eppsinycteris* (Hooker, 1996: pls. 1 and 2) illustrate that mesial elongation of the trigonid is barely distinguishable in this

form, and our survey of dental variation suggests that a bilobed p4 is common in many families of bats. In our opinion, no feature of *Eppsinycteris* (as it is currently known) clearly link it with any extant family. However, position of the hypoconulid on the lower molars indicates that *Eppsinycteris* was either nyctalodont or myotodont (the teeth are too worn to determine which morphology is present), indicating that this genus probably belongs somewhere within the microchiropteraform clade. On this basis, we place *Eppsinycteris* in Microchiropteraformes incertae sedis.

In the yangochiropteran part of the tree, we refer *Philisis* and *Dizzya* to the extinct family Philisidae following Sigé (1985, 1991a), which we in turn place incertae sedis within Yangochiroptera pending additional study. As noted by Sigé (1985), Philisidae may eventually prove to be closely related to Nataloidea if *Vampyravus* is shown to be a synonym of *Philisis*. As discussed previously, we refer *Honrovits* and *Aegina* to Nataloidea incertae sedis following suggestions made by Beard et al. (1992). We also refer *Stehlinia* and *Chadronycteris* to Nataloidea incertae sedis based on recommendations of the same authors. We place *Wallia* and *Cuvierimops* in Molossidae: Molossinae incertae sedis following McKenna and Bell (1997) based on arguments developed in Legendre and Sigé (1983) and Legendre (1985). Finally, we follow Sigé (1985) and McKenna and Bell (1997) in referring *Vampyravus* to Microchiroptera incertae sedis until more material of this form is discovered.

Because relationships among extant megachiropterans are still relatively poorly understood—in part due to incongruence among phylogenies derived from different data sets (Hood, 1989; Kirsch et al., 1995; Colgan and Flannery, 1995; Springer et al., 1995; Hollar and Springer, 1997)—we define Megachiroptera using a stem-modified node-based definition as recommended by Wyss and Meng (1996). Megachiroptera is thus defined as the clade stemming from the most recent common ancestor of *Pteropus* and all Recent mammals more closely related to *Pteropus* than to Microchiroptera or any other mammalian order or suborder. Megachiroptera as thus defined includes all extant Pteropodidae,

but it may not include *Archaeopteropus*. Although *Archaeopteropus* seems to be more closely related to living Pteropodidae than to Microchiroptera, it is too poorly known to be

placed securely either inside or outside Megachiroptera as defined here. Accordingly, we place *Archaeopteropus* incertae sedis in Megachiroptera.

CONCLUSIONS AND SUMMARY

In an essay on the origin and evolution of bats, Jepsen (1970: 40) observed that

A skeleton of an old dead bat doesn't give much direct information about the details of genic history although it may be richly informative about broad evolutionary generalities.

We disagree. As demonstrated in the current study, careful comparisons of fossil and extant specimens provide data that yield a well-resolved, relatively well-supported hypothesis of relationships when analyzed using appropriate cladistic methods. Our analyses indicate that *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* represent a series of consecutive sister-taxa to extant microchiropteran bats (fig. 36). This conclusion stands in sharp contrast to previous suggestions that these fossil forms represent either a primitive grade ancestral to both Megachiroptera and Microchiroptera (e.g., Van Valen's [1979] Eochiroptera), or a separate clade within Microchiroptera (i.e., Smith's [1977] Palaeochiropterygoidea).

To better reflect observed similarities, differences, and phylogenetic relationships among both fossil and extant lineages, we have proposed a new higher-level classification of bats (table 8). This classification combines both node-based and stem-based definitions in a way that we think maximizes both utility and stability (see discussion above). Critical features of this classification include restriction of Microchiroptera to the smallest clade including all extant bats that use sophisticated echolocation, and formal recognition of two more inclusive groups: Microchiropteraformes (Microchiroptera + Palaeochiropterygidae + Hassianycteridae), and Microchiropteraomorpha (Microchiropteraformes + Archaeonycteridae + Icaronycteridae). Megachiroptera is similarly restricted to the the smallest clade including all extant megachiropteran bats (see Simmons [1994] for a list of diagnostic features), and

Megachiropteraomorpha is named for all bats more closely related to Megachiroptera than to Microchiroptera.

Taken together with an assumption of bat monophyly, the phylogeny developed in our study provides a basis for evaluating previous hypotheses concerning the evolution of flight, echolocation, and foraging strategies. Through a combination of character mapping and examination of correlations between morphology and behavior, we find support for several linked hypotheses, many of which were derived from the work of earlier authors. Based on the data presented here, it is clear that flight evolved before echolocation; the first bats most likely used vision for orientation in their arboreal/aerial environment. The evolution of flight was subsequently followed by the origin of low-duty-cycle laryngeal echolocation in early microchiroptera-morphs. This system was probably derived from vocalizations originally used for intraspecific communication. The microchiroptera-morph echolocation system was most likely simple at first, permitting only orientation and obstacle detection and not detection or tracking of airborne prey. However, the energy costs of echolocation to flying bats were low due to the mechanical coupling of ventilation and flight, and the benefits of aerial insectivory apparently led to rapid evolution of a more sophisticated low-duty-cycle echolocation system capable of detecting, tracking, and assessing airborne prey. The need for an increasingly derived auditory system—combined with limits on body size imposed by the mechanics of flight, echolocation, and prey capture—may have resulted in reduction and simplification of the visual system as echolocation became increasingly important.

Our examinations of morphology of the basicranium and auditory region confirm previous suggestions by Novacek (1985a, 1987, 1991) and Habersetzer and Storch (1992)

that *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* were capable of echolocation. Judging from our phylogeny, the earliest morphological transformations in Microchiropteraforma included changes in features associated with production of echolocation calls, transmission of sounds through the middle ear, and some tuning of the inner ear. Subsequent modifications at the level of Microchiropteraformes involved continued tuning of the inner ear, postcranial modifications that may have increased efficiency of the ventilation system and its connections to the flight mechanism, and evolution of a calcar, which may have been linked to aerial insect capture.

Foraging strategies of *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* were reconstructed based on postcranial osteology and wing form, cochlear size, and stomach contents (table 9). Comparisons with megachiropterans and outgroups also permitted the reconstruction of hypothetical ancestral habits. It seems most likely that the earliest bats (including the earliest microchiropteraforms) used vision for orientation, and foraged by gleaning insects and perhaps some fruits and other edible items from foliage, bark, and perhaps the ground. Detection of potential food items was probably accomplished by a combination of vision and listening for prey-generated sounds. These bats probably had low aspect ratio wings, moderate wing loading, and relatively large wing tips, all of which suggest that they habitually flew close to the ground and near vegetation. This wing morphology was subsequently retained in *Archaeopteropus*, *Icaronycteris*, *Archaeonycteris*, *Palaeochiropteryx*, and some extant megachiropteran and microchiropteran bats (see figs. 43, 44).

Wing morphology, moderate cochlea size, and absence of a calcar suggest that *Icaronycteris* and *Archaeonycteris* were perch-hunting gleaners rather than predators on aerial insects. The first major change in foraging methods in Microchiropteraforma was therefore the addition of echolocation as a tool for orientation and obstacle detection; the basic strategy—gleaning from a perch—would have been the same as seen in the no-echolocating chiropteran ancestors of *Ica-*

ronycteris and *Archaeonycteris*, and in microchiropteraform bats. As in ancestral microchiropteraforms, detection and tracking of prey would have been accomplished principally by a combination of vision and listening for prey-generated sounds.

The earliest microchiropteraforms, *Hassianycteris* and *Palaeochiropteryx*, differ from *Icaronycteris* and *Archaeonycteris* in having a larger cochlea and several derived postcranial features (including a calcar). However, these changes do not seem to have been correlated with any appreciable modifications in wing shape or wing loading. These observations indicate that a major shift in foraging strategy occurred at the level of Microchiropteraformes, but that this shift took place without any large-scale changes in the habitat types exploited. The greatly enlarged cochlea and well developed calcar suggest that *Hassianycteris* and *Palaeochiropteryx* were fully capable of aerial hawking, using echolocation to detect, track, and assess prey and utilizing the uropatagium to capture prey on the wing. This hypothesis is consistent with the analyses of stomach contents and taphonomy of *Hassianycteris* and *Palaeochiropteryx* at Lake Messel.

Many extant bats that hunt from perches also hawk insects in flight, with allocation of time between these two foraging strategies reflecting prey availability. Given that gleaning from a perch probably represents the primitive foraging strategy for the microchiropteran lineage, we suspect that *Palaeochiropteryx* may have used a combination of perch hunting and aerial hawking to capture its prey, much like modern nycterids. Passive means would have been used to locate stationary prey; echolocation would have been used for detecting and tracking flying prey. This hypothesis is consistent with observations of cochlear size and wing morphology in *Palaeochiropteryx*.

Hassianycteris, which diverged from the microchiropteran lineage prior to *Palaeochiropteryx*, is characterized by relatively large body size and significantly higher wing loading than any of the other Eocene bats. These observations, along with a moderately high aspect ratio, a greatly enlarged cochlea, and presence of a calcar, suggest that *Hassianycteris* foraged by fast aerial hawking, most

TABLE 9
Foraging Ecologies of Eocene Bats: Observations and Hypotheses^a

	<i>Icaronycteris</i>	<i>Archaeonycteris</i>	<i>Hassianycteris</i>	<i>Palaeochiropteryx</i>
Wing morphology	Low aspect ratio; low wing tip indices; moderate wing loading	Low aspect ratio; low wing tip indices; moderate wing loading	Low aspect ratio; low wing tip indices; high wing loading	Low aspect ratio; low wing tip indices; moderate wing loading
Calcar	Absent	Absent	Present	Present
Cochlear size	Moderate	Moderate	Large	Large
Stomach contents	Unknown	Coleoptera	Macrolepidoptera; Coleoptera; Blattoidea	Microlepidoptera; Tricoptera; scale-bearing Diptera
Proposed mode of orientation and obstacle detection	Echolocation and vision	Echolocation and vision	Echolocation and vision	Echolocation and vision
Proposed foraging habitat	Near ground and vegetation; along edges of lakes	Near ground and vegetation; along edges of lakes	Well above ground in forest clearings, above forest canopy, and over lakes	Near ground and vegetation; along edges of lakes
Proposed principal foraging style(s)	Gleaning prey from surfaces during short flights from a perch	Gleaning prey from surfaces during short flights from a perch	Fast aerial hawking; prey capture using calcar-supported uroptagium	Perch hunting for both flying and nonflying prey; slow aerial hawking; prey capture using calcar-supported uroptagium
Proposed mode of detection and tracking prey	Vision and/or listening for prey-generated sounds	Vision and/or listening for prey-generated sounds	Echolocation	Echolocation (flying prey); vision and/or listening for prey-generated sounds (nonflying prey)
Proposed echolocation duty cycle	Low duty cycle	Low duty cycle	Low duty cycle	Low duty cycle
Proposed type of echolocation call	Short (≤ 2 msec) multiharmonic calls or broadband FM calls in 30–90 kHz range	Short (≤ 2 msec) multiharmonic calls or broadband FM calls in 30–90 kHz range	Narrowband FM calls or FM calls with both steep and shallow sweeps; calls under 30 kHz	Broadband FM calls in 30–90 kHz range

^a See text for discussion of the data and chain of inferences used to develop these hypotheses.

likely well above the ground in forest gaps or above the canopy. *Hassianycteris* thus represents another shift in foraging strategy, away from combined perch hunting and aerial hawking near vegetation to a fast-flying, continuous aerial hawking foraging strategy similar to that seen in extant rhinopomatids and some vespertilionids. This shift apparently occurred after the lineage leading to *Hassianycteris* diverged from the lineage leading to the microchiropteran crown group.

In summary, we propose that foraging behavior in the microchiropteran lineage evolved in a series of steps. The earliest microchiropteramorph bats (Stage 1 in our hypothesis) probably used vision for orientation and located prey by a combination of vision and listening for prey-generated sounds. Food objects were probably obtained by gleaning during short flights from a perch. The next evolutionary step (Stage 2) involved a switch to the use of echolocation for orientation but not for prey detection. These bats (which included *Icaronycteris* and *Archaeonycteris*) retained the primitive habits of locating and tracking their prey by passive means and gleaning prey from surfaces during short flights from a perch. They may have captured flying prey at times, but relied principally on vision and/or prey-generated sounds for locating and tracking prey. Subsequent evolutionary refinements of the echolocation system began to make detection, tracking, and evaluation of flying prey possible, and we expect that this corresponded with a third stage in the evolution of foraging behaviors, one in which bats continued to hunt from perches for stationary prey, but also used echolocation for detecting and tracking flying prey. To fully exploit this method, these bats would have had to increase signal strength to maximize range and provide the necessary time to track and evaluate targets. Environmental clutter (which produces many distracting echoes) would have presented difficulties at this stage, so we suggest that flycatching using echolocation to detect and track prey probably evolved in bats that frequented forest gaps and the edges of forests along lakes and rivers, places where vegetation (with potential perches) lies

adjacent to relatively clutter-free open spaces. The next evolutionary stage (Stage 4) brought continued refinement of the echolocation and flight systems as well as evolution of a calcar-supported uropatagium used for capturing prey on the wing. Microchiropteriform bats at this stage probably used a combination of perch hunting and continuous aerial hawking. Stationary prey would have been detected by passive means, and aerial prey by echolocation. We expect that this combination of foraging strategies was used by the common ancestor of *Hassianycteris* and *Palaeochiropteryx*, and was subsequently retained in *Palaeochiropteryx*. Finally, Stage 5 brought exclusive reliance on continuous aerial hawking using echolocation for prey detection, tracking, and evaluation. This foraging strategy was apparently used by *Hassianycteris* and the common ancestor of extant microchiropterans.

The presence of representatives of three of stages in the evolution of foraging behavior (Stages 2, 4, and 5) at Messel suggests that evolutionary transformations in foraging strategies occurred rapidly in early members of the microchiropteran lineage. Given the topology of our phylogenetic tree (fig. 36), it seems likely that reliance on continuous aerial hawking was primitive for the microchiropteran crown group. This suggests that gleaning, passive prey detection, and perch hunting among extant microchiropterans represent secondarily derived specializations rather than retentions of primitive habits. Each of these behaviors evolved independently several times in Microchiroptera.

The evolution of continuous aerial hawking may have been the "key innovation" responsible for the burst of diversification in microchiropteran bats that occurred in the Eocene. Fossils referable to six major extant lineages are known from Middle–Late Eocene deposits (table 1), and reconstruction of ghost lineages leads to the conclusion that at least seven more extant lineages were minimally present by the end of the Eocene. It thus appears that *Icaronycteris*, *Archaeonycteris*, *Palaeochiropteryx*, and *Hassianycteris* provide an unprecedented view of steps leading to a major adaptive radiation of mammals.

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APPENDIX 1: SPECIMENS EXAMINED

The following list includes all specimens examined in this study; see Appendix 2 for published data sources. Abbreviations are as follows: AMNH, American Museum of Natural History, New York, New York, USA; BMNH, British Museum (Natural History), London, England; HLMD, Hessisches Landesmuseum, Darmstadt, Germany; LNK, Landessammlungen für Naturkunde, Karlsruhe, Germany; LSU, Louisiana State University Museum of Zoology, Baton Rouge, Louisiana, USA; Me (ME), Messel fossil locality, Germany (used as a supplementary identifier for Messel material housed at several museums); MNB, Muséum d'Histoire Naturelle de Bâle, Basel, Switzerland; MNHN, Muséum National d'Histoire Naturelle, Paris, France; PU, Princeton University, Princeton, New Jersey, USA (specimens now housed in the Peabody Museum, Yale University, New Haven, Connecticut, USA; RSB, Institut Royal des Sciences Naturelles de Belgique, Belgium; SMF, Senckenbergmuseum, Frankfurt am Main, Germany; USNM, United States National Museum, Washington, D.C., USA; UW, University of Wyoming Museum of Geology, Laramie, Wyoming, USA.

Scandentia: *Tupaia glis* (AMNH 103610, 213642; USNM 396664); *Tupaia javanica* (AMNH 107595); *Tupaia tana* (AMNH 106479).

Dermoptera: *Cynocephalus variegatus* (AMNH 14021, 101501, 107136, 120449); *Cynocephalus volans* (AMNH 16697, 187860); *Cynocephalus* sp. (AMNH 207001; USNM 115603).

Pteropodidae: *Aethalops alecto* (AMNH 239600); *Balionycteris maculata* (AMNH 216759); *Boneia bidens* (AMNH 254542); *Cynopterus brachyotis* (AMNH 235564; USNM 197237, 399424, 399426; USNM 20214); *Cynopterus sphinx* (AMNH 55568, 107922); *Dobsonia viridis* (USNM 543177, 543180, 543778, 543798); *Dobsonia moluccensis* (AMNH 198750); *Dobsonia pannietensis* (AMNH 157371, 157372); *Eidolon helvum* (AMNH 86245, 236281); *Eonycteris major* (AMNH 241759); *Eonycteris spelaea* (AMNH 31793, 235566; USNM 458131, 458132); *Epomophorus wahlbergi* (AMNH 168100, 187264, 187265, 187266, 187269, 187270, 187271, 187272, 187273, 187274, 187275, 187276, 187277, 187278, 187279, 187288, 207008; USNM 20215); *Epomops buettikoferi* (AMNH 207007, 207008, 207009, 207010, 239375); *Epomops dobsonii* (AMNH 88072); *Epomops franqueti* (AMNH 241012); *Haplonycteris fischeri* (AMNH 187088; USNM 459100, 459101, 548573, 573419); *Harpionycteris whiteheadi* (AMNH 196435; USNM

458209, 458210, 459103, 459108); *Hypsignathus monstrosus* (AMNH 48654, 244255, 244356, 244357, 244358); *Macroglossus minimus* (AMNH 192755, 250080; USNM 543196, 543197, 543960, 543970, 543997, 544030, 544032, 544046); *Megaerops ecaudatus* (AMNH 87285, 216746); *Megaloglossus woermanni* (AMNH 83803, 236291); *Melonycteris melanops* (AMNH 194333); *Melonycteris woodfordi* (AMNH 99950); *Micropteropus pusillus* (AMNH 239383); *Myonycteris torquata* (AMNH 236244); *Nanonycteris veldkampii* (AMNH 241024); *Notopteris macdonaldi* (AMNH 31588, 119445; USNM 260070, 260071, 260072, 260076); *Nyctimene albiventer* (USNM 543237, 543246); *Nyctimene caelaeno* (AMNH 10515); *Otopterus cartilagonodus* (USNM 573446, 573447); *Paranyctimene raptor* (AMNH 198606); *Penthetor lucasi* (AMNH 106823); *Ptenochirus jagori* (AMNH 187085); *Pteropus alecto* (AMNH 154547, 236510); *Pteropus giganteus* (AMNH 83947, 252525); *Pteropus mariannus* (AMNH 249969, 256890); *Pteropus macrotis* (AMNH 256551); *Pteropus neohibernicus* (AMNH 194668); *Pteropus rayneri* (AMNH 79865); *Pteropus tonganus* (USNM 546347, 546349); *Rousettus aegyptiacus* (AMNH 184438, 265619, 265620, 265621, 265622, 265623, 265627, 265628, 265629, 265630, 265631, 265632, 265633, 265634, 265635, 265636; USNM 278616, 458462); *Rousettus amplexicaudatus* (USNM 278616, 458455, 458462); *Rousettus celebensis* (AMNH 224532); *Scotonycteris zenkeri* (AMNH 239381); *Sphaeris blanfordi* (AMNH 240004); *Styloctenium wallacei* (AMNH 153126, 222981); *Syconycteris australis* (AMNH 108857); *Thoopterus nigriceps* (AMNH 222771).

Icaronycteridae: *Icaronycteris index* (LNK 124/126; UW 2244, 21481a–b; PU 18150 [cast]).

Archaeonycteridae: *Archaeonycteris trigonodon* (SMF 80/1379, ME 214, ME 663, ME 963a, ME 1789b; HLMD Me 9754, Me 10591).

Palaeochiropterygidae: *Palaeochiropteryx spiegelii* (MNB Me 537; RSB Nr. 380a); *Palaeochiropteryx tupaiodon* (MNB Me 719, 861; RSB Nr. 165a, 165b, 166a, 166b, 257, 324a, 1034; SMF ME 788a, ME 788b, ME 1033b); *Palaeochiropteryx* sp. (HLMD Me 329, Me 330, Me 719a, Me 1477a, Me 10000, Me 10586, Me 14479, Me 15008, Me 15010a, Me 15018, Me 15019, Me 15021, Me 15021, Me 15022, Me 15025, Me 15026, Me 15220, Me 15477; RSB Nr. 188a, 188b; SMF ME 505, ME 788a, ME 788b, ME 1590a, ME 1590b, ME 1035, ME 1127, ME 1139a, ME 1151b, ME 1204a, ME 1204b, ME 1205, ME 1487a, ME 1487b, ME 1492a, ME

1492b, ME 1494, ME 1501b, ME 1504, ME 1507, ME 1580a, ME 1580b, ME 1590a, ME 1590b, ME 1790b, ME 2018b, ME 2028a, ME 2028b, ME 2348b, ME 2434a, ME 2434b, ME 2434c, ME 2885).

Hassianycteridae: *Hassianycteris magna* (HLMD Me 7605a, Me 7605b, Me 7998; RSB Nr.100a, 66; SMF ME 1540a, ME 1761, ME 2619b); *Hassianycteris messelensis* (HLMD Me 333a, Me 1116, Me 1469b, Me 7480; RSB Nr. 127a, 127c; SMF ME 1024b, ME 1414a, 1469a, 1500).

Emballonuridae: *Balantiopteryx io* (AMNH 185765); *Coleura afra* (AMNH 188263); *Cormura brevirostris* (AMNH 74103); *Diclidurus albus* (AMNH 149167, 214183; USNM 120577, 534417); *Diclidurus isabellus* (USNM 388543, 388544); *Diclidurus scutatus* (AMNH 267832); *Emballonura alecto* (USNM 458512, 458543, 459312, 459313, 459318, 459323); *Emballonura raffrayana* (AMNH 153232); *Peropteryx kappleri* (AMNH 239068); *Rhynchonycteris naso* (AMNH 209190, 209191, 209213, 209214, 209215, 248745, 265986); *Saccolaimus flaviventris* (AMNH 107759); *Saccopteryx bilineata* (AMNH 210461, 265963); *Taphozous melanopogon* (AMNH 235571, 235572, 241802).

Rhinopomatidae: *Rhinopoma microphyllum* (AMNH 212070, 244388, 244389); *Rhinopoma muscatellum* (AMNH 244391, 244393, 244394; USNM 327940, 327963).

Craseonycteridae: *Craseonycteris thonglongyai* (BMNH 77.2990, 77.2993, 77.2999, 77.3007, 77.3009, 77.3015).

Nycteridae: *Nycteris gambiensis* (USNM 478656); *Nycteris grandis* (AMNH 206685); *Nycteris hispida* (AMNH 187291, 187293, 187294, 187325); *Nycteris macrotis* (AMNH 187296, 187297, 187298, 187299, 187300, 187302, 187303, 187304, 187305, 187309, 187314, 187317, 187319, 187320, 187322); *Nycteris thebaica* (AMNH 169163, 169164, 187289, 187321, 257153).

Megadermatidae: *Cardioderma cor* (AMNH 187331); *Lavia frons* (AMNH 187339, 187344); *Macroderma gigas* (AMNH 197205, 197206, 197208, 197210, 197211, 236545, 236546); *Megaderma lyra* (AMNH 33130); *Megaderma spasma* (AMNH 109285, 203289; USNM 458574, 573475, 573679).

Rhinolophidae: **Rhinolophinae:** *Rhinolophus affinis* (AMNH 27378, 216809, 257199, 257200); *Rhinolophus arcuatus* (USNM 175795, 175812, 304355, 304356, 459445, 459447); *Rhinolophus darlingi* (AMNH 257157, 257161); *Rhinolophus ferrumequinum* (AMNH 245358); *Rhinolophus hildebrandti* (AMNH 216206, 216209); *Rhinolophus megaphylla* (AMNH 157393); *Rhinolophus*

simulator (AMNH 257165); *Rhinolophus stheno* (AMNH 235577).

Rhinolophidae: **Hipposiderinae:** *Asellia tridens* (AMNH 175962, 175963, 175964, 175965); *Aselliscus tricuspidatus* (AMNH 159379); *Coelops frithi* (AMNH 107509); *Hipposideros abae* (AMNH 49157); *Hipposideros diadema* (AMNH 31800, 31812, 194858, 207561, 237819; USNM 477728, 477732); *Hipposideros ruber* (AMNH 265796, 265797, 265798, 265799, 265800, 265804, 267805, 265806); *Rhinonycteris aurantius* (AMNH 197213, 197214, 197215, 197216); *Triaenops persicus* (AMNH 216236, 216237, 216238).

Phyllostomidae: *Artibeus jamaicensis* (AMNH 244634); *Brachyphylla cavernarum* (AMNH 188225, 188229); *Carollia perspicillata* (AMNH 209374, 209391, 210700, 210717, 246494, 246524); *Desmodus rotundus* (AMNH 14568, 237372, 237373, 237274, 248942); *Diaemus youngi* (AMNH 209742, 209743); *Erophylla sezekorni* (AMNH 176294, 245691, 245692); *Glossophaga soricina* (AMNH 203613, 247936, 247937, 247960, 247961; USNM 312998); *Leptonycteris nivalis* (AMNH 180343); *Lonchophylla robusta* (USNM 306590, 311996, 522757); *Lonchophylla thomasi* (AMNH 210688, 230211, 230284); *Macrotus californicus* (AMNH 180526); *Micronycteris brachyotis* (AMNH 175628); *Micronycteris hirsuta* (AMNH 267093); *Micronycteris megalotis* (AMNH 266020); *Micronycteris minuta* (AMNH 267098); *Micronycteris microtis* (AMNH 267097); *Micronycteris nicefori* (AMNH 266019); *Phyllostomus discolor* (AMNH 254610); *Phyllostomus hastatus* (AMNH 267434); *Platyrrhinus lineatus* (AMNH 205185); *Sturnira lilium* (AMNH 230529, 246568, 260882, 260887, 260888); *Trachops cirrhosus* (AMNH 129075); *Vampyrum spectrum* (AMNH 2644, 42805, 42895, 212951, 256825, 267446; USNM 346252).

Mormoopidae: *Mormoops blainvillii* (AMNH 176148); *Mormoops megalophylla* (AMNH 25589, 25602, 190138, 190139; USNM 431641); *Pteronotus davyi* (AMNH 204960); *Pteronotus parnellii* (AMNH 176183, 176185, 189595, 245607, 267403; USNM 54139, 54140); *Pteronotus personatus* (AMNH 321127).

Noctilionidae: *Noctilio albiventris* (AMNH 95121, 209304, 182706, 209252, 210576, 210577); *Noctilio leporinus* (AMNH 91935, 91941; USNM 382924).

Mystacinidae: *Mystacina robusta* (AMNH 160269, 214243; USNM 120576); *Mystacina tuberculata* (AMNH 214245, 265139; MNHN 1983-1464).

Myzopodidae: *Myzopoda aurita* (AMNH

257130; USNM 448883, 448886, 448932, 578856).

Thyropteridae: *Thyroptera tricolor* (AMNH 67592, 239085, 266356, 266361, 266364, 268576; USNM 281939).

Furipteridae: *Amorphochilus schnablii* (AMNH 28601); *Furipterus horrens* (AMNH 142903, 267214, 265979; USNM 315734, 549598).

Natalidae: *Natalus stamineus* (AMNH 186399, 206696; USNM 362003, 362102, 262103).

Antrozoidae: *Antrozous pallidus* (AMNH 21593, 31173, 121495, 138339, 207615; USNM 244481, 564036); *Bauerus dubiaquercus* (AMNH 256832).

Molossidae: Tomopeatinae: *Tomopeas ravus* (LSU 25072, 25084, 25086, 25087, 25148, 25150, 27170).

Molossidae: Molossinae: *Eumops bonariensis* (AMNH 234699, 234700, 234701, 234717, 235412, 235965); *Eumops perotis* (AMNH 3259/15751, 42379; USNM 270794, 271164); *Molossus molossus* (AMNH 211379, 211380, 211381, 211382, 211383, 211389); *Molossus rufus* (AMNH 268597); *Mops mops* (USNM 20217); *Promops centralis* (AMNH 183866); *Tadarida brasiliensis* (AMNH 18020, 60791, 131663,

145485, 145486, 203937; USNM 52874, 512843).

Vespertilioninae: *Corynorhinus townsendii* (AMNH 170810, 180094); *Eptesicus furinalis* (AMNH 268581); *Eptesicus fuscus* (AMNH 190168); *Lasiurus borealis* (AMNH 139871); *Lasiurus cinereus* (AMNH 15128, 214126); *Lasiurus intermedius* (AMNH 203930, 253712); *Nycticeus humeralis* (AMNH 3955, 3960); *Nyctophilus geoffroyi* (AMNH 160300); *Nyctophilus timoriensis* (AMNH 197281); *Pipistrellus tasmaniensis* (AMNH 197222); *Scotoecus albofuscus* (AMNH 237386); *Scotophilus kuhli* (AMNH 242718); *Vespertilio murinus* (AMNH 206564).

Miniopterinae: *Miniopterus schreibersi* (AMNH 219973, 219974, 219975, 219976, 219977)

Myotinae: *Myotis fortidens* (AMNH 243791); *Myotis lucifugus* (AMNH 141128, 141129, 141130, 208977, 208978, 244863); *Myotis vivesi* (AMNH 180833, 180835).

Murinae: *Murina cyclotis* (AMNH 234204, 234207; USNM 573777); *Murina suilla* (AMNH 217013); *Murina* sp. (USNM 573775).

Kerivoulinae: *Kerivoula hardwickei* (AMNH 109122, 234209); *Kerivoula pellucida* (AMNH 241938); *Kerivoula papillosa* (AMNH 247576, 247577, 247579).

APPENDIX 2: CHARACTER DESCRIPTIONS

The following character descriptions are based on those presented by Simmons (1998). The character descriptions given here have been modified to incorporate some new data from extant forms, and to account for character states seen only in the fossils. The numbers following each character description refer to sources used to define character states and obtain the data presented in appendix 2. Sources are as follows: (1) Agrawal and Sinha, 1973; (2) Andersen, 1912; (3) Baker et al., 1991a; (4) Baron et al., 1996a, 1996b, 1996c; (5) Beard et al., 1992; (6) Bhatnagar and Wible, 1994; (7) Bhiwgade et al., 1992; (8) Blood, 1987; (9) Brown et al., 1971; (10) Butler, 1980; (11) Corbet and Hill, 1992; (12) Cypher, 1996; (13) Davis, 1938; (14) Doran, 1878; (15) Felton et al., 1973; (16) Fenton and Bell, 1981; (17) J. Geisler, personal obs.; (18) Göpfert and Wasserthal, 1995; (19) Griffiths, 1982; (20) Griffiths, 1983; (21) Griffiths, 1994; (22) T. Griffiths, unpubl. data; (23) Griffiths and Smith, 1991; (24) Griffiths et al., 1992; (25) Habersetzer and Storch, 1987; (26) Habersetzer and Storch, 1989; (27) Habersetzer and Storch, 1992; (28) Habersetzer et al., 1994; (29) Hermanson, 1981; (30) Hermanson and Altenbach, 1983; (31) Hermanson and Altenbach,

1985; (32) Hill, 1974; (33) Hill and Harrison, 1987; (34) Hill and Smith, 1984; (35) Hood and Smith, 1982; (36) Hood and Smith, 1983; (37) Horáček, 1986; (38) Humphry, 1869; (39) Jepsen, 1970; (40) Johnson and Kirsch, 1993; (41) E. Kallo, unpubl. data; (42) Koopman, 1994; (43) Leche, 1886; (44) Le Gros Clark, 1924; (45) Le Gros Clark, 1926; (46) Loo and Kanagasuntheram, 1972; (47) Luckett, 1980a; (48) Luckett, 1980b; (49) Luckett, 1980c; (50) Luckett, 1993; (51) MacAlister, 1872; (52) Madkour, 1989; (53) Matthews, 1941; (54) Menu, 1985; (55) Menu and Sigé, 1971; (56) Norberg, 1970; (57) Norberg, 1972a; (58) Novacek, 1980a; (59) Novacek, 1980b; (60) Novacek, 1985a; (61) Novacek, 1987; (62) Novacek, 1991; (63) Novick, 1962; (64) A. Peffley, MS; (65) Pierson, 1986; (66) Pierson et al., 1986; (67) Robin, 1881; (68) Schlosser-Strum and Schliemann, 1995; (69) W. Schutt, unpubl. data; (70) Sigé, 1974; (71) Simmons, 1980; (72) Simmons, 1993b; (73) N. Simmons, personal obs.; (74) Simmons and Quinn, 1994; (75) Smith, 1972; (76) Smith and Madkour, 1980; (77) Smith and Storch, 1981; (78) Storch and Habersetzer, 1988; (79) Strickler, 1978; (80) Surlykke et al., 1993; (81) Vaughan, 1959; (82) Vaughan, 1970b;

(83) Vaughan and Bateman, 1970; (84) Walton and Walton, 1968; (85) Walton and Walton, 1970; (86) Wassif, 1950; (87) Wassif and Madkour, 1963; (88) Weid and Helversen, 1987; (89) H. Whidden, unpubl. data; (90) Wible and Bhatnagar, 1997; (91) Wilkinson et al., 1997; (92) Winge, 1941; (93) Zeller, 1986.

Character 1: Ear pinnae not funnel-shaped (0); or more or less funnel-shaped (1). 11, 42, 73.

Character 2: Tragus absent (0); or present (1). 11, 42, 73.

Character 3: Narial structures absent (0); or dermal ridge present dorsal to nostrils (1); or noseleaf present (2); or dermal foliations with central slit present (3). 11, 32, 73.

Character 4: *M. occipitofrontalis* inserts into connective tissue and skin over nasal region (0); or inserts onto nasal cartilage via common tendon with contralateral muscle (1). 89, 92.

Character 5: Nasopalatine duct present (0); or absent (1). 6, 46, 90.

Character 6: Paraseptal cartilage (= vomeronasal cartilage) J-shaped, C-shaped, U-shaped, or O-shaped (0); or bar-shaped (1); or absent (2). 6, 46, 90.

Character 7: Vomeronasal epithelial tube well developed, neuroepithelium present (0); or tube rudimentary, neuroepithelium absent (1), or epithelial tube absent (2). 6, 46, 90.

Character 8: Accessory olfactory bulb present (0); or absent (1). 6, 46, 90.

Character 9: Premaxilla articulates with maxilla via sutures (0); or premaxilla fused to maxilla (1); or premaxilla articulates with maxilla via ligaments, premaxilla freely movable (2). 17, 32, 42, 73.

Character 10: Nasal branches of premaxillae well developed (0); or reduced or absent (1). 17, 32, 42, 73.

Character 11: Palatal branches of premaxillae well developed (0); or reduced or absent (1). 17, 32, 42, 73.

Character 12: Palatal branches of premaxillae not fused with one another across midline (0); or fused at midline (1). 32, 73.

Character 13: Emargination not present in anterior palate, medial incisors directly adjacent to one another (0); or emargination present between medial incisors (1). 42, 73.

Character 14: Anterior palatal emargination shallow, extends posteriorly no farther than anterior edge of canines (0); or deep, extends posteriorly at least as far as posterior edge of canines (1). This character cannot be scored in taxa that lack an anterior palatal emargination. 42, 73.

Character 15: Hard palate extends posteriorly into interorbital region (0); or terminates either at or anterior to level of zygomatic roots (1). 17, 73.

Character 16: Two upper incisors in each side of jaw (0); or one incisor (1); or incisors absent (2). 10, 17, 42, 73, 77.

Character 17: Three lower incisors in each side of jaw (0); or two incisors (1); or one incisor (2); or incisors absent (3). 10, 17, 39, 42, 73, 77, 78.

Character 18: Three upper premolars in each side of jaw (0); or two premolars (1); or one premolar (2). 10, 17, 39, 42, 73, 77, 78.

Character 19: Middle upper premolar with three roots (0); or with two roots (1); or with one root (2). 10, 17, 39, 42, 73, 77, 78.

Character 20: Three lower premolars in each side of jaw (0); or two premolars (1). 10, 17, 39, 42, 73, 77, 78.

Character 21: Lower first and second molars with primitive tribosphenic arrangement of cusps and cristids; hypoconulid located near anteroposterior midline, postcristid connects hypoconulid with hypoconulid (0); or nyctalodont, hypoconulid shifted lingually to lie adjacent to entoconid, postcristid connects hypoconulid with hypoconulid (1); or myotodont, postcristid bypasses hypoconulid to connect with entoconid (2); or teeth modified for fruit and/or nectar or blood feeding, cusps and cristids not distinct (2). 5, 10, 17, 25, 54, 55, 61, 73, 78.

Character 22: Lower jaw with elongate angular process (0); or without elongate angular process (1). 17, 61, 73.

Character 23: Angular process projects at or below level of occlusal plane of toothrow, well below coronoid process (0); or angular process projects above level of occlusal plane of toothrow, at same level as the coronoid process (1). This character cannot be scored in taxa that lack an angular process. 17, 73.

Character 24: Postorbital process present (0); or absent (1). 17, 42, 73.

Character 25: Pars cochlearis of petrosal sutured to basisphenoid (0); or loosely attached to basisphenoid via ligaments and/or thin splints of bone (1). 17, 59, 61, 62, 73.

Character 26: Cochlea not enlarged (0); or moderately enlarged (1); or greatly enlarged (2). 17, 27, 58, 59, 60, 61, 63, 73.

Character 27: Cochlea cryptocochlear (0); or phanerocochlear (1). 17, 26, 27, 28, 59, 62, 73.

Character 28: Lateral process of ectotympanic weak or absent (0); or well developed, forms tubular external auditory meatus (1). 17, 58, 59, 73.

Character 29: Tympanic annulus inclined (0); or annulus semivertical in orientation (1). 58, 59, 73.

Character 30: Epitympanic recess shallow and broad (0); or deep, often constricted in area (1). 17, 58, 59, 73.

Character 31: Fossa for *m. stapedius* indistinct

(0); or shallow and broad (1); or deep, constricted in area, often a crescent-shaped fissure (2). 17, 58, 59, 73.

Character 32: Fenestra cochleae (= fenestra rotundum) small or of moderate size, maximum diameter <20% of the external width of the first half turn of the cochlea (0); or enlarged, maximum diameter >25% of the external width of the first half turn of the cochlea (1). 17, 58, 73.

Character 33: Aquaeductus cochleae large and obvious (0); or small or absent, difficult to detect (1). 58, 73.

Character 34: *M. tensor tympani* muscle spindle-shaped, inserts via single tendon onto tubercular processus muscularis of malleus (0); or two-headed, inserts via two tendons onto processus muscularis and accessory process (1); or broad sheet of fibers, inserts on crest like processus muscularis (2); or absent (3). 14, 58, 86, 87, 93.

Character 35: Orbicular apophysis small or absent (0), or large (1). 14, 17, 58, 73.

Character 36: Laryngeal echolocation absent (0); or present (1). 16, 18, 41, 63, 71, 80, 88.

Character 37: One pair of submaxillary glands present (0); or two pairs (1). 45, 67.

Character 38: Right lung divided into four lobes (0); or three lobes (1); or two lobes (2); or undivided (3). 67.

Character 39: Left lung divided into two lobes (0); or undivided (1). 67.

Character 40: Tracheal rings subequal in diameter throughout length of trachea (0); or one ring enlarged to form tracheal expansion just posterior to larynx (1); or two to eight rings enlarged to form tracheal expansion just posterior to larynx (2); or nine or more rings enlarged to form a tracheal expansion that is separated from larynx by four or five rings of normal diameter. 19, 20, 21, 22, 23, 24.

Character 41: Midline hyoid strap musculature with *m. geniohyoideus* and *m. hyoglossus* directly attached to basihyal via fleshy fibers (0); or muscles attached indirectly to basihyal via basihyal tendon, resulting in "free-floating" strap muscle condition (1); or basihyal tendon lost, no connection between *m. geniohyoideus* and *m. hyoglossus* and basihyal (2). 19, 20, 21, 22, 23, 24.

Character 42: *M. sternohyoideus* directly attached to basihyal via fleshy fibers (0); or attached indirectly to basihyal via basihyal tendon (1); or no connection between *m. sternohyoideus* and basihyal (2). 19, 20, 21, 22, 23, 24.

Character 43: Deep division of *m. mylohyoideus* absent (0); or present, runs dorsal to midline strap musculature, inserts on basihyal (1). 19, 20, 21, 22, 23, 24.

Character 44: *M. mylohyoideus* runs ventral to midline strap musculature, inserts on basihyal and

basihyal raphe (0); or inserts on basihyal, basihyal raphe, and thyrohyal (1). 19, 20, 21, 22, 23, 24.

Character 45: *M. mylohyoideus* aponeurotic anteriorly (0); or fleshy for entire width from mandibular symphysis to at least basihyal region (1). 19, 20, 21, 22, 23, 24.

Character 46: *M. mandibulo-hyoideus* (= medial part of anterior digastric) absent (0); or present (1). 19, 20, 21, 22, 23, 24.

Character 47: *M. mandibulo-hyoideus* with muscle fibers (0); or reduced to tendinous band (1). This character cannot be scored in taxa that lack *m. mandibulo-hyoideus*. 19, 20, 21, 22, 23, 24.

Character 48: *M. mandibulo-hyoideus* well developed (0); or reduced to small muscle with tendon (1). This character cannot be scored in taxa that lack *m. mandibulo-hyoideus* or have a *mandibulo-hyoideus* that has been reduced to a tendinous band. 19, 20, 21, 22, 23, 24.

Character 49: *M. stylohyoideus* with slip that passes superficial to digastric muscles (0); or superficial slip absent (1). 19, 20, 21, 22, 23, 24.

Character 50: *M. stylohyoideus* with slip that passes deep to digastric muscles (0); or deep slip absent (1). 19, 20, 21, 22, 23, 24.

Character 51: *M. geniohyoideus* origin from flat posterior surface of mandible lateral to symphysis (0); or from pronglike process that extends posteroventrally from symphysis region (1). 19, 20, 21, 22, 23, 24.

Character 52: *M. geniohyoideus* originates by long tendon from the mandible (0); or by very short tendon (1); or medial fibers originate by tendon, lateral muscle fibers arise directly from the bone of the mandible (2); or muscle arises entirely by fleshy fibers from bone (3). 19, 20, 21, 22, 23, 24.

Character 53: *M. genioglossus* originates immediately lateral to mandibular symphysis (0); or origin extended laterally onto medial surface of mandible, occupying anterior one-fourth to one-third of medial mandibular surface (1). 19, 20, 21, 22, 23, 24.

Character 54: *M. genioglossus* and *m. geniohyoideus* not fused (0); or ventralmost fibers of *m. genioglossus* fused to fibers from caudal portion of *m. geniohyoideus* (1). 19, 20, 21, 22, 23, 24.

Character 55: *M. genioglossus* inserts into posterior tongue, no fibers insert onto basihyal (0); or ventralmost fibers insert onto basihyal (1). 19, 20, 21, 22, 23, 24.

Character 56: *M. hyoglossus* originates from entire lateral basihyal and thyrohyal in broad, unbroken sheet (0); or originates from lateral basihyal and lateral thyrohyal in two sheets separated by a space (1); or originates from antimeres in part, and from lateral basihyal and thyrohyal (2); or

originates from lateral basihyal, thyrohyal origin absent (3). 19, 20, 21, 22, 23, 24.

Character 57: *M. styloglossus* with one belly (0); or with two bellies separated by lateral part of *m. hyoglossus* (1). 19, 20, 21, 22, 23, 24.

Character 58: *M. styloglossus* originates from expanded tip of stylohyal and/or adjacent surface of skull (0); or from ventral surface of midpoint of stylohyal (1). 19, 20, 21, 22, 23, 24.

Character 59: *M. ceratohyoideus* inserts at least in part onto ceratohyal (0); or does not insert onto ceratohyal (1). 19, 20, 21, 22, 23, 24.

Character 60: *M. ceratohyoideus* inserts at least in part onto epihyal (0); or does not insert onto epihyal (1). 19, 20, 21, 22, 23, 24.

Character 61: *M. ceratohyoideus* inserts at least in part onto stylohyal (0); or does not insert onto stylohyal (1). 19, 20, 21, 22, 23, 24.

Character 62: *M. thyrohyoideus* inserts onto thyrohyal (0); or muscle enlarged, inserts onto thyrohyal and basihyal (1). 19, 20, 21, 22, 23, 24.

Character 63: *M. sternohyoideus* origin includes entire anterodorsal surface of manubrium (0); or manubrial origin restricted to medialmost surface of manubrium in vicinity of keel (1). 19, 20, 21, 22, 23, 24.

Character 64: *M. sternohyoideus* origin does not extend onto clavicle (0); or origin includes medial tip of clavicle (1). 19, 20, 21, 22, 23, 24.

Character 65: *M. sternohyoideus* relatively broad (0); or reduced to a narrow strip of muscle (1). 19, 20, 21, 22, 23, 24.

Character 66: *M. sternothyroideus* originates from lateral manubrium (0); or from medial tip of clavicle (1); or origin includes both lateral manubrium and medial clavicle (2). 19, 20, 21, 22, 23, 24.

Character 67: *M. omohyoideus* originates from scapula (0); or clavicle (1); or muscle absent (2). 19, 20, 21, 22, 23, 24.

Character 68: Body of basihyal consists of transverse, unadorned bar or plate (0); or body of basihyal consists of curved bar with apex directed anteriorly (1). 19, 20, 21, 22, 23, 24.

Character 69: Curved body of basihyal V-shaped (0); or U-shaped (1). This character cannot be scored in taxa that lack a curved basihyal. 19, 20, 21, 22, 23, 24.

Character 70: Entoglossal process of basihyal absent (0); or present (1). 19, 20, 21, 22, 23, 24.

Character 71: Entoglossal process small (0), or very large, resulting in T-shaped basihyal (1). This character cannot be scored in taxa that lack an entoglossal process. 19, 20, 21, 22, 23, 24.

Character 72: Ceratohyal unreduced, approximately equal in length to epihyal (0); or ceratohyal reduced to half the length of epihyal (1); or

ceratohyal reduced to tiny element or completely absent (2). 19, 20, 21, 22, 23, 24.

Character 73: Epihyal unreduced, approximately equal in length to ceratohyal (0); or epihyal reduced to half the size of ceratohyal (1); or epihyal reduced to very tiny element or completely absent (2). 19, 20, 21, 22, 23, 24.

Character 74: Stylohyal occurs as gently curved bar with no enlargement or other modification to the lateral edge or cranial tip (0); or with cranial tip slightly expanded (1); or with bifurcated tip (2); or with large, flat expansion or "foot" on lateral cranial tip (3); or with very large, flat, axe-shaped enlargement at tip (4); or lateral half of entire stylohyal swollen (5). 17, 19, 20, 21, 22, 23, 24.

Character 75: Posteriorly directed ventral accessory processes not present on centra of cervical vertebrae 2 and 3 (0); or ventral accessory processes present on C2 and C3 (1). 17, 61, 73.

Character 76: Posteriorly directed, ventral accessory processes not present on centrum of cervical vertebra 4 (0); or ventral accessory processes present on C4 (1). 17, 61, 73.

Character 77: Posteriorly directed, ventral accessory processes not present on centrum of cervical vertebra 5 (0); or ventral accessory processes present on C5 (1). 17, 61, 73.

Character 78: Seventh cervical vertebra not fused to first thoracic vertebra (0); or C7 and T1 at least partially fused (1). 17, 56, 64, 73.

Character 79: First and second thoracic vertebrae not fused (0); or T1 and T2 fused (1). 17, 56, 64, 73.

Character 80: Anterior ribs not fused to vertebrae (0); or first rib fused to vertebrae (1); or at least first five ribs fused to vertebrae (2). 17, 56, 64, 73.

Character 81: Width of first rib similar to other ribs (0); or first rib at least twice the width of other ribs (1). 17, 56, 73.

Character 82: First costal cartilage not ossified or fused with manubrium or first rib (0); or first costal cartilage ossified and fused to manubrium (where it appears to form a winglike lateral process of the manubrium) and fused to first rib (1).

Character 83: Second costal cartilage articulates with sternum at manubrium–mesosternum joint (0), or second rib articulates with manubrium, no contact between rib (or costal cartilage) and mesosternum (1). 17, 56, 73.

Character 84: Second rib articulates with sternum via costal cartilage (0), or second rib fused to sternum, costal cartilage absent or ossified (1). 17, 56, 73.

Character 85: Mesosternum articulates with at least five costal cartilages posterior to second rib (0); or articulates with four costal cartilages pos-

terior to second rib (1); or articulates with only three costal cartilages posterior to second rib (2). 17, 37, 56, 73.

Character 86: Ribs with no anterior laminae (0); or anterior laminae present (1). 17, 73.

Character 87: Anterior laminae on ribs narrow, lamina width less than that of main body of rib (0); or anterior laminae wide, equal to or wider than main body of rib (1). This character cannot be scored for taxa that lack anterior laminae on the ribs. 17, 73.

Character 88: Ribs with no posterior laminae (0); or posterior laminae present (1). 17, 73.

Character 89: Posterior laminae on ribs narrow, lamina width less than that of main body of rib (0); or posterior laminae wide, equal to or wider than main body of rib (1). This character cannot be scored for taxa that lack posterior laminae on the ribs. 17, 73.

Character 90: Anterior face of manubrium small (0); or broad, defined by elevated ridges (1). 17, 56, 73.

Character 91: Ventral process of manubrium absent (0), or ventral process present, distal tip blunt or rounded (1); or ventral process present, distal tip laterally compressed (2). 17, 56, 73.

Character 92: Angle between axis of ventral process and body of manubrium acute (0); or approximately 90° (1); or obtuse (2); or ventral process bilobed with one acute and one obtuse process (3). This character cannot be scored in taxa that lack a ventral process on the manubrium. 17, 56, 73.

Character 93: Length of manubrium posterior to lateral processes >2.5 times the transverse width (0); or length <2 times the transverse width (1). 17, 56, 73.

Character 94: Mesosternum narrow, mean width less than half the distance between clavicles at sternoclavicular joint (0); or mesosternum broad, mean width greater than three-fourths the distance between clavicles (1). 17, 37, 56, 73.

Character 95: Xiphisternum without keel (0); or with prominent median keel (1). 17, 56, 73.

Character 96: Posterior xiphisternum with wide lateral flare (0); or not laterally flared (1). 17, 56, 73.

Character 97: Acromion process without medial shelf (0); or with shelf that projects medially over supraspinous fossa or medial base of acromion process (1). 17, 56, 73.

Character 98: Tip of acromion process without anterior projection (0); or with triangular anterior projection (1). 17, 56, 73.

Character 99: Distal acromion process without posterolateral projection (0); or with triangular posterolateral projection (1). 17, 56, 73.

Character 100: Dorsal articular facet (for tro-

chiter of humerus) absent from scapula (0); or present (1). 17, 68, 73.

Character 101: Dorsal articular facet faces dorsolaterally and consists of small groove on anteromedial rim of glenoid fossa (0); or faces dorsolaterally and consists of an oval facet on anteromedial rim of glenoid fossa (1); or faces dorsally and consists of a large, flat facet clearly separated from glenoid fossa (2). 17, 68, 73.

Character 102: Infraspinous fossa of scapula narrow, length ≥ 2 times the width (0); or wide, length ≤ 1.5 times the width (1). 17, 56, 73.

Character 103: Infraspinous fossa with one facet (0); or two facets (1); or three facets (2). 17, 56, 73.

Character 104: Intermediate infraspinous facet narrower than posterolateral facet (0); or facets subequal (1); or intermediate facet wider than posterolateral facet (2). This character cannot be scored in taxa that have only one or two infraspinous facets. 17, 56, 73.

Character 105: Lateral/posterolateral facet of infraspinous fossa restricted, does not extend into infraglenoid region anteriorly or wrap around intermediate facet at posterior (caudal) angle of scapula (0); or posterolateral facet more extensive, extends into infraglenoid region and wraps around caudal end of intermediate facet (1). 17, 56, 73.

Character 106: Thick lip present along axillary border of scapula (0); or thick lip with bladelike lateral edge present (1); or thick lip absent, axillary border flat or slightly upturned (2). 17, 56, 73.

Character 107: Pit for attachment of clavicular ligament absent from scapula (0), or present anterior and medial to glenoid fossa (1). 17, 73.

Character 108: Anteromedial edge of scapula without projections or flanges (0); or with triangular anteromedial flange (1). 17, 56, 73.

Character 109: Coracoid process stout and of moderate length (0); or very long and thin (1). 17, 56, 73.

Character 110: Coracoid process curves ventrolaterally (0); or curves ventrally (1); or curves ventromedially (2). 17, 56, 73.

Character 111: Tip of coracoid process not flared, approximately same width as coracoid shaft (0); or tip distinctly flared (1); or bifurcated (2). 17, 56, 73.

Character 112: Suprascapular process present (0); or absent (1). 17, 56, 73.

Character 113: Clavicle articulates with or lies in contact with acromion process (0); or is suspended by ligaments between acromion and coracoid processes (1); or articulates with or lies in contact with coracoid process (2). 17, 29, 56, 73, 79.

Character 114: M. subclavius originates from

first costal cartilage (0); or from first costal cartilage and lateral process of manubrium (1). 30, 31, 43, 56, 79, 81, 82.

Character 115: Anterior division of *m. pectoralis profundus* originates from first costal cartilage (0); or from first costal cartilage and clavicle (1); or from clavicle only (2). 30, 31, 43, 56, 79, 81, 82.

Character 116: *M. dorsi patagialis* absent (0); or present (1). 43, 44, 45, 79.

Character 117: *M. humeropatagialis* absent (0); or present (1). 43, 79, 81, 82.

Character 118: *M. occipitopollicalis* absent (0); or present (1). 31, 43, 44, 45, 56, 79, 81, 82.

Character 119: *M. occipitopollicalis* with no tendinous attachments to the anterior division of *m. pectoralis profundus* (0); or with tendinous attachment to the anterior division of *m. pectoralis profundus* (1). This character cannot be scored in taxa that lack *m. occipitopollicalis*. 79, 83.

Character 120: *M. occipitopollicalis* with no tendinous attachments to the posterior division of *m. pectoralis profundus* (0); or with tendinous attachment to the posterior division of *m. pectoralis profundus* (1). This character cannot be scored in taxa that lack *m. occipitopollicalis*. 79.

Character 121: *M. occipitopollicalis* without muscle belly between cranial muscle belly and band of elastic tissue (0); or with small intermediate muscle belly (1). This character cannot be scored in taxa that lack *m. occipitopollicalis*. 56, 79.

Character 122: *M. occipitopollicalis* insertional complex includes muscle fibers distal to band of elastic tissue (0); or entirely tendinous distal to band of elastic tissue (1). This character cannot be scored in taxa that lack *m. occipitopollicalis*. 79.

Character 123: *M. occipitopollicalis* inserts into pollex and metacarpal of digit II (0); or inserts on pollex only (1); or inserts into wing membrane anterior to metacarpal of digit II. This character cannot be scored in taxa that lack *m. occipitopollicalis*. 56, 79, 81, 82.

Character 124: *M. spinotrapezius* not differentiated from anterior trapezius complex (0); or clearly differentiated from *acromiodeltoideus* (1). 30, 31, 43, 44, 45, 56, 79, 81, 82.

Character 125: Origin of *m. acromiotrapezius* includes thoracic vertebra 4 (0); or does not include T4 (1). This character cannot be scored in taxa that lack differentiation of *m. acromiotrapezius* from *m. spinotrapezius*. 30, 31, 43, 44, 45, 56, 79, 81, 82.

Character 126: Origin of *m. acromiotrapezius* does not include thoracic vertebra 5 (0); or does include T5 (1). This character cannot be scored in taxa that lack differentiation of *m. acromiotrapezius* from *m. spinotrapezius*. 30, 31, 43, 44, 45, 56, 79, 81, 82.

*z*ius from *m. spinotrapezius*. 30, 31, 43, 44, 45, 56, 79, 81, 82.

Character 127: Origin of *m. acromiotrapezius* does not include thoracic vertebra 6 (0); or does include T6 (1). This character cannot be scored in taxa that lack differentiation of *m. acromiotrapezius* from *m. spinotrapezius*. 30, 31, 43, 44, 45, 56, 79, 81, 82.

Character 128: *M. clavotrapezius* not differentiated from *acromiotrapezius* (0); or clearly differentiated (1). 30, 31, 43, 44, 45, 56, 79, 81, 82.

Character 129: *M. levator scapulae* originates from atlas (0); or from three to five vertebrae between C2 and C7 (1); or from C4 and C5 only (2). 30, 43, 44, 45, 56, 79, 81, 82.

Character 130: *M. omocervicalis* absent (0); or present (1). 30, 43, 56, 79, 81, 82.

Character 131: *M. omocervicalis* originates from ventral arch of C2 (0); or from transverse processes of C2 (1); or from transverse processes of C3 and C4 (2). This character cannot be scored in taxa that lack *m. omocervicalis*. 30, 43, 56, 79, 81, 82.

Character 132: *M. omocervicalis* inserts on acromion process of scapula (0); or on clavicle (1). This character cannot be scored in taxa that lack *m. omocervicalis*. 30, 43, 56, 79, 81, 82.

Character 133: Anterior division of *m. serratus anterior* originates from six or more ribs (0); or from four or five ribs (1); or from two ribs (2). 13, 30, 31, 44, 45, 56, 79, 81, 82.

Character 134: *M. latissimus dorsi* inserts on ventral ridge of humerus (0); or muscle divided, inserts on ventral ridge plus distal pectoral crest (1). 31, 43, 44, 45, 56, 65, 79, 81, 82.

Character 135: *M. teres major* inserts into ventral ridge (0); or pectoral crest (1). 30, 31, 43, 44, 45, 56, 79, 81, 82.

Character 136: *M. acromiodeltoideus* originates from acromion process plus $\leq 25\%$ of the length of the transverse scapular ligament (0); or acromion plus $> 50\%$ of transverse scapular ligament (1). 13, 30, 31, 43, 44, 45, 56, 79, 81, 82.

Character 137: *M. spinodeltoideus* originates from vertebral border of scapula plus transverse scapular ligament (0); or from vertebral border only (1); or muscle absent (2). 13, 30, 31, 43, 44, 45, 56, 79, 81, 82.

Character 138: Coracoid head (= short head) of *m. biceps brachii* less than or equal to approximately one-third the size of glenoid head (= long head) (0); or coracoid head approximately one-half the size of glenoid head (1); or coracoid head three-quarters size or subequal to glenoid head (2); or coracoid head one and a half times the size of glenoid head (3). 56, 79, 81, 82, 83.

Character 139: Trochiter does not extend to level of proximal edge of head of humerus (0); or

extends just to level of proximal edge of head (1); or extends proximally well beyond level of head (2). 17, 32, 39, 68, 73, 85.

Character 140: Head of humerus round in outline in medial view (0); or oval or elliptical (1). 17, 32, 68, 73.

Character 141: Humerus with distal articular surfaces displaced laterally from line of shaft (0); or facets in line with shaft, not displaced laterally (1). 15, 17, 18, 32, 55, 73, 75.

Character 142: Epitrochlea broad, width $\geq 40\%$ of width of the articular facets (0); or relatively narrow, width $< 25\%$ width of articular facets (1). 15, 17, 32, 73, 75.

Character 143: *M. brachioradialis* present (0); or absent (1). 2, 30, 43, 44, 45, 56, 57, 81, 82, 83.

Character 144: Sesamoid element dorsal to magnum–trapezium articulation absent (0); or present (1). 12, 17, 56.

Character 145: Sesamoid element ventral to unciform–magnum articulation absent (0); or present (1). 12, 56.

Character 146: Sesamoid element dorsal to lunar–radius articulation absent (0); or present (1). 12, 56.

Character 147: Sesamoid element dorsal to unciform–magnum articulation absent (0); or present (1). 12, 17, 56.

Character 148: Sesamoid element dorsal to trapezium–metacarpal I articulation absent (0); or present (1). 12, 56.

Character 149: Wing digit II with ossified first (proximal) phalanx (0); or first phalanx unossified or absent (1). 17, 32, 56, 79, 85.

Character 150: Wing digit II with ossified second phalanx (0); or second phalanx unossified or absent (1). 17, 32, 56, 79, 85.

Character 151: Wing digit II with ossified third (ungual) phalanx (0); or third phalanx unossified or absent (1). 17, 32, 56, 79, 85.

Character 152: Wing digit III with third (ungual) phalanx completely ossified (0); or third phalanx ossified only at the base (1); or third phalanx unossified or absent (2). 17, 32, 56, 79, 85.

Character 153: Wings folded by flexing all phalanges in digits III, IV, and V anteriorly toward the underside of the wing (0); or proximal phalanx of digits III and IV folded posteriorly, distal phalanges folded anteriorly (1); or distal phalanges of digits III and IV folded anteriorly, proximal phalanges not folded (2). This character cannot be scored in taxa that lack wings. 32, 85.

Character 154: *M. flexor digitorum profundus* inserts on digit II (0); or does not insert on digit II (1). 2, 30, 43, 44, 45, 56, 57, 81, 82, 83.

Character 155: *M. flexor digitorum profundus*

inserts on digit IV (0); or does not insert on digit IV (1). 2, 30, 43, 44, 45, 56, 57, 81, 82, 83.

Character 156: *M. flexor digitorum profundus* inserts on digit V (0); or does not insert on digit V (1). 2, 30, 43, 44, 45, 56, 57, 81, 82, 83.

Character 157: *M. extensor digiti quinti* present (0); or absent (1). 2, 30, 43, 44, 45, 56, 57, 81, 82, 83.

Character 158: No vertebral fusion in posterior thoracic and lumbar series (0); or at least three vertebrae fused (1). 17, 64, 73.

Character 159: Sacrum (defined as including all vertebrae that articulate with the pelvis or are fused with those that do form an articulation) terminates anterior to acetabulum (0); or extends posteriorly to at least the midpoint of the acetabulum (1). 17, 64, 73.

Character 160: Sacral laminae narrow or absent, vertebra width (including laminae) less than or equal to three-fourths vertebral body length (0); or laminae broad, vertebra width equal to or greater than vertebral length. 17, 64, 73.

Character 161: Dorsomedial edge of ascending process of ilium upturned, flares dorsally above the level of iliosacral articulation, iliac fossa large and well defined (0); or dorsomedial edge not upturned, does not extend dorsally beyond the level of the iliosacral articulation, iliac fossa not large or well defined (1). 17, 73.

Character 162: Ischium with large ischial tuberosity that projects dorsally from posterior horizontal ramus (0); or ischial tuberosity small or absent, does not project dorsally beyond level of ramus (1). 17, 73.

Character 163: Pubic spine absent (0); or straight (1); or tip of pubic spine bent sharply dorsally (2). 17, 73.

Character 164: Articulation between pubes in male broad, symphysis long in anteroposterior dimension (0); or contact restricted to small area, consists of an ossified interpubic ligament or short symphysis (1). 43, 73.

Character 165: Obturator foramen normal, rim well defined (0); or foramen partially infilled with thin, bony sheet along posteroventral rim (1). 17, 73.

Character 166: *M. psoas minor tendinosus* for approximately half of length (0); or thick and fleshy throughout length (1). 13, 43, 44, 45, 51, 73, 81, 82.

Character 167: *M. gluteus superficialis* not differentiated (0); or differentiated into *m. gluteus maximus* and *m. tensor fascia femoris* (1). 8, 13, 38, 43, 44, 45, 51, 73, 81, 82.

Character 168: *M. piriformis* present (0); or absent (1). 13, 38, 43, 44, 45, 51, 73, 81, 82.

Character 169: Shaft of femur straight (0); or

with bend that directs distal shaft dorsally (1). 17, 73.

Character 170: Fibula complete, well-developed (0); or fibula thin and threadlike (1); or absent or entirely unossified (2). 17, 73, 84, 85.

Character 171: Calcar absent (0); or present (1). 2, 17, 73, 85.

Character 172: Digits II–V of foot with three phalanges (0); or two phalanges (0). 17, 73, 85.

Character 173: Digital tendon locking mechanism absent (0); or present, consists of tubercles on flexor tendon and plicae on adjacent tendon sheath (1); or present, with plicae but no tubercles (2). 69, 74.

Character 174: Baculum absent (0); or present (1). 1, 9, 33, 34, 47, 48, 52, 53, 71, 76, 87.

Character 175: Baculum saddle-shaped or slipper-shaped (0); or baculum elongated with long central shaft (1). This character cannot be scored in taxa that lack a baculum. 1, 9, 33, 34, 47, 48, 52, 53, 71, 76, 87.

Character 176: Pubic nipples absent in females (0); or one pair present (1). 72, 73.

Character 177: Female external genitalia with transverse vulval opening (0); or vulval opening oriented anteroposteriorly (1). 46, 47, 53, 66, 73.

Character 178: Clitoris small, not elongated anteroposteriorly (0); or clitoris elongated (1). 43, 47, 53, 66, 73.

Character 179: External uterine fusion minimal, uterine horns more than 70% length of common uterine body (0); or fusion more extensive, uterine horns less than 50% length of common uterine body (1). 35, 36, 43, 44, 45, 52, 53, 73.

Character 180: Internal uterine fusion absent, two cervical openings into vagina (0); or common uterine lumen present (1). 35, 36, 43, 58, 73.

Character 181: Common uterine lumen short in comparison to length of cornual lumina (0); or common uterine lumen large, cornual lumina either join immediately within common uterine body or are reduced to tubular intramural uterine cornua (1). This character cannot be scored in taxa that lack a common uterine lumen. 35, 36, 43, 53, 73.

Character 182: Uterotubal junction with oviductal papillae or complex folds (0), or simple, no papillae or complex folds (1). 35, 36.

Character 183: Blastocyst stage attained in uterus (0); or attained in oviduct (1). 47.

Character 184: Implantation superficial (0); or secondarily interstitial (1). 47.

Character 185: Embryonic disc oriented toward tubo-uterine junction (0); or consistently antimesometrial (1). 47, 48, 49, 50.

Character 186: Yolk sac development includes spread of mesoderm and expansion of exocoelom over embryonic half of yolk sac only; no vascu-

larization or hypertrophy of yolk sac endoderm (0); or development includes spread of mesoderm and expansion of exocoelom over embryonic half of yolk sac only; embryonic half becomes vascular and exhibits endoderm hypertrophy (1); or mesoderm spreads over entire yolk sac, but exocoelom expands to cover only embryonic half of yolk sac; hypertrophy occurs in vascular yolk sac at embryonic pole (2); or mesoderm spreads over entire surface of yolk sac, exocoelom expands to separate yolk sac completely from chorion; free, vascular yolk sac subsequently collapses and endodermal cells hypertrophy (3). 47, 50, 51.

Character 187: Allantoic vesicle large, occupies at least half of circumference of chorion during limb-bud stage (0); or small, occupies less than half the circumference of the chorion (1); or vesicle does not form, allantois remains tubular and vestigial throughout gestation (2). 47, 48, 49, 50.

Character 188: Primordial amniotic cavity does not form at any stage in development; amniogenesis is by folding (0); or primordial amniotic cavity forms but is transitory, lost in later development (1); or primordial amniotic cavity persists as definitive amniotic cavity (2). 47, 48, 49, 50.

Character 189: Definitive chorioallantoic placenta endotheliochorial (0); or hemochorial (1). 7, 47, 48, 49, 50.

Character 190: Spinal cord with angle between dorsal horns 70° – 80° (0); or 35° – 50° (1); or 0–25 (2). 40.

Character 191: Inferior colliculus significantly smaller than superior colliculus (0); or inferior colliculus larger than superior colliculus (1). 40.

Character 192: Olfactory bulb connected to brain via a “compact connection” by way of a short, thick olfactory peduncle containing paleocortical cells (0); or via a “thin connection” by way of a longer and thinner olfactory peduncle containing mainly olfactory fibers with nerve cells only in its most caudal part (1). 4.

Character 193: Left central lobe of liver fused with left lateral lobe (0); or separate from other lobes or partially fused with right central lobe (1). 13, 67.

Character 194: Gall bladder located in right lateral fissure of liver (0); or in umbilical fissure (1). 13, 67.

Character 195: Caecum present (0); or absent (1). 47, 48, 67.

Character 196: rDNA restriction site 20 present (0); or polymorphic, either present or absent (1). 3.

Character 197: rDNA restriction site 28 absent (0); or present (1). 3.

Character 198: rDNA restriction site 29 absent (0); or present (1). 3.

Character 199: rDNA restriction site 37 absent (0); or present (1). 3.

Character 200: rDNA restriction site 38 absent (0); or present (1). 3.
 Character 201: rDNA restriction site 40 absent (0); or present (1). 3.
 Character 202: rDNA restriction site 43 absent (0); or present (1). 3.
 Character 203: rDNA restriction site 44 absent (0); or present (1). 3.
 Character 204: rDNA restriction site 45 absent (0); or present (1). 3.

Character 205: rDNA restriction site 46 absent (0); or present (1). 3.
 Character 206: rDNA restriction site 47 absent (0); or present (1); or polymorphic, either present or absent (2). 3.
 Character 207: rDNA restriction site 50 absent (0); or present (1). 3.
 Character 208: One copy of R1 tandem repeat present in D-loop region of mtDNA (0); or three to nine copies of R1 repeat present (1). 91.

APPENDIX 3: DATA MATRIX

The data matrix given below contains all of the data used for Analyses 1, 2, and 3. See appendix 2 for character descriptions. This data set is also available electronically via the World Wide Web at <ftp://ftp.amnh.org/pub/mammalogy>.

Scandentia
 00000 00000 000-0 00000 00000 00000 00?30
 00000 00000 0--00 00000 00000 00000 000-0
 -0000 00000 00000 0-0-0 0-000 00000 -00--00000
 00000 000-? ---00 00020 --000 02{01}00 000??
 ???00 00-00 00001 01000 0{01}000 0000-
 {01}?101 0???0 00001 0?001 ????? ????? ??
 Dermoptera
 000?0 00000 000-1 00101 ?1-00 00010 00000
 0???0 00000 0--11 00001 00010 10010 120-0
 -0050 00000 00000 0-0-1 12100 00000 -00--
 00000 00011 010-? ---00 00001 00?00 00?00
 011?? ?????0 00-00 0?000 10010 00000 0010-
 00000 -?000 01111 0?001 00000 01000 00?
 Pteropodidae
 00000 121{01}0 1{01}0-0 {012}{123}{01}10
 31-00 {01}0{01}00 11000 0{01}000 {01}2010
 10011 00001 10000 10000 000-0 -000{01} 00000
 0000{01} {01}010{01} 2{123}{01}00 {01}0000
 -0{12}10 00000 0{01}00{12} {01}{01}100
 00000 00001 21200 0{01}{123}00 00100 00000
 02001 10010 10110 00{01}00 {01}0110 00000
 -0101 30200 00100 00{01}00 00100 {02}00
 Icaronycteris
 ????? ???00 0???? ?0000 000?? 1?0?0 ?????1
 ????? ?????? ?????? ?????? ?????? ?????? ?????1
 00000 00000 0-10? 12100 00000 -01-0 00000
 010?? ?????? ?????? ?????? ?????? ???10 00?0? ?0?00
 00??? ?0111 001?0 ???00 00??? ?????? ??????
 ?????? ?????? ?????? ?????? ???
 Archaeonycteris
 ????? ???00 ?????0 00010 00001 1?0?? ?????1
 ?????? ?????? ?????? ?????? ?????? ?????? ?????? ?????1
 100?? ?0000 ?????0 11100 10?0? ?01-0 0?000
 01??? ?????? ?????? ?????? ?????? ???10 00??? ???00
 02??? ?0?0? ?11?0 ???00 00??? ?????? ?????? ??????
 ?????? ?????? ?????? ?????? ???
 Hassianycteris

????? ???00 ?????0 00{01}10 1000? 210?? ?1???
 ?????? ?????? ?????? ?????? ?????? ?????? ?????? ?????1
 10??0 ?0000 ?0110 2?10? 000{01}1 101-0 00000
 01??? ?????? ?????? ?????? ?????? ???20 00??? ???00
 12??? ?000? 00?00 ???01 10??? ?????? ?????? ??????
 ?????? ?????? ?????? ???
 Palaeochiropteryx
 ?????? ???00 ?????0 00010 {12}0001 210?0 21???
 ?????? ?????? ?????? ?????? ?????? ?????? ?????? ?????1
 11000 00000 10110 22100 00001 011-0 0?100
 01??? ?????? ?????? ?????? ?????? ???10 00??? ???00
 12??? ?0111 001?0 ???01 10??? ?????? ??????
 ?????? ?????? ?????? ?????? ???
 Emballonuridae
 01000 {01}{12}120 10{01}1{01} {01}{01}1-1
 1000{01} 21000 201{02}1 1120{012} 00011
 0--01 00000 {01}010{01} {01}0010 110-0
 -10{12}1 11000 00000 {01}01{01}0 2{12}101
 {01}000{01} 00210 {01}{01}000 {01}{01}202
 01110 10{01}10 11{01}01 01200 0{01}111
 10?10 00011 121?? ?010 10110 ???01 10110
 00000 -0?01 3?102 1{01}100 01000 01000 100
 Rhinopomatidae
 01100 01120 100-1 112-1 10011 21000 21111
 10313 00010 10101 02000 00100 10101 210-1
 12021 11000 01000 11110 11100 00000 -01-0
 20000 01001 00111 01110 00101 01211 00110
 00??? ???00 120?? ?010 10111 ???01 00110
 10001 0?00? 3010? 1{01}001 00000 00000 00?
 Craseonycteridae
 011?? ???20 11101 112-1 11011 21001 21???
 1???3 00010 0--01 02000 00110 10101 010-1
 12011 11101 01001 10100 21101 00001 101-0
 21000 002?? ?????? ?????? ?????? ?????? ???20 00???
 ???01 122?? ?0110 10110 ???01 002?? 100??
 ?????? ?????? 11??? ?????? ?????? ???
 Nycteridae
 01301 22121 000-1 002-1 1{01}001 2{01}111
 00021 11311 00001 0--01 01000 2010{01} 10000
 {01}10-1 00{01}01 11{01}00 10101 11110
 23011 00001 001-0 21000 01212 01101 01110
 11101 11111 01110 00?11 00011 120?? ?0001
 10110 ???13 10111 00000 -???? ?????? 11000
 11100 01100 010

Megadermatidae

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10111 10200 {01}{01}000 10101 03000
2010{01} 10000 010-1 00001 11100 11101
11111 10101 00001 {12}0221 21000 01212
11101 01111 11111 11211 11211 00?? ????
120?? ??{01}10 10210 10011 10111 10001 0?00?
2110? 1{01}001 10001 10000 000

Rhinolophinae

00200 01121 000-1 111-0 10011 2{01}011 00101
1{01}31{0123} 00000 10110 00000 20100 10000
0{12}0-1 01031 11102 11111 0-111 10101 10001
20221 21000 01211 10101 01111 11110 --210
11221 00?? ???? 111 120?? ???? 00201 ????
10111 10001 0000? 30102 1{01}010 00100
01000 000

Hipposiderinae

00200 01121 000-{01} 11{12}-1 {01}0011
2{01}011 001{01}1 1131{0123} 00000 10110
00000 20{01}00 10000 0{012}0-1 0{12}031
11112 11111 0-111 {12}0100 00001 {02}0221
21000 00211 ?0?? ???? 111?0 --2?? ?0221
00000 10011 12010 11{01}00 00201 10011
1111{01} 10001 0???? ???? 10010 01000 01000
000

Phyllostomidae

0120{01} {01}{01}{01}10 010-{01}
{01}{123}{012}{12}{01} {123}0011
{12}{01}{01}{01}0 21001 11000
{12}{12}10{01} 0--11 0{013}000
{12}0{01}{01}0 {01}00{01}0 1{02}0-{01}
0{01}011 11000 0000{01} {01}010{01}
{12}{01}{01}0{01} 00001 {12}1{12}00
1{01}000 1{01}2{01}{12} {01}{01}1{01}1
0{01}010 {01}{01}101 11{02}0{01}
1{01}{23}20 00111 00101 1001{01} 10010
10110 101{01}{01} {01}000- 01111 111{01}1
12212 10100 00000 00101 000

Mormoopidae

{01}100{01} {01}{012}{01}10 010-0 011-0
10011 2{01}011 01001 1??2 11100 0--11 00000
11100 10010 1{02}0-1 0{01}011 11{01}00
00000 11110 2{12}101 00101 1{01}210 11000
10202 11111 01010 11101 11201 10121
{01}0011 01101 10010 00110 10110 ????
100{01}? 01111 11?? ???? 10?? 00011 00010
000

Noctilionidae

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02011 11000 00000 11100 22100 00100 -1200
10000 00102 11101 00010 11101 11200 11111
00?01 11101 122?? ???? 10110 ???? 1010-
01111 01101 12202 10100 00011 00011 00?

Mystacinidae

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1??0 11101 10011 03000 11110 10100 020-1
01011 11000 00000 0-0-0 12101 00101 211-0

00000 ?01?? ????? ????? ????? ????? 11???
???? 101?? ???? 11110 ????? 1001? 00101
00?? ????? ????? ????? ????? ???

Myzopodidae

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1??0 11010 11-01 13111 21100 11000 020-0
-0041 11000 00000 10110 22100 10101 20210
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???? 100?? ???? 10110 ???? 110?? 00001
0???? ????? ????? ????? ????? ???

Thyropteridae

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00000 10101 10101 11010 01101 01200 00120
00?? ???? 100?? ???? 10111 ???? 110??
00011 01?10 21?1? ????? 00000 00000 00?

Furipteridae

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10101 1??0 11100 10011 11111 21100 11100
000-1 10211 11100 00001 11110 23111 11101
111-0 20011 001?? ????? ????? ????? ????? 11??
00?? ???? 110?? ???? 10110 10110 ???? 100??
00011 0???? ????? 10?? 00000 10000 00?

Natalidae

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1??0 11100 10011 11111 21100 01100 020-1
00011 11100 00000 11101 20111 01001 111-0
20111 01102 10101 11010 00001 21100 10120
00?00 01011 110?? ???? 10110 10110 ???? 10010
00001 0???? ????? 10?? 00000 10000 20?

Antrozoidae

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1??0 00010 10111 00000 01110 11000 12111
12011 11000 00001 0-100 12100 00101 211-0
00100 00102 ????? ???? 00001 10100 10320
11?? ???? 110?? ???? 10110 ???? 10110
00001 0???? ????? ????? ????? ???

Tomopeatinae

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-2011 11100 00000 0-100 12000 00111 211-0
00112 011?? ????? ????? ????? ????? 11??
???? 110?? ???? 11110 ????? 101?? 000??
???? ????? ????? ????? ????? ???

Molossinae

01011 {01}{12}110 {01}{01}{01}1{01}
1{012}{12}-1 {12}0011 2{01}000 201{01}1
11000 1210{01} ???? 00000 21110 00000
02110 -2011 11100 00000 {01}0{01}0{01}
{12}2000 0{01}111 2{01}2{01}0 001{01}2
10102 01111 01010 01001 00100 10421 11110
01001 11111 01011 11110 01100 101{01}0
00001 00000 31112 10100 00000 01000 210

Vespertilioninae

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{12}0011 21000 {12}0101 11{01}10 11100
11-11 01000 11110 11000 12100 -2011 11000

0000{012} 101{01}0 {12}{12}1{01}{01} 00101
 21{12}10 0010{012} {012}010{12} 10110
 10{12}10 0100{01} 10100 10320 11100 00101
 1{12}010 10011 10110 ??01 101{01}{01}
 00001 00000 2111? 10100 ????? ????? ??1

Minopterinae

01010 00010 10110 001-0 10011 21000 20101
 11010 11101 11-11 01000 11110 01000 10100
 -2011 11000 00001 11110 23111 01101 211-0
 00102 101?? ????? ????? ????? ????? ??21 11??
 ??01 112?? ?011 10110 ??01 1000- 00001
 0???? ??1? 10100 ????? ????? ??0

Myotinae

01010 12110 10110 00{01}2{01} {12}0011
 21000 10101 1??0 11101
 11-11 01000 11110 01000 12100 -2011 11000
 0000{01} 10110 21111 00101 21210 00101

0010{01} 101{01}{01} {01}0010 01001 00100
 10{23}20 0110? 0??01 11010 10011 10110
 01101 10110 00001 00000 21112 1???? 00000
 00000 001

Murininae

010?? ???10 10110 001-1 10011 21000 201?1
 1??0 11101 0--11 01000 21110 01010 120-1
 02011 11000 00002 10110 21111 00001 20220
 20100 011?? ????? ????? ????? ????? ??20 01??
 ??01 110?? ?011 10110 ??01 10110 00001
 0???? ????? 1?? ???? ????? ??0

Kerivoulinae

110?? ???10 10110 000{12}0 20011 20000 201?1
 11??0 11101 0--11 00000 11111 01000 12100
 -2211 11000 00002 10110 21111 01101 21210
 00100 011?? ????? ????? ????? ????? ??20 01??
 ??01 110?? ?011 10110 ??01 10210 00001
 0???? ????? 10100 ????? ????? ??0