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Chiropteran evolution

Where are the limits?

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Introduction

The order of bats (*Chiroptera*), composed, in the present of over 1.100 species (Simmons, 2005), represents 20% of the diversity found in the mammalian class. Bats, the only mammals capable of self-powered flight, are found on every continent (except the Poles) and play a vital ecologic role on Earth, as seed dispersers and insect predators (Patterson *et al.*, 2003). They can be characterized with an elevated ecological and morphological diversity, unique sensory adaptations and an extreme life-history (Jones, 2002), aspects which offered them the possibility to become the second largest order within *Mammalia* (the first being *Rodentia*). These unique characters include self-powered flight, echolocation, hibernation, nocturnality, gregarious life, and at last, but not least, the use of a great variety of food resources and habitats.

Despite the achieved high diversity and abundance, bat origins are difficult to assess, due to limited fossil presence and missing key elements in the ancestral bat lineage (Simmons, 2005). Mammal phylogeny (with special attention on the position of bats relative to mammals) as well as taxonomical uncertainties for major group classifications was a widely debated subject in the last years (Mindell *et al.*, 1991; Shoshani & McKenna, 1998; Nikaido *et al.*, 2001; Springer *et al.*, 2003; Reyes, 2004). The theories about megabats being more closely related to primates than to microbats was a hotspot of phylogeny for several years (Pettigrew, 1986; Pettigrew *et al.*, 1989; Pettigrew, 1991; Pettigrew, 1995), until the emergence of a series of reliable conclusions through morphological (Simmons, 1994; Simmons & Geisler, 1998; Gunnell & Simmons, 2005) and molecular surveys (Lin & Penny, 2001; but see Teeling *et al.*, 2005 for final conclusions), that failed to gather evidence in support of this theory, and in contrary, prove the closer link between mega and microbats. Also, studies about internal bat phylogeny (Colgan & da Costa, 2002; Teeling *et al.*, 2002; Giannini & Simmons, 2003) were highly debated. Today, the order *Chiroptera* is presented as being monophyletic, with first representatives arising on the Cretaceous/Tertiary boundary, some 60-70 Mya (Simmons, 2005), and primate-chiropteran lineage relationships finalized. Through morphological and molecular studies (see citations above), extant bat species are separated in two major groups, the *Megachiroptera* (large, non-echolocating, fruit eating bats, found mostly in the

tropics) and the *Microchiroptera* (small sized, echolocating omnivorous bats, found throughout the globe) (see also Fig. 2.).

Bats represent a uniquely challenging group to study (and to highly protect), due to their various adaptations to their surrounding environment. Bats are among the (very small) group of vertebrates to achieve self-powered flight, the others being the birds and the extinct *Pterosaurs*. The acquisition of echolocation for orientation, communication and hunting for prey is a rarely occurring evolutionary event, present only in a few existing animals (dolphins, whales, and a bird). Another interesting character of bats is the use prolonged torpor (eg. hibernation) when temperatures and food availability drops. This feature of bats is shared with other animals from various taxa. Understanding its physiological interactions and genetic background can have direct applications in human medicine (surgery, implant organ preservation, etc.). Other striking features found in bats include nocturnality, gregarious life and an extreme life history. These, together with the above mentioned characters place bats in the spotlight of evolutionary biology. Understanding the functional mechanism behind these adaptations could lead to practical applications and human benefits. Equally important must be applications in conservation biology, due to the highly endangered status of several bat taxa.

1. Chiropteran phylogeny, intraordinal taxonomy and their position on the tree of life

Phylogenies of living or extinct taxa (in this case, mammals and especially bats) are hard to understand in lack of a wide-ranging sampling and methods that do not result in unreliable or partial results. Also, it is essential to provide comparable datasets, which can be re-applied or refined in future surveys. The question of whether to use morphological, anatomical or molecular methods is an essential one, because of different results given by each method when applied alone. The most reliable results are of course those that rely on the simultaneous use of these methods (ex. Simmons, 1994; Teeling *et al.*, 2005). This was the case of bat phylogeny, where several studies, using different methods confirmed different hypotheses. Two aspects were generally debated about chiropterans, this being the position of bats on the phylogenetic tree of Mammalia, and higher taxons (Mindell *et al.*, 1991; Shoshani & McKenna, 1998; Nikaido *et al.*, 2001; Springer *et al.*, 2003; Reyes, 2004), and the internal phylogeny

of the order (Colgan & da Costa, 2002; Teeling *et al.*, 2002; Giannini & Simmons, 2003).

About the position of the *Chiroptera* group among the lineages of mammals, through mostly anatomical (neural adaptations, visual pathways, etc.), several morphological features and some molecular data (mtDNA, amino acid sequences, RFLP) Pettigrew (1986, 1991, and 1995) argued that the superorder *Megachiroptera* is more closely related to evolved primates than to the *Microchiroptera*. Several theories have been proposed (“flying primate”, “deaf fruit bat”, “blind cave bat”, “fallen angel”), but most of them required many evolutionary changes. The (seemingly most acceptable) “flying primate” hypothesis (Fig. 1.), states that the capability of self-powered flight evolved two times, once in microbats and once in the separate lineage leading to megabats (Pettigrew, 1991 and 1995). However, flight is a rare evolutionary event (found only in three vertebrate classes and insects), with far ranging anatomical and morphological adaptations (reviewed in Maina, 2000), so in consequence, it is very unlikely that it evolved twice in independent lineages.

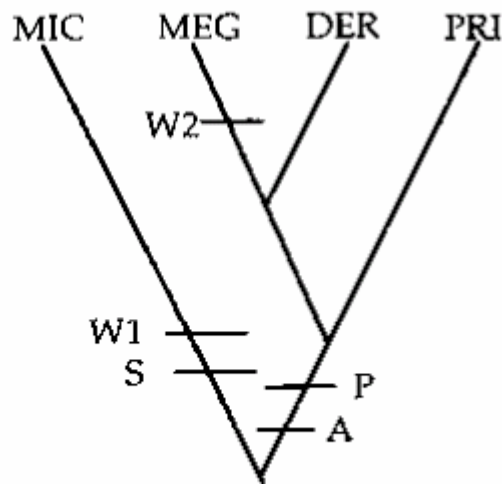


Fig. 1. The “flying primate” hypothesis (reproduced from Pettigrew, 1991)
(MIC – microbats, MEG – megabats, DER – dermopterans, PRI – primates, W – wings, S – sonar (echolocation), P – primate features, A – archontan skeletal features)

Despite the strong evidence of the existence of the highly evolved retinotectal pathway leading from eye to midbrain (which is a definitive classification character of primates) in megabats (and other characters, reviewed in Pettigrew, 1991), and their missing status in microbats, the primate-megabat link could not be sustained positively. Several recent morphological and/or molecular studies (Simmons, 1994;

Simmons & Geisler, 1998; Lin & Penny, 2001; Gunnell & Simmons, 2005) have proven the contrary, namely that microbats and megabats are more closely related to each other, than to any other mammalian lineage, or even primates. Mindell *et al.* (1991), using 12S rRNA gene and COI from various mammalian taxa, excluded the possibility of the dual evolution of flight. Furthermore, based on simultaneous analysis of several complete mtDNA genomes, Lin & Penny (2001) have proposed that the closest relatives of bats are cetferungulates (including Cetacea, Artiodactyla, Perissodactyla and Carnivora), but other studies, based mostly on nuclear genes (ex. Reyes *et al.*, 2004) show other possibilities for mammalian radiation. Result bias derives from the separate use of nuclear and mitochondrial markers. Currently bats are presented as being enclosed in the superorder Laurasitheria (Teeling *et al.*, 2002), together with insectivores, carnivores and ungulates (Jones, 2002). Arising problems in proposed radiation theories could be attributed to sampling under-representation of some taxa, or the singular use of a restricted number of genetic markers.



Fig. 2. Classical representatives of microbat (left) and megabat (right) suborders
(source: www.co.hunterdon.nj.us)

At the intraordinal level, it has been several times proposed that the microchiropteran suborder may be paraphyletic, with the family Rhinolophoidea being more closely related to megabats, than to any other microbat family. Jones *et al.* (2002) reanalyzed 105 estimates of bat phylogenetic relationships published since 1970, and theoretically rejected microbat parphyly, in support of microbat monophyly. However, Teeling *et al.* (2002), with a wide-ranging taxon sampling (nine outgroups, twenty bat species, including all extant rhinolophoid families) and 7.1Kb of analyzed nuclear sequences, found genetic evidence in support of the former theory, (eg. microbat paraphyly), grouping extant megabats, as well as *Megaderma*,

Rhinolophidae and *Rhinopomatidea* in the suborder *Yinpterogochiroptera* (*sensu* Springer *et al.*, 2001). Nevertheless, many intraordinal taxonomic mysteries remain unresolved in both suborders, despite several attempts, for example in *Megachiroptera* (Colgan & da Costa, 2002; Giannini & Simmons, 2003). The most comprehensive results are from Teeling *et al.* (2005), a study which also illuminates the divergence time and geographical origin of bats (Fig. 3.; see also section 2.).

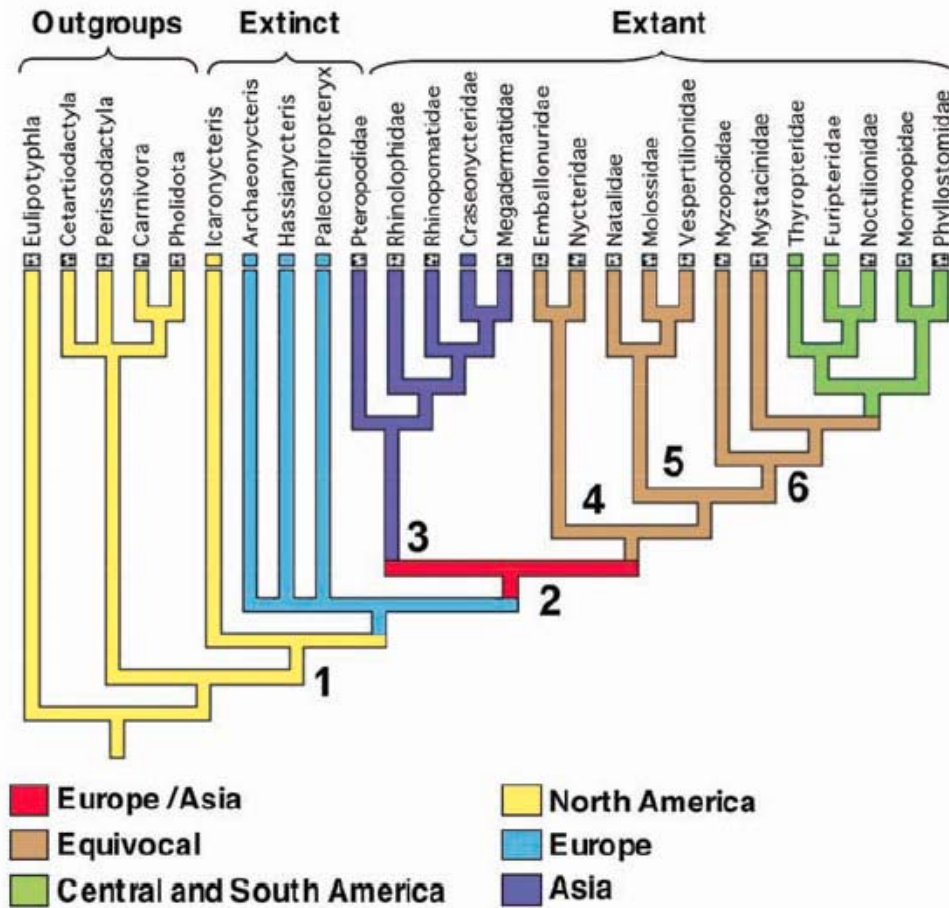


Fig. 3. Geographic distributions, origins and phylogenetic relationships among extant and extinct chiropterans (reproduced from Teeling *et al.*, 2005). (1 – Chiroptera, 2 - Yangochiroptera, 3 – Yinpterogochiroptera, 4 – Emballonurioidea, 5 – Vespertilionoidea, 6 - Noctilionoidea)

2. Fossil history and the geographical origins of bats

The period between the Upper Cretaceous and the Paleocene, often referred to as the Cretaceous/Tertiary (K/T) boundary (some 70 Mya) is marked with several major changes in the history of life on Earth. In a generally tropical climate, first there is a burst in diversification of plants, insects and placental mammals, followed by the severe extinction of dinosaurs (Donovan, 1989). Early studies investigating this

explosion of diversity failed to conclude the timing of diversification in placental mammals, due to limited taxon sampling, use of single calibration points and unwarranted molecular clocks that incorporate only lineage specific rate variations (Springer *et al.*, 2003). In order to these eliminate these missing elements Springer *et al.* (2003) constructed a phylogenetic tree, correcting all the misleading factors. They place the mean date of the placental root to approx. 105 Mya, the interordinal divergence of placental mammals before the K/T boundary (70 Mya), and intraordinal splits mostly after (60-65 Mya). Results are more of less in agreement with fossil history.



Fig. 4. Holotype specimen of *Icaronycteris index*, from the Green River Formation, early Eocene, southwestern Wyoming, USA (picture taken from Gunnell & Simmons, 2005).

The earliest confirmed (and surprisingly well preserved) bat fossil, *Icaronycteris index* (Fig. 4.), dates from the early Eocene (approx. 51 Mya) in North America (Gunnell & Simmons, 2005) from the Green River Formation, southwestern Wyoming, but other early taxa are also present in European, African and Australian fossil deposits. These include skeletons (often with soft tissue outline) of *Palaeochiropteryx*, *Archeonycteris*, *Hassianycteris* and *Tachypteron*. Surprisingly fossil bats show nearly all the key innovative morphological adaptive elements of extant bat taxa (ex. fully developed flight and echolocation) (Simmons & Geisler, 1998), thus major evolutionary refinements must predate the Eocene period, which in its turn could present a diversification period of modern taxa. In the middle/late

Eocene and early Oligocene period (33-55 Mya) many bat fossils taxa already represent extant bat families, meaning that modern radiations may have occurred then or slightly earlier (Gunnell & Simmons, 2005). However, the major part of fossil bats represents microchiropteran species. Megachiropteran origins are known only from isolated tooth or partial skeletons (ex. *Archeopteropus transiens*). Regardless the relatively high abundance of microchiropteran fossils, comparisons with mammalian sister taxa and molecular studies (Teeling *et al.*, 2005) indicate a 56-86% of missing elements, with nearly all fossil history missing for *Megachiroptera*. Newest findings in bat fossil history are *Tanzanycteris mannardi* (Gunnell *et al.*, 2003) from early Lutetian (46 Mya) sediments in north-central Tanzania, respectively *Phyllops silvai* (Suárez & Diaz-Franco, 2003) from late Pleistocene (1.8 Mya) cave deposits in Cuba.

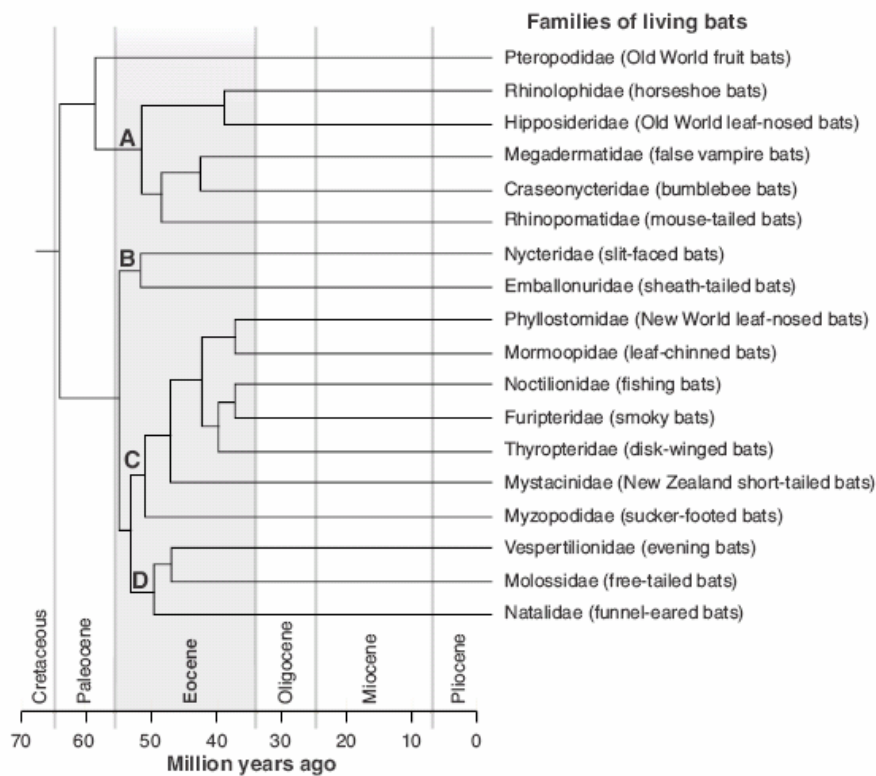


Fig. 5. Temporal pattern of bat diversification, dating major diversifications on the Cretaceous/Tertiary boundary and slightly after (reproduced from Simmons, 2005).

In tracing bat geographic origins Simmons & Geisler (1998) failed to present a clear picture, due to omnipresent bat fossils on most continents (Simmons, 2005). In contrast, Teeling *et al.* (2005) managed to include in their study all extant bat families and to produce a well resolved phylogenetic tree (see also Fig. 3.). Results delimit the appearance of major bat lineages, indicated also in other studies (ex. Springer *et al.*,

2003), in consensus with placental mammal diversification on the K/T boundary. Based on this major bat lineages appeared some 50-52 Mya, coincident with a global rise in temperature, increase in plant and insect diversity/abundance. The dataset from Teeling *et al.* (2005) suggests that bats originated in Laurasia, possibly in North America (Fig. 3.), with megabats originating in Asia and microbat lineages in Laurasia, except for noctilionids (Gondwana – possibly South America).

3. Evolution of flight and echolocation, with theories about ancestral bat aspects and possible causes for nocturnality

Flight and echolocation are two unique characters found together in the order *Chiroptera*, fact which has generated many theories about their evolutionary relatedness (eg. they evolved in parallel manner), or that they evolved linearly (echolocation first or flight first) (reviewed in Speakman, 2001). Conclusive arguments are limited by missing key elements in the existing chiropteran fossil history.

Different theories exist regarding flight evolution (see below), but every one suffers from missing elements, due to incomplete fossil history or early flight. The three most acceptable theories are:

- flight evolved in order to efficiently escape predators
- flight evolved in order to catch airborne prey
- flight evolved in order to efficiently travel from one place to the other

Animal flight is a highly energetically expensive form of locomotion, but in terms of cost per unit distance covered, powered flight is a very efficient mode of transport (Maina, 2000). The development of flight and its anatomical, biochemical and morphological properties in only four animal taxa (the extinct pterosaurs, extant insects, birds and bats) gives direct evidence of its high energetical and biophysical costs (reviewed in Maina, 2000). Birds and bats have used different approaching strategies to obtain self-powered flight, and both differed from pterosaurian characters and strategies. The most striking morphological feature is that birds fly with their hands, pterosaurs flew with one of their fingers, whereas bats use all of their fingers to obtain propulsion (see Fig. 6.). Also, the inclusion of the hind limb in the structure of the wing is present only in bats and pterosaurs, while missing in birds. Nevertheless,

in all forms of flying animals a prerequisite factor for flight was the evolution of enhanced oxygen uptake, transfer and utilization.

Bats evolved much later than pre-birds (eg. *Archaeopteryx litographica*, some 150 Mya, in the Upper Jurassic), from pre-bats (earliest fossil being the fully developed *Icaronycteris index*, 50 Mya, in the Eocene period), so their adaptation took place between the limitations and confinements of the pre-bat (also early mammal) body. Nevertheless, bats achieved a nearly equal oxygen uptake capability to that of birds. This specializations involved (i) a large heart with huge cardiac output, (ii) a high haematocrit, hemoglobin concentration, erythrocyte count and blood oxygen-carrying capacity, (iii) superior pulmonary structural parameters (eg. a large lung), and (iv) an efficient capillary blood supply to the flight muscles (Maina, 2000).

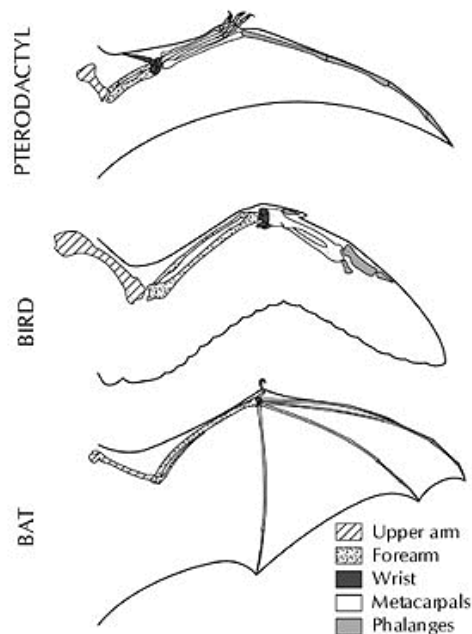


Fig. 6. Schematic representations of vertebrate wing types.
Note the different evolutionary use of forelimbs in the three taxa

In the comparison of flight speed of birds and bats, the winner are clearly birds, with the maximum recorded speed belonging to the peregrine falcon (*Falco peregrinus*), with a 403 km/h during complete dive on a prey (Tucker, 1998). Bats are slower, with recorded speeds of 16 km/h (*Pipistrellus pipistrellus*), 30-50 km/h (*Myotis lucifugus*), and 64 km/h (*Eptesicus fuscus*). But through exploring a great variety of habitat types (meaning increasing habitat complexity), bats have evolved, in parallel with flight, distinct neural features, associated with hearing, olfaction and spatial memory (larger hippocampus and inferior colliculi) (Safi & Dechmann, 2005)

and some morphological features, that increase flight maneuverability (ex. inclusion of the hind limb and tail in the structure of the wing) (Dudley, 2002).

Flight in bats (as also in birds) can be the result of either a “ground up” or a “tree down” evolution (Gunnell & Simmons, 2005). In the first case (“ground up”) proto-bats would had to jump up from the ground to acquire flying prey with their webbed hands or primitively evolved wings (Pirlot, 1977), ultimately achieving self-powered flight. Other authors give trust to the second hypothesis (“tree-down”) and under this assumption proto-bats may have been simple gliders (with the use of increasing patagia), and selection favoring longer glides, increased maneuverability and longer periods of aerial locomotion, resulting in active flight (Gunnell & Simmons, 2005). The latter hypothesis seems more plausible, based on fossil and morphological studies (Simmons & Geisler, 1998).

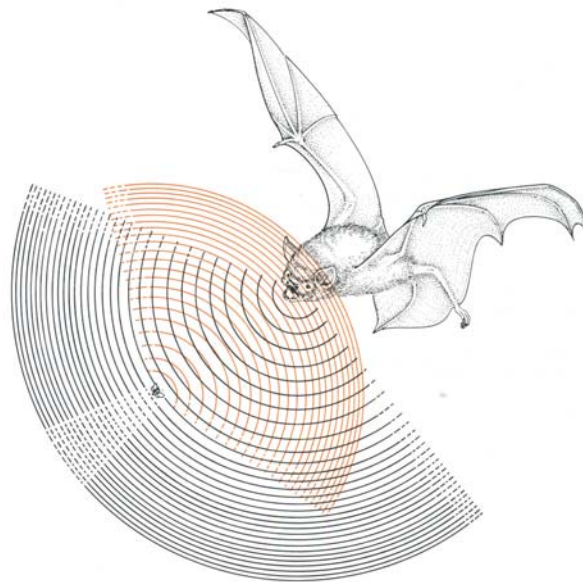


Fig. 7. Schematic representation of bat echolocation.
(dark waves – emitted signal, red waves – returning signal)

Echolocation, as primal source for orientation and food acquisition has evolved (as did active flight) only in a restricted number of animal taxa. These include bats, dolphins, whales (ex. the humpback whale *Megaptera novaeangliae*) and the bird *Streptopelia caripensis*, and their presence evidences convergent evolution for this trait in different habitats. Primitive forms of echolocation detections may be present in some moth species, due to the fact that these can successfully avoid being eaten by echolocating bats. The few existing fossil bats show already evolved echolocation characters (Simmons & Geisler, 1998), which can point to its much earlier appearance in the bat lineage, dating back to the late Paleocene (Gunnell & Simmons, 2005). The

general scheme of echolocation (Fig. 7.) is as it follows: (i) bats emit ultrasonic sounds (ranging from 10 to 150 KHz (Simmons & Stein, 1980)) (ii) the emitted signals reach the target surface and (iii) produce echoes, detected by the bats sophisticated ears. Different signal wavelengths of the combined use of different wavelengths permit bats to forage and orientate in open (ex. above forests) or highly cluttered space (ex. between trees and foliage), with many ghost-echoes present. The diversification of echolocation probably boosted the evolution of bats, resulting in gleaners, aerial hawkers, etc.

From the two extant bat superorders, only the *Microchiroptera* have the capability to echolocate, with only one genus of Megachiroptera (*Rousettus*) being able to produce primitive tongue “clicks” (Simmons & Stein, 1980). Several studies and reviews were produced about echolocation diversity and classification in bats based on emitted echolocation signals (Simmons & Stein, 1980; Arita & Fenton, 1997, Schnitzler *et al.*, 2003 and citations therein), but only recently became possible the phylogenetic reconstruction of present echolocation traits. The two major hypothesis about the evolution of echolocation in bats state that (i) echolocation evolved once in the early lineage, with subsequent loss in *Megachiroptera*, or (ii) it evolved independently in different microbat lineages. Springer *et al.* (2001) reconstructed an echolocating evolutionary tree, but failed to choose between the two above mentioned hypotheses, when examining molecular and morphological data only from extant bat species. However, after incorporating fossil data from extinct bat species, the former hypothesis was supported, eg. echolocation evolved once in the bat lineage, with subsequent loss in *Megachiroptera*.

Several scenarios were proposed to account for evolutionary bat appearance (60-70 Mya) but most of them can't find fertile ground (reviewed in Speakman, 2001), due to missing proto-bat fossils. Generally it is presumed that the proto-bat was a arboreal, insectivorous, under-branch hanger and nocturnal (Gunnell & Simmons, 2005) animal. However, much debate is about the evolution of flight and echolocation, more precisely what trait evolved first, and what did follow, or if they evolved in parallel manner. The “flight first” theory (Simmons & Geisler, 1998) assumes that the proto-bat was in the beginning a branch-to branch jumping insectivorous animal with the subsequent transition to a gliding animal with prolonged fingers, to finally achieve self-powered flight. With this new trait, proto-bats could have explore new habitats, some becoming insectivorous (through the evolution of

echolocation), whereas others becoming frugivorous (with evolved visual adaptations). The “echolocation first” theory assumes that insectivorous, nocturnal proto-bats used echolocation for communication, with subsequent adaptations to promote aerial prey tracking. Phalanges were already slightly evolved, through the transition from ground to arboreal life, and were used to catch airborne prey. With the use sophisticated echolocation to track and localize prey, proto-bats begun to jump on their targets, these jumps ever increasing in length, and finally becoming a glide or even self-powered flight. The tandem evolution theory states that the two characters evolved in parallel manner (Arita & Fenton, 1997). Simmons & Geisler (1998) argued in support of the “flight first” theory, but Gunnell & Simmons (2005) presented evidence in support of the simultaneous evolution of the two traits, with the inclusion of morphological aspects of the newest bat fossils found (*Tanzanycteris mannardi* (Gunnell et al., 2003) and an unnamed bat fossil from the Green River formation in Wyoming). In his review about chiropteran flight and echolocation evolution, Speakman (2001) summarized actual hypothesis, presented evidence against and supporting them, and added a new, radical scenario. Based on this, arboreal the proto-bat was not nocturnal and insectivorous, but diurnal and frugivorous (due to the Cretaceous angiosperm diversification). Using his well developed visual characters, this proto-bat would jump ever longer to access fruit resources, eventually yielding in self-powered flight. Later, some taxa would acquire insectivorous habits, due to nitrogen balance problems related to frugivory, and lack of any natural competitors (because of absence of insectivorous birds in the Cretaceous period). In the Tertiary period, there is a burst in bird diversification, yielding in a highly competitive environment, and forcing bats to acquire a nocturnal life. Consequences of nocturnality were in the case of megabats, the enhanced evolution of neural and morphological characters for night vision, and in microbats, the evolution of echolocation (Speakman, 2001). But this final theory awaits (molecular and fossil) arguments pro or contra, and the evolution of nocturnality could have undergone a different scenario.

Studies about bat nocturnality have focused on three aspects which could have facilitated the appearance of nocturnality in formerly diurnal bats: (i) competition with insectivorous and frugivorous birds, (ii) risk of avian predation and (iii) risk of hyperthermia (reviewed in Speakman, 1995). The bases of the first theory (eg. avian competition for food) come from observations about bats being attacked by

competitive birds, although this remains generally a rare event. However, bats lacking any natural competitor (ex. *Desmodus rotundus* feeding on blood) are also nocturnal, suggesting that avian competition does not force bats into the nocturnal world (Speakman, 1995). If the theory about avian predation on bats would be accepted, we could assume that bats living in predator-absent areas can be diurnally active. Seemingly only pteropodid fruit bats to fit in these theory (some species actually fly in daylight when predators absent), but here we find exception too, leading to the consideration that predation risk is not or only in low proportion responsible for chiropteran nocturnality (Speakman, 1995). Also the predation of nocturnal birds (ex. owls) on bats far exceeds the rate of daytime predation. The third hypothesis, hyperthermia in diurnal bats during the day, is plausible, because of inefficient dissipation of endogenous heat resulting from flight. This theory predicts that with decreasing temperature, there could be an increase in bat activity. Winter activity of bats seem to conclude with this, also laboratory tests in wind tunnels (where bats do not receive solar heat) find that at ambient temperatures exceeding 28-30°C, bats are unable to regulate their body temperature. Opposing evidence is found in the Samoan fruit bat (*Pteropus samoensis*), showing that this bat is highly active when solar activity and temperature reach daytime peaks. In conclusion, all three theories about evolution of nocturnality suffer from the lack of any coherent evidence (with the avian competitor theory being the most improbable, Rydell & Speakman, 1995)), so chiropteran nocturnality awaits further evaluation.

4. Gregarious social life, roosting habits and diets found in bats

Bats exploit a broad spectrum of habitats, food resources and do this in various ways, meaning foraging techniques, roosting structures, etc. This high adaptive capability resulted in remarkable levels of bat global diversity (Patterson *et al.*, 2003), with its peak in the geographical tropics. Consequences can also be found at the level of social organizations in bats, with solitarily living bats (or just males of several species), to colonies of thousand (or more) individuals (over 20 million individuals in the case of the Brazilian free-tailed bat *Tadarida brasiliensis*, see Fig. 8.), evidencing a highly gregarious way of life. Various social life organization types exist in living animals, reaching from isolated nocturnal primates (Radhakrishna, 2005) to highly organized

gregarious structures in insects, bats, etc. Social life organization (excluding cognitive organizations) seems to be independent from taxonomical position. The evolution of gregariousness in bats could be traced back to benefits of its use. In hibernating bats, body temperature could become less dependent from ambient temperature, when individuals are surrounded with conspecifics, having similar requirements. Also, in maternity colonies, bat pups are often grown not only by the mother but other individuals as well. Ultimately, bat aggregations can be the source of protection from predators for the individual (ex. when emerging from roosts, see Fig. 8.), eg. lower chance of being eaten when numbers are great. Roosting in a colony can also be advantageous (ex. against snakes preying on bats), increasing numbers decreasing individual predation. Gregariousness evolved several times independently in highly different animal taxa (ex. insects, bats), indicating its evolutionary beneficial value.



Fig. 8. Emergence of Brazilian free-tailed bats (*Tadarida brasiliensis*) from cave roost (source: Bat Conservation International)

Bats use several types of roost and can be classified accordingly. They roost in caves, crevices, tree cavities, on trees (especially *Megachiroptera*), in tree foliage (Kunz, 1982), and recently (few hundred years), due to human civilization, in man made structures. The choice of roost type is dependent on availability, dimensions, energetic considerations (ex. in hibernation) and risks of predation. Bats show seasonally varying roosting preferences, dependent on special demands. The use of the great variety of roosts, as well as man made structures provides the evidence of the order being very adaptative and sometimes opportunistic in roost choice (Kunz, 1982). Paradoxally, consequences of deforestation, building restoration, modification

of underground environment (eg. recreation, tourism), and often vandalism, indicates sensitivity of bats.

Bats exploit a great range of food resources, ranging from simple frugivory to blood consumption, and exploit it in extreme efficient ways. For example, the greatest bat colony in the world, located in North America, consisting of some 20 million Brazilian free-tailed bats (*Tadarida brasiliensis*), can eat every night 250 tones of insects. Most temperate zone bats are insectivorous, but in the tropic, insectivorous bats also dominate their communities. Other types of animalivory in bats include fish, frogs, other bats, and blood (three species) as food supplies (Patterson *et al.*, 2003). In the latter case, one species (*Desmodus rotundus*) prefers mammalian, the other two (*Diaemus youngi* and *Diphylla ecaudata*) avian blood (Patterson *et al.*, 2003). The other major type of bat diet is herbivory, including species which feed on nectar and pollen, fruit and foliage, although in the latter case, there is no dependence on it (Patterson *et al.*, 2003). Evolution of this diverse feeding spectrum is possibly linked with the timing of bat diversification (50-52 Mya, Teeling *et al.*, 2005) and also, not surprisingly, with the diversification of plants and the peak of insect diversity on the K/T boundary.



Fig. 9. *Desmodus rotundus*, a bat with blood-based diet (source: www.naturepl.com, Barry Mansell)

Given the great variety of roost and diets exploited, it is understandable how bats can achieve this high species diversity (more than 1.100 extant species), this great variety sometimes resulting in some regions where over 100 bat species coexist with apparently no competitive difficulties (Patterson et al., 2003). The evolution of flight and sophisticated echolocation was the prerequisite for this great diversity, offering the possibility to exploit new, unused habitats and food resources. Understanding evolutionary processes underlining social organizations, roost selection and diet preference in bats could have direct applications in bat protection.

5. Unique life-history traits, hibernation and its genetic background in bats

Body temperature and body size are two major factors influencing animal functioning (Speakman & Thomas, 2003). Temperature affects the rate of all the metabolic processes in the body, and hence affects muscle contractions, nerve conductance, enzyme activities, etc. Body size determines food necessities, with larger animals requiring more nutrition, but it has effects on temperature requirements, with larger animals supporting lower ambient temperatures. Bats, however, show extreme thermolability and exhibit a large scale of body, ranging from the 2 g *Craseonycteris thonglongyai* to 1.5 kg heavy *Pteropus* species. These varying traits gave bats the possibility to evolve a unique life-history trait, characterized by long life regardless small size (Barclay & Harder, 2003).

Different animal taxa have different life-history traits, altogether described as the “fast-slow” continuum of life histories (Speakman *et al.*, 2002). The “fast” end includes species that reach sexual maturity at young age, produce many small offspring and live short lives. The “fast” end includes for ex. insectivores, small mammals, etc. At the opposite end of the continuum are usually large animals that mature late, produce few, but large offspring and live long lives (Barclay & Harder, 2003). Bats have been more or less ignored in the study of life histories in mammals, despite the fact of their unique characters. Bat can be characterized as small sized mammals that reach sexual maturity at relative young age (in bat terms), and give birth to few but large offspring, and live long lives. These facts could place bats at both ends of the “fast-slow” continuum, because of the simultaneous presence of “fast” and “slow” traits in their life history. Bats live unusually long life (maximum

recorded age in the family *Rhinolophiodes*, M=23.3 years, (Barclay & Harder, 2003)), in comparison with similar sized mammals (ex. rodents) and give birth annually to usually one (sometimes two) large offspring. Several studies and reviews arose about the link between body size, energy and lifespan (Speakman, 2005) and different hypothesis have been proposed to explain unusual bat life history evolution (Jones & MacLarnon, 2001; Barclay & Harder, 2003), but most are not supported, due to insufficient data or missing cross-taxa comparisons. Barclay & Harder (2003) proposed that low extrinsic mortality, a constrained number of ova produced at one time and the limited food availability is responsible for this unusual life history found in bats.

Hibernation is an anatomical and physiological adaptation found in many animal taxa (ex. snakes, mammals, etc.) to cope with limited food availability and/or low ambient temperatures. In order to cope with severe (annually) environmental changes these animals undergo a prolonged state of torpor, when the body's every function and process (heart rate, oxygen consumption, breathing, etc.) is being reduced to its minimum. This assures a survival in these severe periods, with the criteria that enough fat reserves have been accumulated during the periods before entering torpor. Hibernation (and in general, thermoregulation) in mammals has been (Lyman, 1961) and is (Srere *et al.*, 1992; Hittel & Storey, 2002; Carey *et al.*, 2003; DiBona, 2003) one of the intensely studied physiological aspects in modern science, because of its possible applications in modern surgery and organ implant preservation.

The majority of existing studies about hibernation (Lyman, 1961; Srere *et al.*, 1991; Hittel & Storey, 2002; Carey *et al.*, 2003) in mammals describe different stages of entering torpor, but these are confined to small mammals (ex. ground squirrel, golden hamster, etc.) and not bats. This is possibly due to the fact that bats are highly sensitive animals, and can react to the slightest of changes in the surrounding environment. However, we can assume similar patterns of physiological stages and changes, due to convergent evolution.

Physiological stages of hibernation are detailed in Lyman (1961). Based on this, a prerequisite for entering hibernation is a drop in heart rate, respiratory rate and oxygen consumption before a decline in body temperature. Throughout the hibernation period a high blood pressure is maintained, but respiration is severely reduced (from 100-200 to 4-6/min), as well as heart rate (from normal 200-300 to 3-5/min). Arousal from hibernation is a highly coordinated physiologic event in which

the anterior of the body is warmed rapidly by shivering and other heat generating mechanisms, while heated blood is shunted from the posterior of the animal by differential vasoconstriction until the anterior (including heart, lungs, brain, etc.) reaches 37°C. A general model depicting the genetic mechanisms in entering hibernation (Fig. 10.) are thought to start with environmental signals reaching the brain, from where the cascade of molecular responses start to prepare the body for entering hibernation.

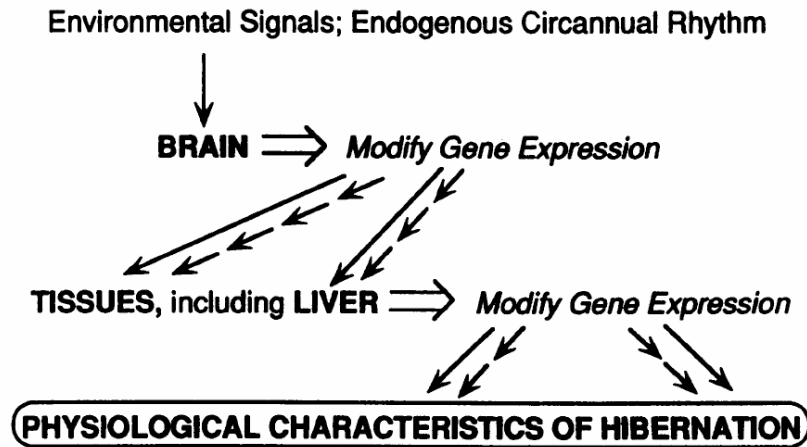


Fig. 10. General schematic representation of genetic signals in entering hibernation (reproduced from Srere *et al.*, 1990)

Despite several attempts, molecular signals involved in hibernation remain unresolved. Partial results identify a protein, α -macroglobulin, which increases in concentration in hibernating mammals (Srere *et al.*, 1991) and a differential expression of Cox1 mRNA (Hittel & Storey, 2002). These studies hypothesize that hibernating mammals may increase the expression of the mitochondrial genome, and Cox1 specifically, to prevent or minimize the damage to the electron transport chain during cold periods. Cellular and molecular aspects involved in hibernation are reviewed in Carey *et al.* (2003).

Conclusions and future aspects

The chiropteran order has a global distribution, with over 1.100 extant bat species, representing 20% of living mammal species. Through their evolutionary history, bats have acquired the unique combination of several key attributes, like flight, echolocation, nocturnality, hibernation, etc., which are probably the cause of their

great diversity and abundance. Studying these evolutionary traits may help to understand the evolution of other animal taxa sharing these traits, but the human benefit factor is also very important. For example, the elucidation of molecular and cellular signals involved in hibernation, may have direct applications in biomedicine (reviewed and summarized in Carey *et al.*, 2003), like the use of hypothermia in surgery, transplant organ preservation or the study of mechanisms involving the increase of tolerance to skeletal muscle atrophy and dysfunction, etc. A more extreme bat character adaptation could be the treatment of stroke victims and heart patients, with the anticoagulant from vampire bat saliva. But more generally, ecological demands imply the maintenance of diversity found in the chiropteran order, due to their vital ecologic role on Earth, as seed dispersers and insect predators. In order to maintain this high bat diversity, efficient protection of bat colonies, roost and feeding sites must be achieved, to reduce or even reverse the already alarming endangered status of several bat taxa.

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