Convergences in the diversification of bats

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Abstract Twenty-five characters or suites of characters from bats are considered in light of changes in bat classification. The characters include some associated with flower-visiting (two), echolocation (12), roosting (six), reproduction (two) and three are of unknown adaptive function. In both the 1998 and 2006 classifications of bats into suborders (Megachirottera and Microchirottera versus Yinpterochiroptera and Yangochiroptera, respectively), some convergences between suborders are the same (e.g., foliage roosting, tent building), but others associated with echolocation differ substantially. In the 1998 phylogeny convergences associated with echolocation (high duty cycle echolocation, nasal emission of echolocation calls) occurred among the Microchirottera. In the 2006 phylogeny, they occur between Yinpterochiroptera and Yangochiroptera. While some traits apparently arose independently in two suborders (e.g., foliage-roosting, tent building, low intensity echolocation calls, noseleafs, nasal emission of echolocation calls, high duty cycle echolocation behaviour), others appear to have been ancestral (roosting in narrow spaces, laryngeal echolocation, stylohyal-tympanic contact, oral emission of echolocation calls, and small litter size). A narrow profile through the chest is typical of bats reflecting the thoracic skeleton. This feature suggests that the ancestors of bats spent the day in small crevices. Features associated with laryngeal echolocation appear to be ancestral, suggesting that echolocation evolved early in bats but was subsequently lost in one yinpterochiropteran lineage [Current Zoology 56 (4): 454–468, 2010].

Key words Flower-visiting, Echolocation, Roosting, Reproduction, Ancestral bat

Evolution has provided spectacular examples of the development of similar lifestyles and morphology among different lineages. In vertebrates, the exploitation of krill as a food source has coincided with striking similarities in body form and feeding mechanisms among some cartilaginous fishes, ichthyosaurs, and baleen whales. Among the Chondrichthyans, two separate lineages are planktivorous (whale sharks and megamouths) (Nakaya et al., 2008) – one using gill rakers as strainers, the other its mouth. Shonisaurus, a Triassic ichthyosaur was over 20 m long, and the absence of teeth suggests that it fed on plankton (Nicholls and Manabe, 2004) probably using a mechanisms analogous to those of baleen whales. As striking, but perhaps more different in some details, are birds, bats and pterosaurs, the three groups of flying chordates (Padian, 1983).

The diversity of living bats and a growing number of fossil specimens provides biologists with data about variation among bats and the opportunity to place these data in a phylogenetic context. In such exercises the problem of recognizing ancestral features and distinguishing between parallel and convergent evolution is a recurring challenge for understanding the diversification of animals. For bat biologists, changes in the subordinal classification and in phylogeny (Fig. 1) that occurred between 1998 and 2009 (Simmons and Geisler, 1998; Teeling, 2009) expanded the field of examples of convergences within the diversification of bats. The ~1200 living species are arrayed in 19 families and exhibit an interesting blend of convergences among species of different lineages living in different areas. Refinements to phylogenetic relationships among extant bats provide an opportunity to consider the consistency of these convergences in the face of changes in our understanding of their evolutionary history.

In 1998, living bats were arrayed in two suborders, Megachirottera and Microchirottera, but since 2006 the two suborders now are called Yinpterochiroptera (previously known as Pteropodiformes) and Yangochiroptera (previously referred to as Vespertilioniformes but including the Emballonuridae and Nycteridae) (Hutcheon and Kirsch, 2006). Wetterer et al. (submitted a and b) argue for Yinpterochiroptera and Yangochiroptera as the corrects names of the suborders of bats. The distribution of families differs between the old and the new subordinal arrangement (Table 1). While focusing on changes in phylogeny, it is easy to forget that when Jepsen (1966) described the Eocene Icaronycteris index there was no data-based phylogeny of Chiroptera.
Our understanding of bat diversification is further enriched by the explosion in our knowledge about bats. Allen's (1939) classic book about bats predates the discovery of echolocation, a topic that today is addressed in hundreds of publications. Another reflection of the explosion of knowledge is that the 1988 book about ecological and behavioral methods for studying bats was 588 pages long, about half that in the second (2009) edition (Kunz, 1988; Kunz and Parsons, 2009). The increase in information about bats extends from behaviour and social systems to reproduction and basic biology.
Table 1  A comparison of the previous and current classifications (to family) of extant bats

<table>
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<th>Previous classifications</th>
<th>Current classifications</th>
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<tr>
<td>1998 Simmons and Geisler, 1998</td>
<td>2006 Wetterer et al. submitted a and b</td>
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<td>suborder Megachiroptera</td>
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<tr>
<td>suborder Microchiroptera</td>
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<td>suborder Yangochiroptera</td>
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<td>family Furipteridae</td>
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Recognition of Miniopteridae as a family follows Miller-Butterworth et al. (2006).

The capacity for flapping flight distinguishes bats from all other mammals, and there is general agreement that the origin and diversification of bats began with flight (Speakman and Racey, 1991; Fenton et al., 1995; Simmons and Geisler, 1998). Currently, there is no agreement about when echolocation evolved in bats with some (e.g., Simmons and Geisler, 1998) supporting the hypothesis that flight evolved first, others echolocation first (Fenton et al., 1995), and still others favour simultaneous evolution of flight and echolocation (Speakman and Racey, 1991). Simmons et al. (2008) argued that the Eocene Onychonycteris finneyi’s ability to fly is clear from the morphology of its shoulder girdles, but proposed that the combination of size of the orbicular process of the malleus, size of the auditory bulla and structure of the proximal end of the stylohyal strongly suggested that it could not echolocate.

The purpose of this paper is to examine the diversification of bats and determine how often examples of convergences have changed with changes in the classification of bats. The examples begin with flower-visiting species, extend to echolocation, roosting and reproduction. Convergences include morphological, histological and neurobiological features. Specifically, I examine 25 characters or suites of characters, two associated with flower-visiting, 12 associated with echolocation, six with roosting, two with reproduction and three of unknown functional significance. These convergences may have occurred between species in two suborders, or among species in different families and I will determine which, if any, of these patterns have changed between the 1998 and 2006 phylogenies (and classifications). I will use this information in an effort to identify some ancestral features of bats.

1  Flower-visiting

In bats and other animals, feeding at flowers (eating nectar and pollen) at least involves specialization of heads and tongues, and bats follow this pattern. Flower-visiting is a well known convergence among suborders of bats. In 1998 the convergences were between Megachiroptera and Microchiroptera, now between Yinpterochiroptera and Yangochiroptera. In the Old World, several species of Pteropodidae have long rostra and long tongues allowing them to feed at flowers (e.g., Gould, 1978) and the same is true in the Phyllostomidae in the New World (Fleming and Valiente-Banuet, 2002). At least two lineages of Pteropodidae (Hollar and Springer 1997; Alvarez et al. 1999) and two of Phyllostomidae (Baker et al., 2000; Wetterer et al., 2000; Dávalos and Jansa, 2004) have evolved similar specializations for feeding at flowers.

Furthermore, in the New World, some flowers of some species of plants have ultrasonic nectar guides that facilitate bats’ use of the resource (Von Helversen and Von Helversen, 1999). The nectar guides ensure that bats are lined up on the best course to obtain nectar. This floral specialization has not been documented in the Old World where most flower-visiting bats are not known to echolocate. In Old and New World, flowers of plants that depend upon bats for pollination (chiropterophilous) also show convergences in at least colour, odour, position on the plant, and time of flowering. There also are spectacular examples of bat and flower specializations (e.g., Muchhala and Thomson, 2009).

2  Echolocation

Echolocation is an active mode of orientation and involves use of echoes of sounds animals produced to
collect information about their surroundings. The differences between what an echolocator says and what it hears provide the data used to collect information about their surroundings (Thomas et al., 2004). This means that outgoing pulses must be registered in the echolocator’s brain to provide a template for comparison with echoes. Echolocation has evolved several times in birds and mammals. As both Teeling (2009) and Maltby et al. (2009) noted, there are several potential scenarios for the evolution of echolocation in bats and no unequivocal evidence about which is correct. Did flight evolve first (Simmons and Geisler, 1998) or echolocation (Fenton et al., 1995), or both simultaneously (Speakman and Racey, 1991)? Options for the evolution of echolocation in bats influence the details of incidences of convergence among bats in the area of echolocation.

2.1 Sound production

Among bats, most echolocating species use echoes of signals produced in the larynx, but a few species in the genus *Rousettus* (family Pteropodidae) use tongue-clicks (Holland et al., 2004). No other pteropodids are known to echolocate, although Gould (1988) suggested that *Eonycteris spelaea* uses wing claps as echolocation signals. Experimental results demonstrate that *Rousettus aegyptiacus* echolocate with tongue clicks, and, based on roosting in the total darkness of caves, it is likely that some other species in the genus (e.g., *R. leschenaulti*) also do so. *Lissonycteris angolensis*, sometimes considered to be a *Rousettus* (Juste et al., 1997) does not echolocate (Lawrence and Novick, 1963).

If laryngeal echolocation is ancestral in bats, then pteropodids lost the ability. Echolocation later evolved in a few pteropodids using echoes of signals produced by tongue clicks or wing claps. All other bats known to echolocate, whether in the Yinpterochiroptera (Rhinolophoidea) or Yangochiroptera (all families), use sounds produced in the larynx. The alternate hypothesis proposes that echolocation evolved independently in the two suborders of bats.

2.2 Stylohyal-tympanic connection

Veselka et al. (2010) demonstrated that in laryngeally echolocating bats (Yinpterochiroptera and Yangochiroptera) the stylohyal bone always contacts and sometimes is fused to the tympanic bone, while in pteropodids (whether non-echolocating or using by tongue clicks to echolocate) there is no contact between these two structures (Fig. 2). Veselka et al. (2010) proposed that this connection between bulla and hyoid allowed neural registration of outgoing echolocation pulses (= reaffecterent connection) in the bats’ brain.

![Fig. 2](image2.png)

Again, if laryngeal echolocation is ancestral in Chiroptera, stylohyal contact with tympanic has evolved once and then subsequently lost in one group of Yinpterochiroptera (Pteropodidae). If laryngeal echolocation is not ancestral, the stylohyal-tympanic contact must have evolved independently in the Yinpterochiroptera and Yangochiroptera. The proximal shape of the stylohyal in some Eocene bats, but not *Onychonycteris finneyi*, has been interpreted as indicative of the capacity for laryngeal echolocation (Simmons et al., 2008) but Veselka et al. (2010) found that contact between stylohyal and tympanic is a more consistent indicator of laryngeal echolocation than the shape of the proximal end of the stylohyal. The preservation of *O. finneyi* does not provide a clear indication of the relationship between stylohyal and tympanic bones leaving unanswered the question of whether or not it could echolocate.

2.3 Sound emission

Most species of echolocating bats emit echolocation
sounds through open mouths, but a few emit them through nostrils (Griffin, 1959; Novick, 1977). If laryngeal echolocation is ancestral, the details of laryngeal structures (e.g., Griffiths, 1978) or oral versus nasal emission (e.g., Pederson 1993a, b) reflect a common ancestor. Nasal versus oral emission of signals has appeared twice, once in each suborder (Yinpterochiroptera, Yangochiroptera). If laryngeal echolocation is not the ancestral condition, then oral and nasal emission have each evolved at least twice in bats.

2.4 Signal intensity

Signals used by echolocating bats range from high to low intensity (>130 to ~60 dB SPL @ 10 cm, respectively - decibels Sound Pressure Level measured 10 cm from source; Holderied et al. 2005; Surlykke and Kalko 2008). Griffin (1958) noted the dichotomy in signal strength and distinguished high intensity echolocating bats from ‘whispering’ bats. The impacts of attenuation, spreading loss (Lawrence and Simmons, 1982a), and directionality (Surlykke et al., 2009) mean that even using 130 dB SPL@10 cm signals, the range of bats’ echolocation is limited. Kick (1982) demonstrated that the high intensity echolocating Eptesicus fuscus first detects a 19 mm diameter sphere at 5 m, a graphic demonstration of short range detection of a prey-sized object. Fenton et al. (1995) argued that high intensity echolocation signals had to have developed before bats could use echolocation to detect and track flying prey (insects) because of the limited range of low intensity signals. If this argument is correct, then high intensity signals are ancestral.

Echolocating species in both suborders use either high or low intensity signals, but as we obtain more data from bats in the field, our knowledge of the details change. For example, it now is clear that not all phyllostomids produce low intensity echolocation calls (Mora and Macias, 2007; Brinklav et al. 2008) even though earlier impressions were different (Griffin, 1958). Low intensity echolocation calls often coincide with the use of prey-generated cues to find food (e.g., Schnitzler and Kalko, 2001).

2.5 Signal design

The echolocation signals used by tongue-clicking bats are short, broadband clicks (Fig. 3a), while those of laryngeal echolocators exhibit structured changes in frequency over time (= are tonal; Fig. 3b through l). Maltby et al. (2009) argued that early laryngeal echolocating bats used short, broadband, multiharmonic signals, presumably with structured changes in frequency over time (e.g., Fig. 3b). Tonal signals may be broad in bandwidth meaning large changes in frequency over short duration (e.g., Fig. 3 c, d, e, f, g), or narrow in bandwidth meaning little change in frequency over time (Fig. 3h, i). Echolocation signals range in duration from < 1 millisecond (ms) to over 50 ms. People studying bat echolocation use acronyms to describe the signals from FM (frequency modulated for broadband signals) to CF (constant frequency) or QCF (quasi constant frequency) (Kalko and Schnitzler, 1993). The acronyms may describe calls but not necessarily echolocation behaviour (Fenton, 1999). There is a diversity of signal design in almost all branches of the phylogeny of bats using laryngeal echolocation (Jones and Teeling, 2006), although Maltby et al. (2009) recognized seven basic types of search phase echolocation calls.

The ability of laryngeally echolocating bats to adjust their signals to maximize the information available to them means that there is considerable flexibility in call design among these bats. The changes in call design as an individual searches for, detects, approaches and attacks a flying insect (Fig. 4) is a demonstration of call flexibility.

Flexibility in the design of echolocation calls extends to adjustments made depending upon habitat (proximity of targets to background; e.g., Moss et al., 2006), general setting (Gillam and McCracken, 2007; Surlykke et al., 2009), as well as alternating call patterns (Figs. 2h, 4a; see also Kingston et al., 2003; Denzinger et al., 2001). Variation in echolocation calls may be a way to overcome the directionality of echolocation (Surlykke et al., 2009). The situation is further complicated because echolocation calls can be influenced by social setting (Fig. 3l; e.g., Gillam et al., 2007) and one bat's echolocation calls may be used by another and serve a communication function (Ulanovsky et al., 2004; Bayefsky-Anand et al., 2008; Deehan et al., 2009).

2.6 Tragus

The tragus (Fig. 5) of some echolocating bats influences perception of echoes by reducing sidelobes (Mueller, 2004; Mueller et al., 2006) which may influence vertical localization of targets (Lawrence and Simmons, 1982b). Tragi are well developed in some species (families) in both suborders, notably among the Megadermatidae (Yinpterochiroptera) and in several families of Yangochiroptera. But tragi are reduced substantially in some species in both suborders (e.g., Rhinolophidae – Yinpterochiroptera; Molossidae - Yangochiroptera). Mueller et al. (2006) noted that the thickened lower margin of the pinnae contributed to the function of the tragus in Nyctalus plancyi (Vespertilionidae)
Fig. 3  Variations in the echolocation calls of bats
Included are one tongue click from *Rousettus aegyptiacus* (a) as well as a sampling of the tonal echolocation calls produced by laryngeally echolocating bats (b through l). Tonal calls vary from being short and multiharmonic (b), to frequency modulated with broad bandwidth and short duration (c, d, e, f, g), frequency modulated and broadband with harmonics (c, d), long, narrowband frequency modulated signals (h, i), short upward-sweeping frequency modulated signals (f), short, broadband calls of low intensity (g), or signals dominated by one frequency but terminating (and sometimes beginning) with a frequency modulated sweep (j, k). In k there are the calls of two species, one producing shorter (a hipposiderid), the other longer calls (a rhinolophid). Calls in a through l and those in l are produced at low duty cycle. Calls in j and k at produced high duty cycle, *Pteronotus pammelii* (j) and the hipposiderid and rhinolophid. When two species are flying in the same airspace they may be distinguishable by their calls (l).
Fig. 4  Feeding buzzes, high pulse repetition rates associated with attacks on flying insects, produced by two different low duty cycle molossid bats

The first buzz is from *Molossus ater*, the second (which shows two buzzes) from *Tadarida teniotis*. Changes in patterns of frequency change over time, call duration and interpulse interval are obvious.

2.7 Duty cycle

Most echolocating animals separate pulse and echo in time to minimize self-deafening or forward masking (Fenton et al., 1995). These animals, from shrews to birds, toothed whales and most bats are low duty cycle echolocators whose short signals are separated by long periods of silence. Low duty cycle echolocators cannot broadcast and receive at the same time because the outgoing signal is so much more intense than the returning echo. Low duty cycle echolocation is the prevalent behaviour and has evolved several times in mammals and birds (Thomas et al., 2004). The differences in calling patterns are clear (Fig. 5), but there are no documented morphological features (such as nose-leaves or stylohyal-tympanic connections) unique to high duty cycle bats.

Some echolocating bats avoid self-deafening by separating pulse and echo in frequency. These high duty cycle echolocators produce signals of longer duration separated by short periods of silence. High duty cycle echolocation occurs in the Rhinolophidae and Hipposideridae (Yinpterochiroptera) and in one species of Mormoopidae (*Pteronotus parnellii*) in the Yangochiroptera. This dichotomy in duty cycle appears in the Old World and the New World. High duty cycle echolocators have specialized auditory systems (an acoustic fovea - Schuller and Pollak, 1979) and use flutter detection to identify flying targets (usually insects) in areas where there are many echoes from background (e.g., Schnitzler and Kalko, 2001). The specializations of the acoustic fovea are morphological and neurological and differ between Old World and New World high duty cycle echolocators (Schuller and Pollak, 1979).
At one site at the same time a recording of the echolocation calls of a high duty cycle (Rhinolophus hipposideros – most energy over 100 kHz) and a low duty cycle bat (Pipistrellus bodenheimeri – most energy < 75 kHz) High duty cycle echolocation is characterized by long calls separated by short intervals. Low duty cycle echolocation is characterized by short calls and long interpulse intervals.

The evolution of high duty cycle echolocation in both suborders of bats is an impressive convergence (Teeling, 2009). Doppler shift compensation is a behavioural indication of high duty cycle echolocation and has been demonstrated in both hipposiderid and rhinolophid bats as well as in P. parrnelli. At least one other mormoopid species that uses low duty cycle echolocation use Doppler shift compensation (Smotherman and Guillen-Servent, 2008), perhaps offering an example of the steps involved in the evolution of such specialized behaviour.

2.8 Noseleafs

Facial structures such as noseleafs, affect the pattern of sound radiation away from the bat's face. There is a variety of facial structures among bats, from obvious leaf-like projections usually standing above the rostrum, to flaps of skin around the mouth. Noseleafs (Fig. 6) are conspicuous in the Phyllostomidae (Yangochiroptera) and Megadermatidae (Yinpterochiroptera) and other

![Fig. 5](image)

**Fig. 5** At one site at the same time a recording of the echolocation calls of a high duty cycle (Rhinolophus hipposideros – most energy over 100 kHz) and a low duty cycle bat (Pipistrellus bodenheimeri – most energy < 75 kHz)

![Fig. 6](image)

**Fig. 6** This selection of bats illustrates some of the variety in tragi and noseleafs

The bats depicted are Balantiopteryx plicata (a), Nyctalus noctula (b), Eptesicus fuscus (c), Otonycteris hemprichi (d), Murina leucogaster (e), Pteronotus personatus (f), Pteronotus parnellii (g), Rhinopoma hardwickei (h), Megaderma lyra (i), Phyllostomus discolor (j), Rhinolophus ferrumequinum (k), Nycterus grandis (l), Axilla tridens (m), Desmodus rotundus (n), Mimon bennetti (o), and Tonatia evotis (p). Tragi are conspicuous in a, b, c, d, e, f, g, h, i, n, o, and p. Noseleafs are obvious in i, j, k, o and p. There is a small noseleaf in h, and variations on a noseleaf in i, m, and n. Tubular nostrils are obvious in e.
facial modifications are evident in Rhinolophidae, Hipposideridae, and Rhinopomatidae (Yinpterochiroptera) as well as in Nycteridae, and Mormoopidae (Yangochiroptera). Some vespertilionids (Yangochiroptera) also have facial features suggesting a leaflike structure (Nyctophilus spp., Idionycteris). Noseleaves in Phyllostomidae vary considerably in size and shape, from huge (Lonchorhina) to much reduced (Centurio, Sphaeronycteris, Desmodus, Diphylla, Daeamus, Erophylla, Brachyphylla, Phyllonycteris). Some bats with noseleaves emit echolocation calls through the nostrils and the orientation of their facial skeletons relative to the bases of their skulls is different from that of oral emitters. The skull orientation is the same for most bats with noseleaves (Phyllostomidae, Rhinolophidae, Megadermatidae – Pederson, 1993a, b).

In Carollia perspicillata the orientation of the noseleaf influences the pattern of sound radiation away from the bat (Hartley and Suthers, 1987). In Rhinolophus ferrumequinum some features of facial ornamentation influence the terminal frequency modulated sweep of the echolocation call (Zhuang and Mueller, 2006). Although we know that facial structures can influence the pattern of sound radiation away from the bat, the full impact of noseleaf design on echolocation calls remains unclear (Bogdanowicz et al., 1997).

In summary, among these features related to echolocation, the following appear to be ancestral for bats: use of laryngeal signals in echolocation, connection between stylohyal and tympanic bones, high intensity signals, tonal signals, oral emission and low duty cycle pattern of producing echolocation calls. Although the tragus occurs in both suborders, there is no other evidence that it is ancestral. Using tongue clicks as echolocation calls, noseleaves and high duty cycle echolocation appear to be derived features. Of these only the tongue clicks are restricted to one group of bats (some Pterpodidae in the Yinpterochiroptera).

3 Roosting

The roosts used by bats today can be broadly categorized as hollows, crevices, foliage, or specialized (Fenton, 2001). If the ancestral stock from which bats evolved was arboreal and nocturnal, it may be correct to assume that an inconspicuous and safe place to spend the day has always been important for survival. I hypothesize that the ancestral condition in bats was a body form that allowed the ability to squeeze into small spaces, such as crevices under bark, or small openings providing access to hollows in trees. Consistent with this hypothesis is the narrow thoracic profile of bats reflecting the arrangement of flight muscles (Vaughan, 1970a, b) and thoracic skeleton (Vaughan, 1970b; DesRoche et al., 2007). Specifically, muscles responsible for raising the wing are on the dorsum, those producing the downstroke are ventral. Keel-like structures are on the manubrium of the sternum (DesRoche et al., 2007) where they do not appreciably increase the thickness of the chest (unlike the sternal keels of most birds).

The impact of roosting on the social behaviour and organization of bats will undoubtedly provide many other examples of convergences in Chiroptera. It is important to remember that for social and thermoregulatory reasons at least, the bats in a roost may be as important as the roost itself (e.g., Kunz and Lumsden, 2003). The prevalence of fission-fusion 'societies' among bats may provide other examples (e.g., Wilkinson, 1985; Kerth et al., 2006; Rhodes, 2007; Willis and Brigham, 2004). In fission-fusion ‘societies’ extended groups of individuals may seldom use the same roost on any given day, but perhaps more often use different roosts.

3.1 Flattened skulls

Some species in the Vespertilionidae and Molossidae (Yangochiroptera) have conspicuously flattened skulls (Fig. 7) and roost under rocks (the molossids) or in spaces accessible through narrow openings (the vespertilionids). In South America, Neoplatymops mattogrosensis has been found roosting under flat rocks in open areas, while in Africa, the same is true of Sauromys petrophilus and Platymops setiger. In Southeast Asia, two species of vespertilionids (Tylonycteris) with conspicuously flattened skulls, roost in hollows between nodes in bamboo stems and enter through small openings made by bruchid beetles (Marshall, 1971). Other bats that roost

Fig. 7 Flattened skulls (a, c) are compared with a more normal skull (b)

Shown here are side views of the skulls of Tylonycteris robustula, Promops nasutus and Platymops setiger. Scale units are 1 mm.
in narrow spaces do not have flattened skulls (e.g., Tómopeas, a vespertilionid, and many molossids) and there are no Yinpterochiroptera with this characteristic. Apart from gaining access to or roosting in narrow places, no other function has been ascribed to the flattened skulls of bats.

3.2 Adhesive disks

Among the Yangochiroptera, Myzopoda in Madagascar and Thyroptera in the Neotropics, have adhesive disks on their wrists and ankles. Although the mechanism for producing adhesion differs between the two bats (Myzopodidae and Thyropteridae), in both cases the disks give the bats purchase on slippery surfaces (Riskin and Fenton, 2001; Riskin and Racey, 2010). Thyroptera spp. roost in furled leaves with heavy waxy cuticles, roost sites also used by vespertilionids that lack the adhesive disks, e.g., Myotis bocagel (Brosset, 1976), Pipistrellus nanus (Taylor, 2000). Other vespertilionids (Glishropus spp) have thickened thumbs that may be important for roosting and many roost in new banana leaves (Payne, et al., 1985). Unlike many other bats, these species are heads up in the furled leaves so they are facing the exits to their roosts.

3.3 Foliage roosting

Foliage roosting is common in pteropodid bats, less common in other Yinpterochiroptera, and variable among Yangochiroptera. While it has been known for a long time that some bats roost in foliage, we still do not know where many species roost. Radio-tracking makes it possible to find the roosts of many bats, revealing, for example, that Perimyotis subflavus roosts in foliage (Veilleux et al., 2003) rather than in hollows as I had thought, or confirming that Sturnira lilium roosts in foliage (Fenton et al., 2000). In the case of S. lilium, Centurio senex (Fenton et al., 2001), Lasiusurus borealis or Lasiusurus cinereus (Hickey and Fenton, 1999, 1996), in spite of intensive looking in the tree or bush in which the bats roosted, my colleagues and I never succeeded in spotting a roosting, radio-tagged bat. In the case of S. lilium, on one occasion at least 10 bats took flight (including the one with the transmitter) when we shook the bush. These small (mostly < 30 g) bats are notoriously difficult to see in their roosts. Even larger (80 – 100 g) Echphonhorous species can be difficult to locate in their roosts, except when the signal from a radio transmitter narrows the search area to one tree or bush (e.g., Fenton et al., 1985). This experience suggests that bats may often roost in foliage are difficult to locate because of some combination of camouflage (Bartholomew et al., 1970), disruptive colouration (Fenton, 1993) and behavour (Chalinolobus variegatus - Obrist et al., 1989; Pteropus samoensis - Brooke et al., 2000). Some researchers have had better fortune in spotting and observing roosting Lasiusurus cinereus (Barclay, 1989; Willis et al., 2006).

3.4 Tents

Some species of bats in both suborders chew to modify foliage or other plant parts to enhance their effectiveness as roosts (Kunz et al., 1994). Arguably, uses of tents is an extension of foliage roosting and one that strongly influences group size and social behaviour in the bats (e.g., Campbell, 2008; Campbell et al., 2006; Chavierri and Kunz 2006; Kunz and McCracken 1996). At least three other bats (Lophostoma silvicolum, L. brasiliense, L. carrikeri) use biting to modify termite nests to make them useful as roosts (Dechmann et al., 2004; Dechmann et al., 2009; Campbell et al. 2006).

4 Reproduction and Development

The details of aspects of reproduction in bats suggest convergences in this area (Crichton and Krutzsch, 2000). With the exception of Lasiusurus borealis (a vespertilionid) where females occasionally have litters of three or four, one or two young per litter is characteristic of bats (Crichton and Krutzsch, 2000) and this has consequences for life history strategies among bats (Barclay and Harder, 2003). Two features, energy rich placentae and implantation at the blastocyst stage (below) appear to be derived features in bats.

4.1 Energy-rich placenta

The development of an energy-rich placenta appears to have arisen twice in bats, in pteropodids (Yinpterochiroptera) and in molossids (Yangochiroptera). This trait may be an adaptation to reduce energy demands on pregnant females as they approach term (Rasweiler, 1990; Rasweiler and Badwaik, 2000). Energy-rich placentae appear to have evolved at least twice in Chiroptera.

4.2 Blastocyst implantation

In several species of bats, delayed implantation is relatively common (e.g., the phyllostomid Macrotus californicus or Miniopterus spp.), but in some species implantation of the blastocyst, occurs >10 days after conception (Crichton and Krutzsch, 2000). This occurs in Yinpterochiroptera (Pteropodidae) as well as in some Yangochiroptera (Emballonuridae, Mystacinidae, Noctilionidae and Phyllostomidae) (Badwaik and Rasweiler 2000; Rasweiler and Badwaik, 2000). This departure from the typical mammalian condition correlates with a post partum oestrous and may serve to maximize the time for post partum development of the lining of the uterus,
facilitating implantation and could reflect hormonal levels during this early stage of development.

The current view that bats are monophyletic (e.g., Simmons 1994), albeit one that is not unanimous (Pettigrew, 2008), would be further supported if elongation of wing elements in both suborders proves to be under the same genetic control (Sears et al., 2006). The same would apply to apoptosis or lack thereof if the development of forelimbs and hindlimbs in bats was under similar genetic control (Weatherbee et al., 2006).

5 Convergences of Unknown Function

There are at least three other striking examples of convergences among bats for which there do not appear to be adaptive explanations. These three examples appear to be derived features.

5.1 Tubular nostrils

Tubular nostrils are distinctive features of some bats in the Yinpterochiroptera (Pteropodidae - Nyctimene, Paranyctimene) and others in the Yangochiroptera (Vespertilionidae - Murina, Harpicephalus). Tubular nostrils coincide with strong, well developed premaxillae. While the pteropodids are not known to echolocate and are frugivorous (Dumont and O’Neal, 2004), the tube-nosed vespertilionids use laryngeal echolocation and are insectivorous (Kingston et al., 1999). The function of tubular nostrils in bats remains to be demonstrated.

5.2 Naked backs

Some Yinpterochiroptera (Pteropididae - Dobsonia spp) and some Yangochiroptera (Mormoopidae - Pteronotus) appear to have “naked backs” because their wing membranes join in the middle of the back. In both groups there is fur on the back under the wing membranes but the function of this feature remains unclear.

5.3 Vestigial thumbs

Many species of bats use their thumbs to manipulate food and thumbs are prominent in most species of bats. Strikingly reduced thumbs are most obvious in species of Furipteridae (Furipterus and Amorphochilus), they also occur in some Emballonuridae (Diclidurus). While furipertids roost in caves or hollows in trees (Simmons and Voss, 1998), Diclidurus roost under palm fronds in a typical emballonurid stance. Once again there is no obvious adaptive explanation for this feature and no evidence of it among the Yinpterochiroptera.

5.4 Diversification of bats

The diversification of bats has produced several convergences based on their appearances in both suborders. Examples include roosting in foliage, roosting in tents, tubular nostrils and naked backs, as well as enriched placentae and implantation at the blastocyst stage. Other features, such as vestigial thumbs, flattened skulls, and adhesive disks have appeared in more than one lineage of Yangochiroptera. Apart from features associated with echolocation, the new phylogeny of bats has not resulted in fundamental changes in levels of convergences (at subordinal versus family levels), suggesting that many convergences reflect diversification in different zoogeographic areas. Some of these convergences may stem from periods of diversification, e.g., 30 – 50 million years ago as suggested by Jones et al. (2005). As more genetic analyses emerge, e.g., of olfactory genes (Hayden et al., 2010), we can expect more convergences to emerge.

As intriguing will be convergences between bats and other animals. Obvious examples are those associated with flower-visiting and will involve bats and birds (notably hummingbirds, sunbirds, and other flower specialists), or bats and insects. Recent indications of convergences involving the gene Prestin between laryngeally echolocating bats and odontocete cetaceans (Liu et al., 2010; Li et al., 2010) are exciting examples. Of particular note in this context is that the convergences between these two groups appears to focus on the cochlea (Prestin) and sound reception but there is no convergence in the arrangement of the stylohyal and tympanic between odontocetes and laryngeally echolocating bats (Veslka et al., 2010).

5.5 The Ancestors of bats

I hypothesize that bats evolved from small, nocturnal, insectivorous stock. These animals had narrow body profiles allowing them access to daytime refuges in small crevices or in hollows entered through small openings. The legacy of this situation is apparent in the thoracic skeletons of living and fossil bats.

If exploiting flying nocturnal insects as prey was key to the origin and diversification of bats, then the ability to detect and track, and then pursue flying targets would have been essential. Fenton et al. (1995) argued that echolocation was key to the detection and tracking of prey and here the development of more intense signals was fundamental because low intensity signals provide minimal range partly because of spreading loss and atmospheric attenuation. Short, broadband, multiharmonic signals (Maltby et al., 2009) would have provided the ancestors of bats with a greater operational range. Frequency-dependent (Lawrence and Simmons, 1982a) differences in atmospheric attenuation across harmonics could have delivered a combination of effective range
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