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 (Megachiroptera and Microchiroptera 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 Microchiroptera. 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 Chondrichthyes, 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.
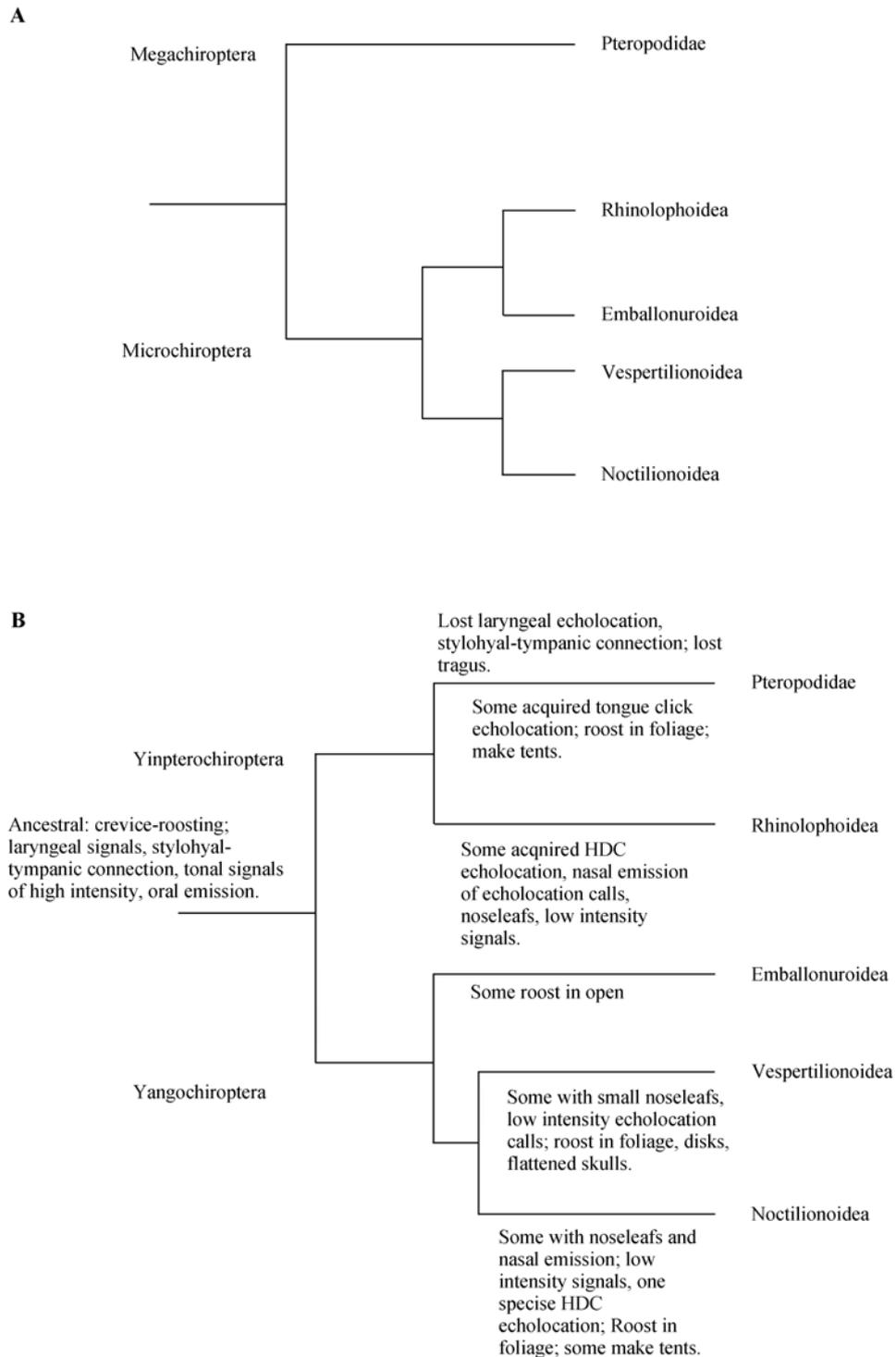
In 1998, living bats were arrayed in two suborders, Megachiroptera and Microchiroptera, but since 2006 the two suborders now are called Yinpterochiroptera (previously known as Pteropodiformes) and Yangochiroptera (previously referred to as Vespertilioniformes but including the Emballonuridae and Nycteridae) (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.

A

Megachiroptera ———————————— Pteropodidae

Microchiroptera
—— Rhinolophoidea
—— Emballonuroidea
—— Vespertilionoidea
—— Noctilionoidea

B

Lost laryngeal echolocation, stylohyal-tympanic connection; lost tragus.

Pteropodidae

Some acquired tongue click echolocation; roost in foliage; make tents.

Yinpterochiroptera

Rhinolophoidea

Ancestral: crevice-roosting; laryngeal signals, stylohyal-tympanic connection, tonal signals of high intensity, oral emission.

Some acqnired HDC echolocation, nasal emission of echolocation calls, noseleafs, low intensity signals.

Emballonuroidea

Some roost in open

Vespertilionoidea

Yangochiroptera

Some with small noseleafs, low intensity echolocation calls; roost in foliage, disks, flattened skulls.

Noctilionoidea

Some with noseleafs and nasal emission; low intensity signals, one specise HDC echolocation; Roost in foliage; some make tents.

Fig. 1 A comparison of the 1998 (A) and 2006 (B) phylogenies of bats (after Teeling 2009) showing the changed subordinal classifications and, in B, a selection of ancestral and derived characters

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

Previous classifications	Current classifications
1998	2006
Simmons and Geisler, 1998	Wetterer et al. submitted a and b
suborder Megachiroptera	suborder Yinpterochiroptera
family Pteropodidae	family Pteropodidae
suborder Microchiroptera	family Rhinolophidae
family Emballonuridae	family Hipposideridae
family Craseonycteridae	family Rhinopomatidae
family Rhinopomatidae	family Craseonycteridae
family Nycteridae	family Megadermatidae
family Megadermatidae	suborder Yangochiroptera
family Rhinolophidae	family Nycteridae
family Hipposideridae	famly Emballonuridae
family Mystacinidae	family Mystacinidae
family Noctilionidae	family Noctilionidae
family Phyllostomidae	family Phyllostomidae
family Mormoopidae	family Mormoopidae
family Molossidae	family Natalidae
family Miniopteridae	family Miniopteridae
family Vespertilionidae	family Vespertilionidae
family Myzopodidae	family Molossidae
family Natalidae	family Thyropteridae
family Thyropteridae	family Furipteridae
family Furipteridae	family Myzopodidae

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 diversifycation 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 (= reafferent connection) in the bats' brain.
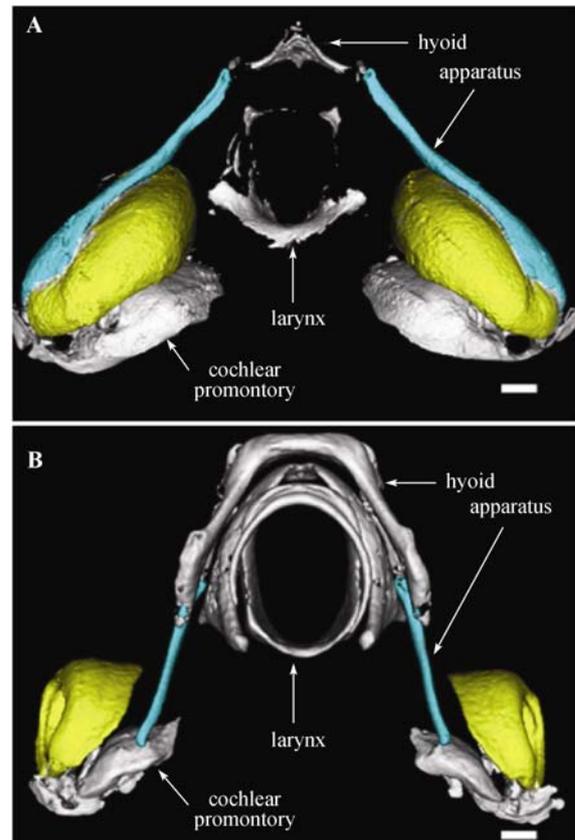
Fig. 2 A comparison of the arrangement of the stylohyal (turquoise) and tympanic (yellow) bones in a laryngeally echolocating bat *Desmodus rotundus* and a non echolocating bat *Sphaerias blanfordi*
Note that in *Desmodus* the stylohyal contacts the tympanic, but not in *Sphaerias*. After Veselka et al. (2010).

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 largyngeal echolocators exhibit structured changes in frequency over time (= are tonal; Fig. 3 b through l). Maltby et al. (2009) argued that early laryngeally 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 largyneal 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; Dechman 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)
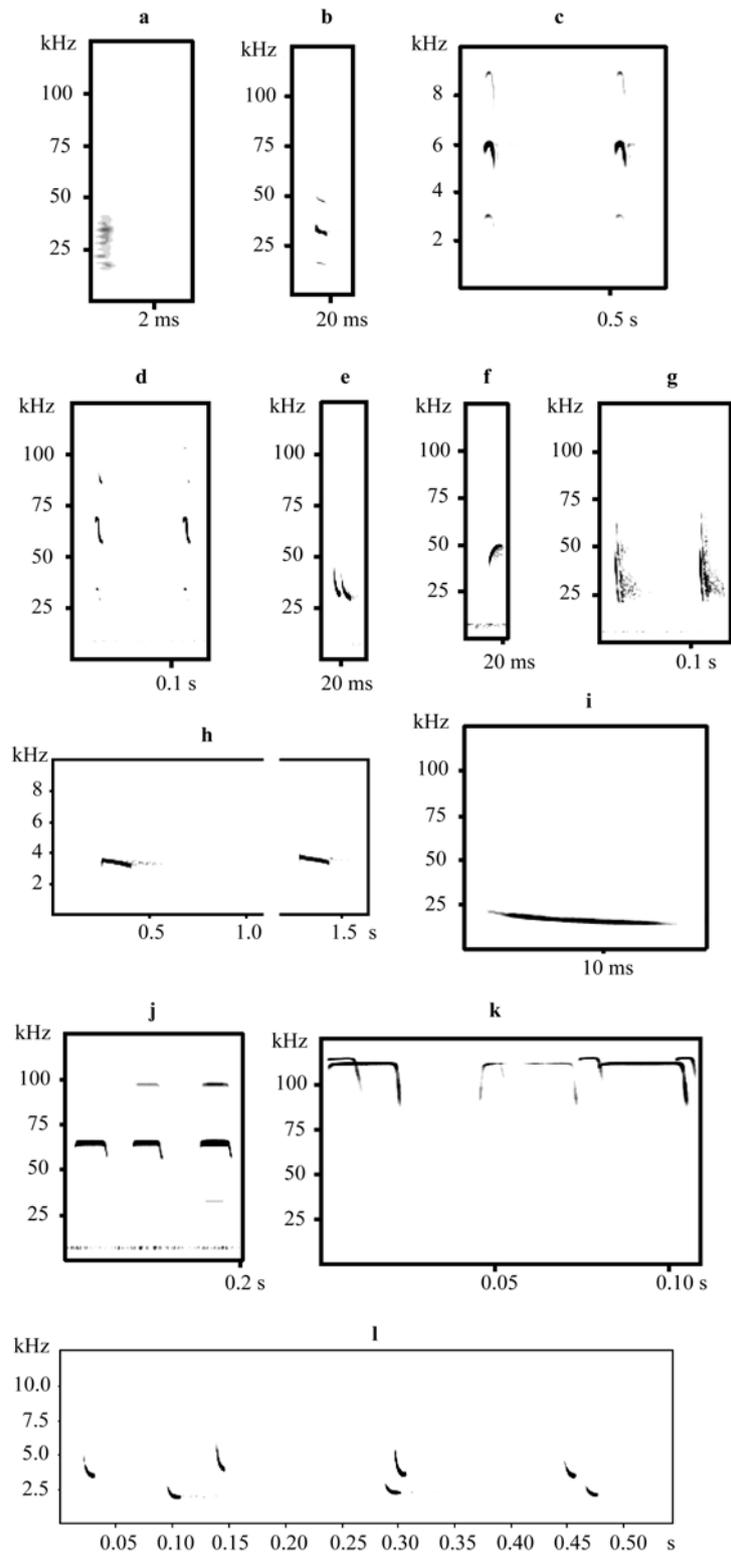
Fig. 3 Variations in the echolocation calls of bats

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 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 I and those in l are produced at low duty cycle. Calls in j and k at produced high duty cycle, *Pteronotus parnellii* (j) and the hipposiderid and rhinolophid. When two species are flying in the same airspace they may be distinguishable by their calls (l).
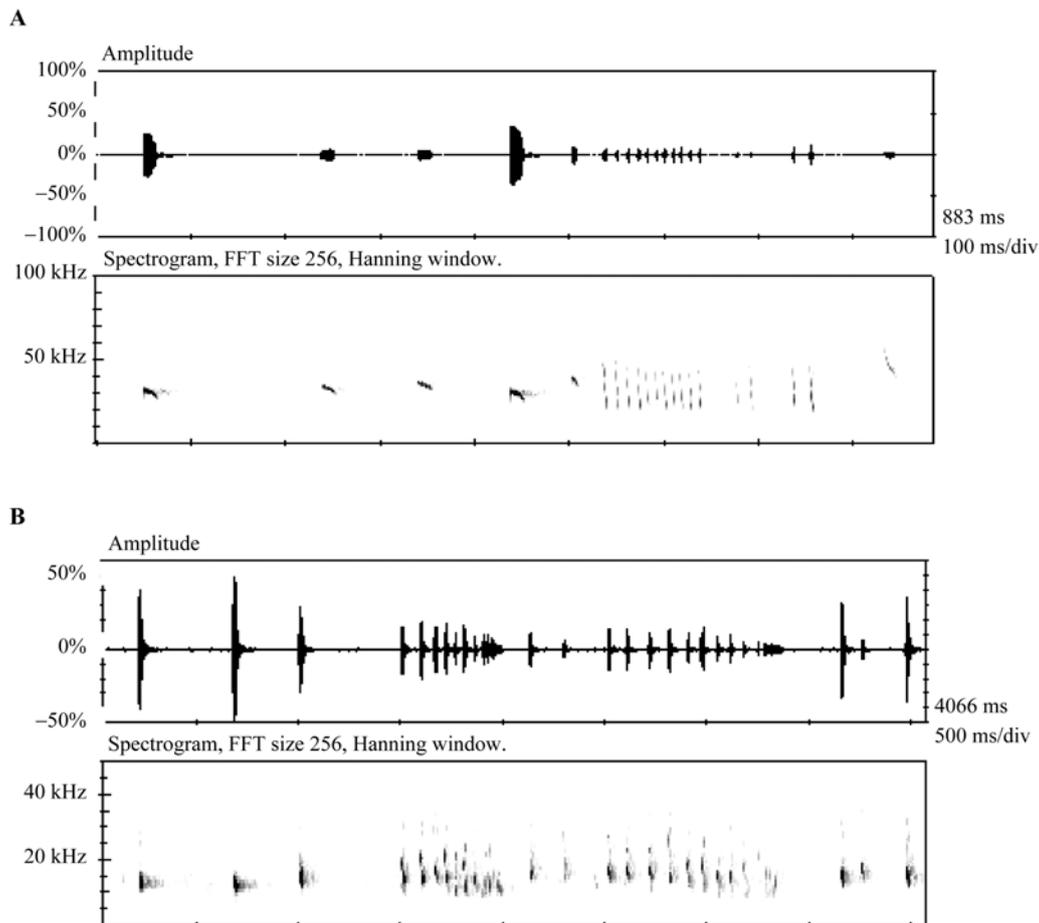
Fig. 4   Feeding buzzes, high pulse repetition rates associated with attacks on flying insects, produced by two different low duty cycle mlossid bats

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.

demonstrating that the collective structures (pinnae and tragi) contribute to function. There is no compelling evidence that tragi are ancestral characters but it seems likely that they evolved early in response to selection pressure for improved echolocation performance.

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-leafs 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).
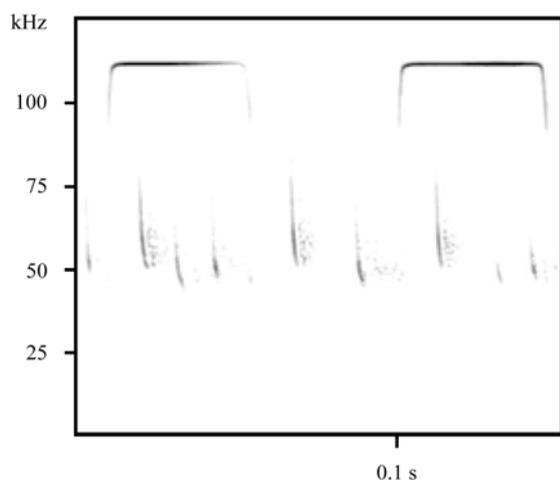
Fig. 5   At one site at the same time a recording of the echolocation calls of a high duty cycle (*Rhinolophus hipposideros* – most   energy over 100 kHz) and a low duty cycle bat (*Pipistrellus bodenheimeri* – most energy < 75 kHz)
High duty cycle echolocation is characterized by long calls separated 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. parnellii*. 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. 6   This selection of bats illustrates some of the variety in tragi and noseleafs
The bats depicted are *Balantiopteryx plicata* (a), *Nytalus 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), *Nycteris grandis* (l), *Asellia 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 l, 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*). Noseleafs in Phyllostomidae vary considerably in size and shape, from huge (*Lonchorhina*) to much reduced (*Centurio, Sphaeronycteris, Desmodus, Diphylla, Diaemus, Erophylla, Brachyphylla, Phyllonycteris*). Some bats with noseleafs 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 noseleafs (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, noseleafs 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
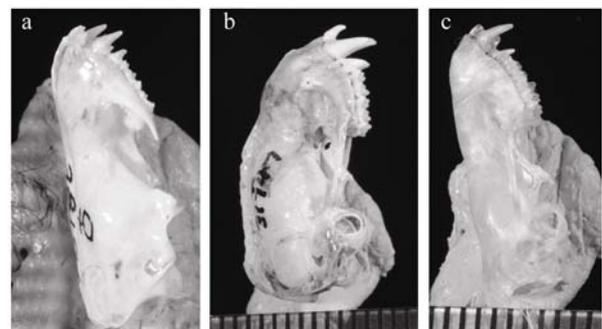
Fig. 7   Flattened skulls (a, c) are compared with a more normal skull (b)
Shown here are side views of the skulls of *Tylonycteris robustula, Promops nasutus* and *Platymops setiger*. Scale units are 1 mm.

in narrow spaces do not have flattened skulls (e.g., *Tomopeas*, 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 bocagei* (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), *Lasiurus borealis* or *Lasiurus cinereus* (Hickey and Fenton, 1990, 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) *Epomphorous* 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 be-

haviour (*Chalinolobus variegatus* - Obrist et al., 1989; *Pteropus samoensis* - Brooke et al., 2000). Some researchers have had better fortune in spotting and observing roosting *Lasiurus 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 *Lasiurus borealis* (a vespertilonid) 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 plancentae and impantation 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 implantaton

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 oestrus 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, Harpiocephalus*). 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 furipterids 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 vestigal 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

and detail about targets.

The hypothesis that echolocation was ancestral in the evolution of bats is suggested by contact between stylohyal and tympanic bones, a characteristic of largyneal echolocators occurring in both suborders. If echolocation and flight are ancestral features of bats that had appeared before the divergence that produced Yinpterochiroptera and Yangochiroptra, then seven of the 12 features I examined are ancestral. If echolocation appeared after this divergence, 10 of 12 features are derived. The development of high duty cycle echolocation in two separate lineages of bats demonstrates the power of selective pressure associated with increased efficiency in prey detection.

References

Alvarez Y, Juste JB, Tabares E, Garrido-Pertierra A, Ibanez C et al., 1999. Molecular phylogeny and morphological homoplasy in fruitbats. Mol. Biol. Evol. 16: 1061−1067.

Badwaik NK Rasweiler JJ IV. 2000. Pregnancy. In: Crichton EG, Krutzsch PH ed. Reproductive Biology of Bats. New York: Academic Press, 221−293

Baker RJ, Porter CA, Patton JC, Van Den Busche RA, 2000. Systematics of bats of the family Phyllostomidae based on *RAG2* DNA sequences. Occ. Pap. Mus. Texas Tech Univ. 202: 1−16.

Barclay RMR, 1989. The effect of reproductive condition on the foraging behavior of female hoary bats *Lasiurus cinereus*. Behav. Ecol. Sociobiol. 24: 31−37.

Barclay RMR, Harder LD, 2003. Life histories of bats: Life in the slow lane. In: Kunz TH, Fenton MB ed: Bat Ecology. Chicago: University of Chicago Press, 209−256

Bartholomew GA, Dawson WR, Lasiewski RC 1970. Thermoregulation and heterothermy in some of the smaller flying foxes (Megachiroptera) of New Guinea. Z. vergl. Physiol. 70: 196−209.

Bayefsky-Anand S, Fenton MB, Skowornski MD, Korine C, Holderied M, 2008. Variations in the echolocation calls of the European free-tailed bat. J. Zool. (Lond.) 275: 175−123.

Bogdanowicz W, Csada RD, Fenton MB, 1997. Noseleaf structure, echolocation and foraging behavior in the Phyllostomidae (Chiroptera). J. Mammal. 78: 942−953.

Brinklav S. Kalko EKV, Surlykke A, 2008. Intense echolocation calls from two 'whispering' bats, *Artibeus jamaicensis* and *Macrophyllum macrophyllum* (Phyllostomidae). J. Exp. Biol. 212: 11−20.

Brooke AP, Solek C, Tualaulelei A, 2000. Roosting behavior of colonial and solitary flying foxes in American Samoa (Chiroptera: Pteropodidae). Biotropoica 32: 338−350.

Brosset A, 1976. Social organization in the African bat *Myotis bocagei*. Z.Tierpyschol. 42: 50−56.

Campbell P, 2008. The relationship between roosting ecology and degree of polygyny in harem-forming bats: Perspectives from *Cynopterus*. J. Mammal, 89: 1351−1360.

Campbell P, Akbar Z, Adnan AM, Kunz TH, 2006. Resource distribution and social structure in harem-forming old world fruit bats: Variations on a polygynous theme. Anim. Behav. 72: 687−698.

Chaverri G, Kunz TH, 2006. Roosting ecology of the tent-roosting bat *Artibeus watsoni* (Chiroptera: Phyllostomidae) in southwestern Costa Rica. Biotropica 38: 77−84.

Crichton EG, Krutzsch PH, 2000. Reproductive Biology of Bats. New York: Academic Press.

Dávalos LM, Jansa SA, 2004. Phylogeny of Lonchophyllini (Chiroptera: Phyllostomidae). J. Mamma   85: 404−413.

Dechmann DKN, Kalko EKV, Kerth G. 2004. Ecology of an exceptional roost: Energetic benefits could explain why the bat *Lophostoma silvicolum* roosts in active termite nests. Evol. Ecol. Res. 6: 1037−1050.

Dechmann DKN, Heucke SL, Giuggioli L, Safi K, Voigt CC et al., 2009. Experimental evidence for group hunting via eavesdropping in echolocating bats. Proc. Roy. Soc. Biol.Sci. 276: 2721−2728.

Dechmann DKN, Santana SE, Dumont ER, 2009. Roost making in bats: Adaptations for excavating active termite nests. J. Mammal. 90: 1461−1468.

Denzinger A, Siemers BM, Shaub A, Schnitzler HU, 2001. Echolocation by the barbastelle bat *Barbastella barbastellus*. J. Comp. Physiol. A187: 521−528.

DesRoches K, Fenton MB, Lancaster WC, 2007. Echolocation and the thoracic skeletons of bats: A comparative morphological study. Acta Chiropter. 9: 483−494.

Dumont ER, O'Neal R, 2004. Food hardness and feeding behavior in old world fruit bats (Pteropodidae). J. Mammal. 85: 8−14.

Fenton MB, 1992. Pelage patterns and crypsis in roosting bats: *Taphozous mauritianus* and *Epomophorus* spp. Koedoe 35: 49−55.

Fenton MB, 1999. Describing the echolocation calls and behavior of bats. Acta Chiropter.1: 127−136.

Fenton MB. 2001. Bats. Revised edition. New York: Facts On File Inc..

Fenton MB, Audet D, Obrist MK, Rydell J, 1995. Signal strength, timing and self-deafening: The evolution of echolocation in bats. Paleobiology 21: 229−242.

Fenton MB, Brigham RM, Mills AM, Rautenbach IL, 1985. The roosting and foraging areas of *Epomophorus wahlbergi* (Pteropodidae) and *Scotophilus viridis* (Vespertilionidae) in Kruger National Park, South Africa. J. Mammal. 66: 461−468.

Fenton MB, Vonhof MJ, Bouchard S, Gill SA, Johnston DS et al., 2000. Roosts used by *Sturnira lilium* (Chiroptera: Phyllostomidae) in Belize. Biotropica, 32: 729−733.

Fenton MB, Bernard E, Bouchard S, Hollis L, Johnston DS et al., 2001. The bat fauna of Lamanai, Belize: Roosts and trophic roles. J. Trop. Ecol.17: 511−524.

Fleming TH, Valiente-Banuet A, 2002. *Columnar cacti* and Their Mutalists. Tucson: University of Arizona Press.

Gillam EH, McCracken GF, 2007. Variability in the echolocation of *Tadarida brasiliensis*: Effects of geography and local acoustic environment. Anim. Behav. 74: 277–286.

Gould E, 1978. Foraging behavior of Malaysian nectar-feeding bats. Biotropica 10: 184–193.

Gould E, 1988. Wing-clapping sounds of *Eonycteris spelaea* (Pteropodidae) in Malaysia. J. Mammal. 69: 378–379.

Griffin DR, 1958. Listening in the Dark. New Haven: Yale University Press.

Griffiths TA, 1978. Modification of *M. cricothyroideus* and the larynx in the Mormoopidae, with reference to amplification of high-frequency pulses. J. Mammal. 59: 724–730.

Hartley DJ, Suthers RA, 1987. The sound emission pattern and the acoustical role of the noseleaf in the echolocating bats *Carollia perspicillata*. J. Acoust. Soc. Am. 82: 1892–1900.

Hayden S, Bekaert M, Crider TA, Mariani S, Murphy WF et al., 2010. Ecological adaptation determines functional olfactory subgenomes. Gen. Res. Doi/10.1101/gr/099416.109.

Hickey MBC, Fenton MB, 1990. Foraging by red bats *Lasiurus borealis*: do intraspecific chases mean territoriality? Can. J. Zool. 68: 2477–2482.

Hickey MBC, Fenton MB, 1996. Behavioural and thermoregulatory responses of female hoary bats *Lasiurus cinereus* Beauvois (Chiroptera: Vespertilionidae) to variations in prey availability. Ecoscience 3: 414–422.

Holderied MW, Korine C, Fenton MB, Parsons S, Robinson S et al., 2005. Echolocation call intensity in the aerial hawking bat *Eptesicus bottae* (Vespertilionidae) studied using stereo videogrammetry. J. Exp. Biol. 208: 1321–1327.

Holland RA, Waters DA, Rayner JMV, 2004. Echolocation signal structure in the megachiropteran bat *Rousettus aegyptiacus* Geoffroy 1810. J. Exp. Biol. 207: 4361–4369.

Hollar LJ, Springer MS, 1997. Old World fruitbat phylogeny: Evidence for convergent evolution and an endemic African clade. PNAS 94: 5716–5721.

Hutcheon JM, Kirsch JAW, 2006. A moveable face: Deconstructing the Microchiroptera and a new classification of extant bats. Acta Chiropter. 8: 1–10.

Jepsen GL, 1966. Early eocene bat from Wyoming. Science 154: 1333–1339.

Jepsen GL, 1970. Bat origins and evolution, In: Wimsatt WA ed. Biology of Bats. Vol 1. New York: Academic Press, 1–64

Jones G, Holderied MW, 2007. Bat echolocation calls: Adaptation and convergent evolution. Proc. Roy. Soc. Biol Sci. B274: 905–912.

Jones G, Teeling EC, 2006. The evolution of echolocation in bats. TREE 21: 149–156.

Jones KE, Bininda-Emonds ORP, Gittleman JL, 2005. Bats, clocks, and rocks: Diversification patterns in Chiroptera. Evolution 59: 2243–2255.

Juste BJ, Ibanez C, MacHordom A, 1997. Evolutionary relationships among the African fruit bats: *Rousettus aegyptiacus, R. angolensis* and *Myonycteris.* J. Mammal. 78: 766–774.

Kalko E KV, Schnitzler HU, 1993. Plasticity in the echolocation sig-

nals of European pipistrelle bats in search flight: Implications for habitat use and prey detection. Behav. Ecol. Sociobiol. 33: 415–428.

Kerth G, Ebert C, Schmidt C, 2006. Group decision making in fission-fusion societies: Evidence from two-field experiments in Bechstein's bats. Proc. Roy. Soc.Biol. Sci. B. 273: 2785–2790.

Kick SA, 1982. Target-detection by the echolocating bat *Eptesicus fuscus*. J. Comp. Physiol. A145: 431–435.

Kingston T, Jones G, Akbar Z, Kunz TH, 2003. Alternation of echolocation calls in five species of aerial-feeding insectivorous bats from Malaysia. J. Mammal. 84: 205–215.

Kingston T, Jones G, Akbar Z, Kunz TH, 1999. Echolocation signal design in Kerivoulinae and Murininae (Chiroptera : Vespertilionidae) from Malaysia. J. Zool. (Lond) 249: 359–374.

Kunz TH, 1988. Ecological and Behavioral Methods for the Study of Bats. Washington: Smithsonian Institution.

Kunz TH, Lumsden LF, 2003. Ecology of cavity and foliage roosting bats. In: Kunz TH, Fenton MB ed. Bat Ecology. Chicago: University of Chicago Press, 1–89

Kunz TH, Fujita MS, Brooke AP, McCracken GF, 1994. Convergence in tent architecture and tent-making behavior among neotropical and paleotropical bats. J. Mammal. Evol. 2:57–78.

Kunz TH, McCracken GF, 1996. Tents and harems: Apparent defence of foliage roosts by tent-making bats. J. Trop. Ecol. 12: 121–137.

Kunz, TH, Parsons S, 2009. Ecological and behavioral methods for the study of bats. 2nd edn. Washington: Smithsonian Institution Press.

Lawrence B., Novick A, 1963. Behavior as a taxonomic clue, relationships of *Lissonycteris* (Chiroptera). Brevoria 184: 1–15.

Lawrence BD, Simmons JA, 1982a. Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. J. Acoust. Soc. Am.71: 585–590.

Lawrence BD, Simmons JA, 1982b. Echolocation in bats: The external ear and perception of the vertical positions of targets. Science 218: 481–483.

Li Y, Liu Z, Shi P, Zhang J, 2010. The hearing gene *Prestin* unites ecolocataing bats and whales. Current Biology R55–R56.

Liu Y, Cotton JA, Shen B, Han X, Rossiter SJ et al., 2010. Convergent sequence evolution between echolocating bats and dolphins. Current Biology R53–R54.

Maltby A, Jones KE, Jones G, 2009. Understanding the evolutionary origin and diversification of bat echolocation calls. In: Brudzynski SM ed. Handbook of Mammalian Vocalization. Oxford: Academic Press, 37–48

Marshall AG, 1971. The ecology of *Basilia hispida* (Diptera: Nycteribiidae) in Malaysia. J. Anim. Ecol. 40: 141–154.

Miller-Butterworth CM, Murphy WJ, O'Brian SJ, Jacobs DS, Springer MS et al., 2006. A family matter: Conclusive resolution of the taxonomic position of the long-fingered bats *Miniopterus.* Mol. Biol. Evol. 24: 1553–1561.

Mora EC, Macias S, 2007. Echolocation calls of Poe's flower bat *Phyllonycteris poeyi* unlike those of other phyllostomids. Naturwissenschaften 94: 380–383.

Moss CF, Bohn K, Glickenson H, Surlykke A, 2006. Active listening for spatial orientation in a complex auditory scene. PLOS Biology

4:e79 doi 10.1371/journal.pbio.0040079

Mueller R, 2004. A numerical study of the role of the tragus in the big brown bat. J. Acoust. Soc. Am. 116: 3701–3712.

Muchhala N, Thomson JD, 2009. Going to great lengths: Selection for long corolla tubes in an extremely specialized bat-flower mutualism. Proc. Roy. Soc. Biol. Sci. B doi:10.1098/rspb.2009.0102

Mueller R, Lu H, Zhang S, Peremans H, 2006. A helical biosonar scanning pattern in the Chinese noctule *Nyctalus plancyi*. J. Acoust. Soc. Amer. 119: 4083–3092.

Nakaya K, Matsumoto R, Suda K, 2008. Feeding strategy of the megamouth shark *Megachasma pelagios* (Lamniformes: Megachasmidae). J. Fish Biol. 73: 17–34.

Nicholls EL, Manabe M, 2004. Giant ichthyosaurs of the Triassic: A new species of *Shonisaurus* from the Pardonet Formation (Norian: Late Triassic) of British Columbia. J. Vert. Palaeont. 24: 838–849.

Nolte MJ, Hockman D, Cretekos CJ, Behringer JH, Rasweiler IV JJ, 2009. Embryonic staging system for the black mastiff bat *Molossus rufus* (Molossidae) correlated with structure-function relationships in the adult. Anat. Rec. 292: 155–168.

Novick A, 1977. Acoustic orientation. In: Wimsatt WA ed. Biology of Bats. Vol. 3. New York: Academic Press, 74–289

Obrist M., Aldridge HDJN, Fenton MB, 1989. Roosting and echolocation behavior of the African bat *Chalinolobus variegatus*. J. Mammal. 70: 828–833.

Padian K, 1983. A functional analysis of flying and walking in pterosaurs. Paleobiology 9: 218–239.

Payne J, Francis CM, Phillipps K, 1985. Mammals of Borneo. Kuala Lumpur: The Sabah Society and WWF, Malaysia.

Pederson SC, 1993a. Cephalometric correlates of echolocation in the Chiroptera. J. Morph. 218: 86–98.

Pederson SC, 1993b. Cephalometric correlates of echolocation in the Chiroptera. II: Fetal development. J. Morph. 225: 107–123.

Pettigrew JD, 2008. Primate-like retinotectal decussation in an echolocating megabat *Rousettus aegyptiacus*. Neuroscience 153: 226–231.

Rasweiler IV JJ, 1990. Implantation, development of the fetal membranes, and placentation in the captive black mastiff bat *Molossus ater*. Am. J. Anat. 187: 109–136.

Rasweiler IV JJ, Badwaik NK, 1997. Delayed development in the short-tailed fruit bat *Carollia perspicillata*. J. Reprod. Fert. 109: 7–20.

Rasweiler IV JJ, Badwaik NK, 2000. Anatomy and physiology of the female reproductive tract. In: Crichton EG, Krutzsch PH ed. Reproductive Biology of Bats. New York: Academic Press, 157–219.

Rhodes M, 2007. Roost fidelity and fission-fusion dynamics of white-striped free-tailed bats *Tadarida australis*. J. Mammal. 88: 1252–1260.

Riskin DK, Fenton MB, 2001. Sticking ability and locomotion in Spix's disk-winged bat *Thyroptera tricolor* (Microchiroptera: Thyropteridae). Can. J. Zool. 79: 2261–2267.

Riskin DK, Racey PA, 2010. How do sucker-footed bats hold on, and why do they roost head-up? Biol. J. Linn. Soc. 99: 233–240.

Schnitzler HU, Kalko EKV, 2001. Echolocation by insect-eating bats. Bioscience 51: 557–569.

Schuller GS, Pollak G, 1979. Disproportionate frequency representa-

tion in the inferior colliculus of Doppler- compensating greater horseshoe bats: evidence of an acoustic fovea. J. Comp. Physiol. A132: 47–54.

Sears KE, Behringer RR, Rasweiler IV JJ, Niswander LA, 2006. Development of bat flight: Morphologic and molecular evolution of bat wing digits. PNAS 103: 6581–6586.

Simmons NB, 1994. The case for chiropteran monophyly. Am. Mus. Novit. 103: 1–54.

Simmons NB, Seymour KL, Habersetzer J, Gunnell GFl, 2008. Primitive early Eocene bat from Wyoming and the evolution of flight and echolocation. Nature 451: 818–821.

Simmons NB, Geisler JH, 1998. Phylogenetic relationships of *Icaronycteris, Archaeonycteris, Hassianycteris*, and *Palaeochiropteryx* to extant bat lineages in Microchiroptera. Bull. Am. Mus. Nat. Hist. 235: 1–182.

Simmons NB, Voss RS, 1998. The mammals of Paracou, French Guiana: A Neotropical lowland rainforest fauna Part 1. Bats. Bull. Am. Mus. Nat. Hist. 237: 1–219.

Smotherman M, Guillen-Servent A, 2008. Doppler-shift compensation behavior by Wagner's mustached bat *Pteronotus personatus*. J. Acoust. Soc. Am. 123: 4331–4339.

Speakman JR, Racey PA, 1991. No cost of echolocation for bats in flight. Nature 350: 421–423.

Surlykke A, Pedersen SB, Jakobsen L, 2009. Echolocating bats emit a highly directional sonar sound beam in the field. Proc. Roy. Soc. Bio. Sci. B276: 852–860.

Surlykke A, Kalko EKF, 2008. Echolocating bats cry out loud to detect their prey. PLOS ONE 3: 2036.

Surlykke A. Ghose, K, Moss CF, 2009. Scanning of natural scenes by echolocation in the big brown bat *Eptesicus fuscus*. J. Exp. Biol. 212: 1011–1020.

Taylor PJ, 2000. Bats of Southern Africa. Pietermaritzburg: University of Natal Press.

Teeling EC, 2009. Hear, hear: the convergent evolution of echolocation in bats? TREE 24: 351–354.

Thomas JA, Moss CF, Vater M, 2004. Echolocation in Bats and Dolphins. Chicago: University of Chicago Press.

Ulanovsky N, Fenton MB, Tsoar A, Korine C, 2004. Dynamics of jamming avoidance in echolocating bats. Proc. Roy. Soc. Biol. Sci. B 271: 1467–475.

Vaughan TA, 1970a. The skeletal system. In: Biology of Bats. Vol 1. Wimsatt WA ed. New York: Academic Press, 98–139.

Vaughan TA, 1979b. The muscular system. In: Wimsatt WA ed. Biology of Bats. Vol 1. New York: Academic Press, 140–194,

Veselka N, McErlain DD, Holdsworth DW, Eger JL, Chhem R et al., 2010. A bony connection signals laryngeal echolocation in bats. 463: 939–942.

Veilleux J, Whitaker Jr JO, Veilleux SL, 2003. Tree-roosting of reproductive eastern pipistrelles *Pipistrellus subflavus* in Indiana. J. Mammal. 84: 1068–1075.

Von Helversen D, Von Helversen D, 1999. Acoustic guide in bat-pollinated flower. Nature 398: 759–760.

Weatherbee SD, Behringer RR, Rasweiler IV JJ, Niswander LA, 2006. Interdigital webbing retention in bat wings illustrates genetic changes underlying amniote limb diversification. PNAS 103:

15103–15107.

Wetterer AL, Rockman MV, Simmons NB, 2000. Phylogeny of phyllostomid bats (Mammalia: Chiroptera): Data from diverse morphological systems, sex chromosomes and restriction sites. Bull. Am. Mus. Nat. Hist. 248: 1–200.

Wetterer AL, Simmons NB, Gunnell GF, Submitted. Yangochiroptera. In: de Queiroz K, Gauthier J, Cantino P ed. The Phylocode Companion Volume. Berkeley: University of California Press.

Wetterer AL, Simmons NB, Gunnell GF, Submitted. Yinpterochiroptera. In: de Queiroz K, Gauthier J, Cantino P ed. The Phylocode Companion Volume. Berkeley: University of California Press.

Wilkinson GS, 1985. The social organization of the common vampire bat. 1. Pattern and cause of association. Behav. Ecol. Sociobiol.17:

111–121.

Willis CKR, Brigham RM. 2004. Roost switching, roost sharing and social cohesion: Forest-dwelling big brown bats *Eptesicus fuscus* conform to the fission-fusion model. Anim. Behav. 68: 495–505.

Willis CKR, Brigham RM, Geiser F, 2006. Deep, prolonged torpor by pregnant, free-ranging bats. Naturwissenschaften 93: 80–83.

York HA, Foster PF, Jones MF, Schwarz WH, Vezeau AL et al., 2008. Observations of cavity-roosting behavior in Costa Rican *Lophostoma brasiliense* (Chiroptera: Phyllostomidae. Mammal. Biol. 73: 230–232.

Zhuang Q, Mueller R, 2006. Noseleaf furrows in a horseshoe bat act as resonance cavities shaping the biosonar beam. Phys. Rev. Lett. 97: 218701–218704.