

# The evolution of echolocation in bats

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**Recent molecular phylogenies have changed our perspective on the evolution of echolocation in bats. These phylogenies suggest that certain bats with sophisticated echolocation (e.g. horseshoe bats) share a common ancestry with non-echolocating bats (e.g. Old World fruit bats). One interpretation of these trees presumes that laryngeal echolocation (calls produced in the larynx) probably evolved in the ancestor of all extant bats. Echolocation might have subsequently been lost in Old World fruit bats, only to evolve secondarily (by tongue clicking) in this family. Remarkable acoustic features such as Doppler shift compensation, whispering echolocation and nasal emission of sound each show multiple convergent origins in bats. The extensive adaptive radiation in echolocation call design is shaped largely by ecology, showing how perceptual challenges imposed by the environment can often override phylogenetic constraints.**

## Echolocation and the diversity of bats

Bats are perhaps the most unusual and specialized of all mammals. Together with birds, they are the only extant vertebrates that are capable of powered flight. Bats have mastered the night skies largely by using echolocation (biosonar) to perceive their surroundings [1,2]. Indeed flight and echolocation are largely responsible for the global success, species richness and the ability of bats to exploit diverse niches (see Online Supplementary Material). How, when and why did bats evolve these extraordinary capabilities? Here we review new phylogenetic studies that challenge our traditional view of the evolution of echolocation, and also relate variation in echolocation call design to phylogeny to explore adaptive radiation and convergent evolution in this exceptional sensory mechanism.

## The position of bats in the mammalian phylogenetic tree

Questions concerning the evolutionary origin of bats have long intrigued biologists and resulted in many phylogenetic studies, the results of which have caused heated and lengthy debates [3–6]. The position of bats within Mammalia and the monophyly of the order itself were questions that dominated the 1980s and 1990s. Currently, there is overwhelming molecular and morphological evidence to support the monophyly of bats and, thus, a single origin of flight in mammals [7–10]. Recent molecular data from large nuclear datasets [11–13], rare genomic events [14] and complete

mitochondrial genomes [15] convincingly group bats within the superordinal group Laurasiatheria (alongside mammals such as carnivores, whales, moles, horses and anteaters), and do not support a sistergroup relationship between bats and flying lemurs as was previously believed [16,17]. Molecular approaches also give a different perspective on the phylogenetic affinities among the bat families that differ radically from relationships derived by traditional morphological comparisons (Box 1).

## Morphological consensus

Before the dawn of molecular studies, bat systematics was dominated by palaeontological and morphological data. The most prominent morphological tree in the literature during the 1970s and 1980s was derived from the classification system of Miller [18] and was proposed by Smith [19] and Van Valen [20]. This tree was later modified by Koopman [21] and has been supported mainly by both large morphological datasets [17,22] and super-tree consensus studies [23]. The first major division in this tree splits bats into two suborders. All bats that produce echolocation calls in their larynx were placed into the suborder Microchiroptera, and all bats that do not were placed into the suborder Megachiroptera. This seemed a natural subdivision and suggested that echolocation had a single origin in bats. The next major division split the microbats into two infraorders, Yinochiroptera and Yangochiroptera [21]. All bats in Yinochiroptera had either moveable or missing premaxillaries (the bones at the front of the upper jaw bearing the incisor teeth). In all other bats, and indeed in all other mammals, these structures are fused [21]. All these subdivisions deviate from new, strongly supported molecular trees [6,10,24–27] that indicate an association of the rhinolophoid microbats (rhinolophids, hipposiderids, craseonycterids, rhinopomatids and megadermatids) with the megabats, rendering microbats paraphyletic and grouping the remaining two yinochiropteran families (nycterids and emballonurids) within the Yangochiroptera (phyllostomids, mormoopids, noctilionids, furipterids, thyropterids, mystacinids, myzopodids, vespertilionids, molossids and natalids; Box 1).

## Emerging molecular consensus

The major structure of the bat phylogenetic tree based on molecular data (i.e. microbat paraphyly) was apparent with the first molecular phylogenetic studies. Based on transferrin immunological distance data, microbats were found to be paraphyletic; however, this result was initially reported as an artifact because it was so unexpected (E.D. Pierson, PhD dissertation, University of California,

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### Box 1. Bat phylogenetics: past and present

The emerging molecular tree of extant bat families (Figure 1a) unites the pteropodids (which do not echolocate, except by tongue clicking in one genus) with the echolocating superfamily Rhinolophoidea (e.g. horseshoe bats) in the clade Yinpterochiroptera. All other (echolocating) bats are united together into the clade Yangochiroptera. Coloured boxes, branches and names represent the superfamilial groupings of [6]. The position for the newly proposed family *Miniopteridae* is taken from [27] and is indicated by an asterisk. All associations that were not strongly supported by at least one independent molecular study are indicated by hatched lines. Molecular data have also uncovered novel interfamilial relationships. The endemic New Zealand short-tailed bat *Mystacina tuberculata* is related unequivocally to noctilionoid Neotropical bats [6,26,27,68], a finding that has recently been supported by a new morphological dataset, albeit with low bootstrap support [22]. Emballonurids and nycterids, originally included within Yinochiroptera, are sister taxa [6,27]. Vespertilionids, molossids and natalids all share a unique common ancestry [6,27,68] and the Neotropical noctilionids, furipterids and thyropterids also form a clade [6,26,68]. Teeling *et al.* [6] found high

bootstrap support for a sistergroup relationship between craseonycterids and megadermatids, and they also united the monotypic Malagasy myzopodids with mystacinids and Neotropical noctilionids. Mitochondrial datasets [26] and a nuclear intron dataset [27] indicate moderate support for a relationship between myzopodids and vespertilionoids; however, alternative positions for myzopodids could not be rejected [27]. Concatenations of nuclear intron sequence data [27], mitochondrial rRNAs [26] and a nuclear-mitochondrial concatenation [69] suggest that the genus *Miniopterus* should be elevated to familial status from its current position in Vespertilionidae; however, these datasets disagree on its exact phylogenetic position.

The prevailing morphological tree (Figure 1b; reproduced with permission from [22]) unites all echolocating bats in the suborder Microchiroptera. This suborder is subsequently divided into Yinochiroptera and Yangochiroptera based on whether or not the premaxillaries are either moveable or missing in relation to the maxillaries. Hatched lines indicate where the tree differs from that of a competing morphological estimate [21]. Reproduced with permission from [6] (a) and [22] (b).

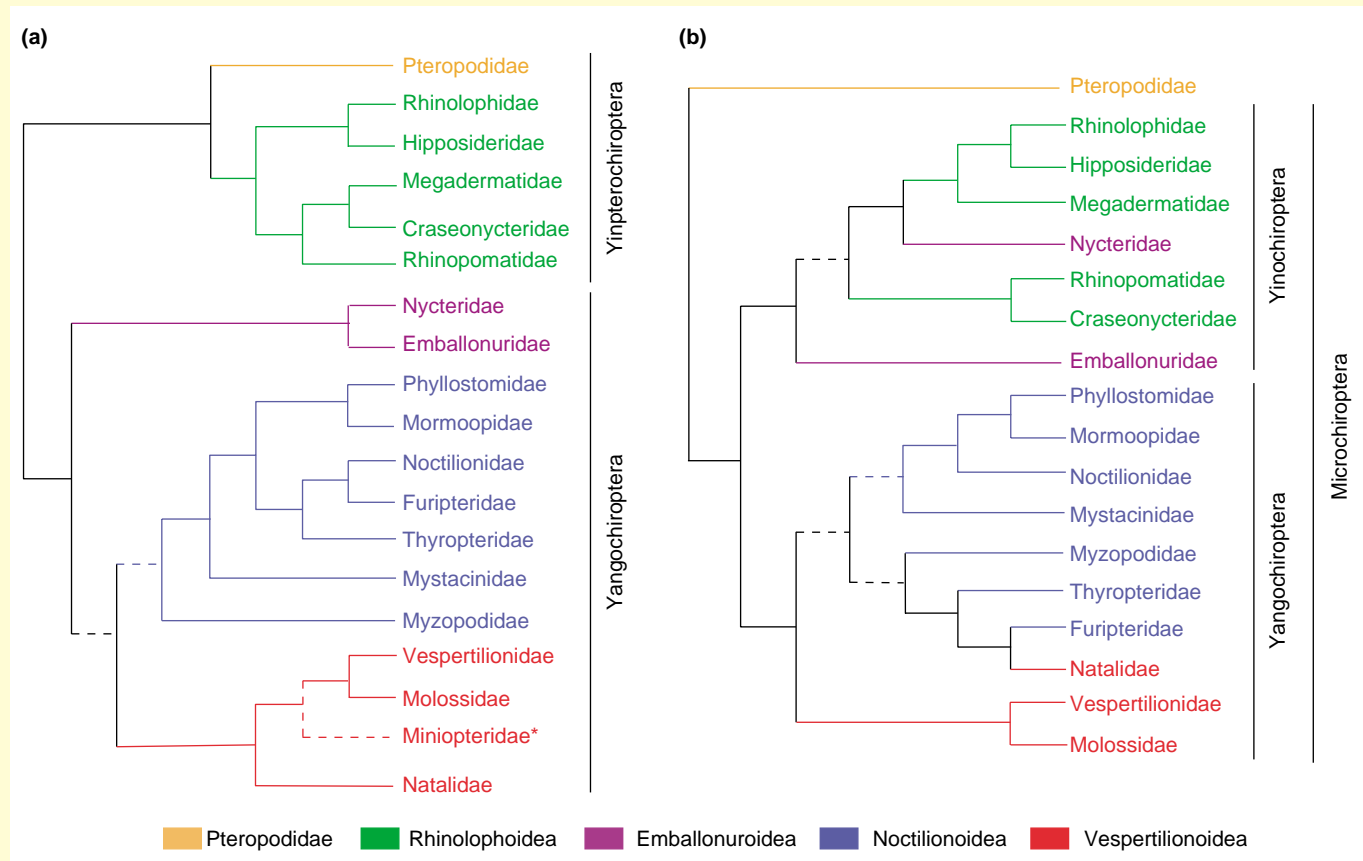


Figure 1.

Berkeley, 1986). Whole genome DNA–DNA hybridization studies also supported the association of rhinolophoid microbats with megabats [28], although the authors again first interpreted their findings as reflecting base composition biases in the genomes of megabats and rhinolophoids [29]. Repetitive elements found in all microbats but not in rhinolophoids also indicated that the suborder was not monophyletic [30]. During the 1990s, although molecular datasets consisting of either a single gene [9,31] or limited total-evidence studies [32] supported microbat paraphyly, these limited datasets suffered from poor taxonomic representation and low bootstrap support.

Solid support for the association of rhinolophoid microbats with megabats and for the inclusion of emballonurids and nycterids within Yangochiroptera was achieved only with the onset of larger molecular datasets that concatenated DNA sequences from numerous nuclear and mitochondrial genes [10,13,24] and included representatives of all recognized bat families [6,27] (although Craseonycteridae was missing from [27]). Support for the main structure of the molecular tree also derives from recent mitochondrial-only datasets [26,33] and rare genomic events [6,25,34] (see Online Supplementary Material). The emerging molecular phylogenies

### Box 2. Did echolocation evolve more than once in bats?

Some fossil bats are sufficiently well preserved that morphological characters associated with echolocation are evident. These include a stylohyal bone expanded cranially at the tip, a large orbicular process on the malleus, and a moderately enlarged cochlea [17]. To determine whether echolocation evolved once in bats and was subsequently lost in pteropodids, the phylogenetic position of extinct bats in relation to extant pteropodids and echolocating taxa needs resolving. Reanalysis of a morphological dataset [17] that includes characters from extinct fossil taxa using the molecular tree as a constraint [6,24] shows that Eocene fossil bats comprise a paraphyletic group at the base of the Chiroptera, with the fossil species *Icaronycteris index* (at least 53 million years old) basal to all bats. Because *I. index* shows morphological features that are similar to those seen in extant echolocating bats, the hypothesis that laryngeal echolocation evolved once in bats and was subsequently lost in pteropodids receives strong support. Laryngeal echolocation might have evolved between ~85 Mya and 65 Mya [70].

Echolocation later re-evolved secondarily in a modified form in some pteropodids. The unique tongue-clicking echolocation used by bats in the genus *Rousettus* is probably not an intermediate stage in

the loss of laryngeal echolocation because *Rousettus* is not basal in the pteropodid radiation [24]. The large eyes of extant pteropodids do not reflect an ancestral state and visual prowess in this group probably evolved after the degeneration of echolocation [24]. Broadband, multiharmonic calls used in communication by extant pteropodids might be legacies of signals used by their ancestors for echolocation [24]. Pteropodids also have a moderately enlarged cochlea, which overlaps in size with those of echolocating bats, perhaps representing another relic from their echolocating past [24].

Eick *et al.* [27], however, argue that echolocation arose independently in rhinolophoids (rhinolophids, hipposiderids and megadermatids) and in all other echolocating bats 'as all rhinolophoids have an ossified first costal cartilage fused to the manubrium and first rib'. This character is not found in any other bats and might be an adaptation to reduce the cost of echolocation when stationary. However, the argument that echolocation evolved independently in rhinolophoid bats is based on just one character that might represent a specialization unique to echolocation in this group. At present, the argument for a single origin of laryngeal echolocation seems more convincing.

support a deep divergence between Pteropodidae, Rhinolophidae, Hipposideridae, Megadermatidae, Craseonycteridae and Rhinopomatidae (all now placed in the putative suborder Yinpterochiroptera [6,24,25]) and the remaining 12 families of bats that are placed in the redefined suborder Yangochiroptera [6,24,25] (Box 1).

What do these new molecular trees mean for the evolution of echolocation? The competing hypotheses and their supporting evidence are outlined in Box 2. The new phylogenies also illustrate some remarkable examples of adaptive radiation and convergent evolution in signal design, both of which are explored next.

### Adaptive radiation and convergent evolution of echolocation calls in extant bats

One recent attempt to categorize bat echolocation calls considered three major types of echolocation call: broadband, narrowband and long constant frequency (CF) with Doppler-shift compensation (DSC) [35]. Other than differing in the pattern of frequency structure over time, bat signals also vary in their intensity and harmonic composition. Sophisticated methods for reconstructing bat flight tracks in three-dimensions [36,37] have enabled the accurate localization of flying bats in relation to measuring microphones, thereby permitting accurate measurements of echolocation call intensities to be made. Typically, bats emitting calls with intensities <75 dB Sound Pressure Level (SPL) at a distance of 10 cm from the mouth of the bat are considered 'low-intensity' echolocators, whereas species calling at intensities >90 dB are held to emit 'high-intensity' calls [38]. Recent measurements of call intensities in some aerial-feeding bats give intensities of >135 dB at 10 cm, making them some of the most intense airborne vocalizations recorded in nature [36,37].



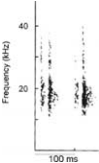

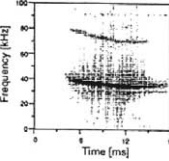

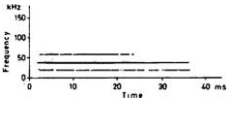

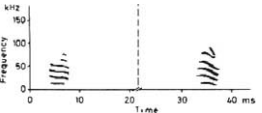

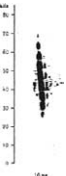

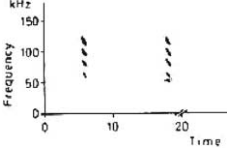

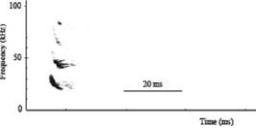

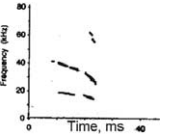

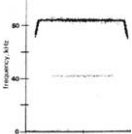

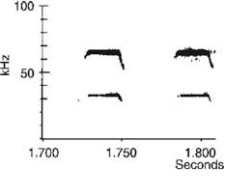
Bat calls, like most sounds, have complex frequency spectra that often comprise a harmonic series. Therefore, the signal consists of components (harmonics) where the frequencies are integer multiples of the lowest, or fundamental, harmonic. Some bats (e.g. many species

in the Vespertilionidae; Table 1) emit signals with strong fundamental harmonics, such that, although higher harmonics are present, their intensity is low compared with that of the fundamental. Many bats emit multiharmonic signals, with the fundamental harmonic not always being the dominant one. For example, bats in Rhinolophidae and Hipposideridae emit calls that are typically dominated by the second harmonic (Table 1). Many gleaning bats (i.e. species that capture prey from surfaces) emit brief broadband calls that contain several strong harmonics, although echolocation can also be switched off when prey echoes are masked by background echoes (i.e. clutter), at which point the bats localize prey by listening for prey-generated sounds [39].

To better understand the adaptive radiation of call design, we will briefly describe eight categories of echolocation calls produced by bats (Table 1). We then relate call design to the emerging molecular phylogeny, and highlight some examples of adaptive radiation and convergent evolution in signal design. Our classification is based on the signals that are emitted when bats are searching for prey in the field (or, in the case of the Old World fruit bat *Rousettus*, flying in caves). We emphasize that the calls described are used to highlight examples of adaptive radiation and convergence in signal design among species in different families; the calls are not representative of all species in any given family. Bats emit calls that vary in design according to habitat [35,40]. Many calls become shorter in duration and emphasize broadband components in clutter, and these changes should be appreciated when considering the calls illustrated in Table 1.

(a) *No echolocation.* Most of the Old World fruit bats (Pteropodidae) do not use echolocation for orientation; this could either reflect the ancestral state within bats or represent a secondary loss of echolocation within pteropodids (Box 2). Most pteropodids have effective vision for orientation at night and have a reflective tapetum lucidum to enhance visual sensitivity at low light levels [41]. Being frugivorous and nectarivorous, pteropodids do not need

**Table 1. The diversity of echolocation calls in bats<sup>a</sup>**

Echolocation call type	Bat species (family)	Spectrogram		Bat species (family)	Spectrogram		Refs
		Yinpterochiroptera			Yangochiroptera		
(a) No echolocation	 <i>Cynopterus brachyotis</i> (Pteropodidae)						
(b) Brief, broadband tongue clicks	 <i>Rousettus aegyptiacus</i> (Pteropodidae)						[43]
(c) Narrowband, dominated by fundamental harmonic				 <i>Lasiurus borealis</i> (Vespertilionidae)			[71]
(d) Narrowband, multiharmonic	 <i>Rhinopoma hardwickii</i> (Rhinopomatidae) <sup>b</sup>			 <i>Taphozous melanopogon</i> (Emballonuridae)			[46]
(e) Short, broadband, dominated by fundamental harmonic				 <i>Myotis daubentonii</i> (Vespertilionidae)			[72]
(f) Short, broadband, multiharmonic	 <i>Megaderma lyra</i> (Megadermatidae)			 <i>Mystacina tuberculata</i> (Mystacinidae)			[46,53]
(g) Long, broadband, multiharmonic				 <i>Myzopoda aurita</i> (Myzopodidae)			[56]
(h) Constant frequency	 <i>Rhinolophus ferrumequinum</i> (Rhinolophidae)			 <i>Pteronotus parnellii</i> (Mormoopidae)			[55,73]

<sup>a</sup>Bats are divided into the suborders Yinpterochiroptera and Yangochiroptera as supported by the emerging molecular consensus. As well as illustrating the adaptive radiation of call types within these clades, examples of convergence can be seen for narrowband, multiharmonic; short, broadband, multiharmonic; and constant frequency signals, with bats in both suborders producing these calls. All photos by G. Jones, except *Myzopoda aurita* by J. Russ, *Pteronotus parnellii* by M.B. Fenton.

<sup>b</sup>Although the calls of *Rhinopoma hardwickii* can contain reverberations, they are still narrowband and multiharmonic.

to use high-frequency echolocation calls to detect small targets such as insects. Neural constraints might preclude the simultaneous evolution of advanced visual and auditory processing [42], forcing bats to strengthen one sense at the expense of another.

(b) *Brief, broadband tongue clicks* (typically <1 ms, 12–70 kHz). Cave-dwelling pteropodids in the genus *Rousettus* produce clicks in pairs (one from each lip) by raising the tongue from the floor of the mouth. This mechanism of sound production is radically different from that used by all other bats, which produce tonal echolocation signals in the larynx. As far as is known, clicks are used for echolocation by all other animals (toothed whales, swiftlets, oilbirds and insectivores) [1,2]. Because clicks are likely to have evolved secondarily in *Rousettus* (see Box 2), it cannot be convincingly argued that they reflect an ancestral condition for bats.

Traditionally, click-like signals have been viewed as offering poor orientation performance and as being somewhat rudimentary. However, the Egyptian rousette bat *Rousettus aegyptiacus* performs as well in obstacle negotiation tasks as some bats emitting tonal signals. Recent evidence [43] suggests that clicks minimize bandwidth at very short durations and hence focus energy into the frequencies at which bats hear best. The signals used by *Rousettus* might be more sophisticated than was previously believed. Similar to horseshoe bats, *Rousettus* moves its ears while echolocating in flight, although probably to improve the directional sensitivity of hearing rather than to assist in localizing targets in the vertical plain as occurs in horseshoe bats [44].

(c) *Narrowband signals dominated by the fundamental harmonic*. These calls are seen in many open-space bats in Vespertilionidae and Molossidae, and in the newly proposed family Miniopteridae. They might have arisen once in the ancestor of this clade. Narrowband calls show limited frequency modulation and relatively long (often >5 ms) durations. These signals are typically emitted by bats flying in open spaces and are suited for detecting targets, such as insects, flying in such spaces [35]. The signals are long because the target objects are distant, and echoes return after the bat finishes calling so that the outgoing pulse does not overlap with the returning echo [35].

(d) *Narrowband multiharmonic signals*. Some bats emit signals where the dominant harmonic is narrowband, but several other strong harmonics are also produced. Each harmonic component is narrowband in such calls. Narrowband multiharmonic signals are emitted by open-space bats and are usually dominated by harmonics other than the fundamental. Such calls are produced in Yinpterochiroptera by bats in Craseonycteridae [45] and Rhinopomatidae [46], and in Yangochiroptera by bats in Emballonuridae [46], Mormoopidae [47] and Thyropteridae [48]. Narrowband multiharmonic signals probably evolved several times independently given their occurrence in several families in both Yinpterochiroptera and Yangochiroptera.

(e) *Short, broadband calls with a dominant fundamental harmonic*. These calls are emitted by bats in the family Vespertilionidae, including species in the genus

*Myotis* [49]. Their use when searching for prey appears to be restricted to bats within this family. Many species that use narrowband signals for detection switch to emitting broadband calls to localize targets. Broadband calls cover a wide range of frequencies over a short time interval (typically <5 ms). They are often emitted by bats flying in cluttered situations and are usually brief so that the bat avoids overlap of echoes returning from nearby objects while still emitting the pulse [35]. Broadband calls are well adapted for localizing targets in three-dimensions, an important aspect of echolocation performance when flying in clutter [35].

(f) *Short, broadband multiharmonic signals*. Bats in a range of families emit these signals. Harmonics potentially improve ranging and discriminative performance [50]. The harmonic containing the frequency of most energy in the call varies among species. Brief multiharmonic signals probably evolved several times independently in bats, with examples being found in both Yinpterochiroptera (Megadermatidae [51]) and Yangochiroptera (Nycteridae [52]; Phyllostomidae [47]; Mystacinidae [53]; Vespertilionidae [54], and Natalidae [55]).

(g) *Long duration broadband calls*. As far as is known, only the monotypic Malagasy sucker-footed bat *Myzopoda aurita* (Myzopodidae) produces signals such as these [56]. The calls are long (up to 23 ms) and multiharmonic, with the most energy being in the second harmonic.

(h) *Pure constant frequency signals* (i.e. pure tones with no bandwidth). These calls are emitted by bats in Rhinolophidae, Hipposideridae, Mormoopidae (only Parnell's moustached bat *Pteronotus parnellii*) and Noctilionidae. CF components are usually terminated with a broadband sweep, which enhances localization performance [35]. CF signals can be relatively long in duration (>30 ms) as used by the horseshoe bats (Rhinolophidae) and *P. parnellii*. Long duration CF signals not only give high performance in target detection, but also enable the classification of targets [35]. For example, bats emitting long CF signals can distinguish small insects from larger ones because the smaller insects beat their wings at a higher rate and thereby introduce more 'acoustic glints' (i.e. small modulations in amplitude and frequency) in the returning long echoes [57]. Long CF signals are often used by bats searching for moving targets in cluttered habitats and are associated with DSC, whereby the bats lower the frequency of the emitted call more the faster they fly to compensate for Doppler shifts induced by their own flight speed [58]. As such, the CF portion of the echo always returns to the bat at a frequency close to that emitted when resting, which happens to be the frequency at which the animal hears best, the 'acoustic fovea' [59]. Bats in Hipposideridae emit relatively short CF signals (often <10 ms) and only show partial DSC [60].

DSC means that the emitted call and the returning echo are at different frequencies. The bats can thus separate pulse and echo in frequency (rather than the time), and can use long-duration calls when flying close to obstacles. Bats in Rhinolophidae, Hipposideridae and *P. parnellii* emit long calls with relatively short gaps between calls and, hence, operate at high-duty cycles (filling much of the echolocating time with sound); their

echolocation is arguably different from that of the noctilionids, which echolocate at lower-duty cycles and do not emit CF signals in an obligate manner [61].

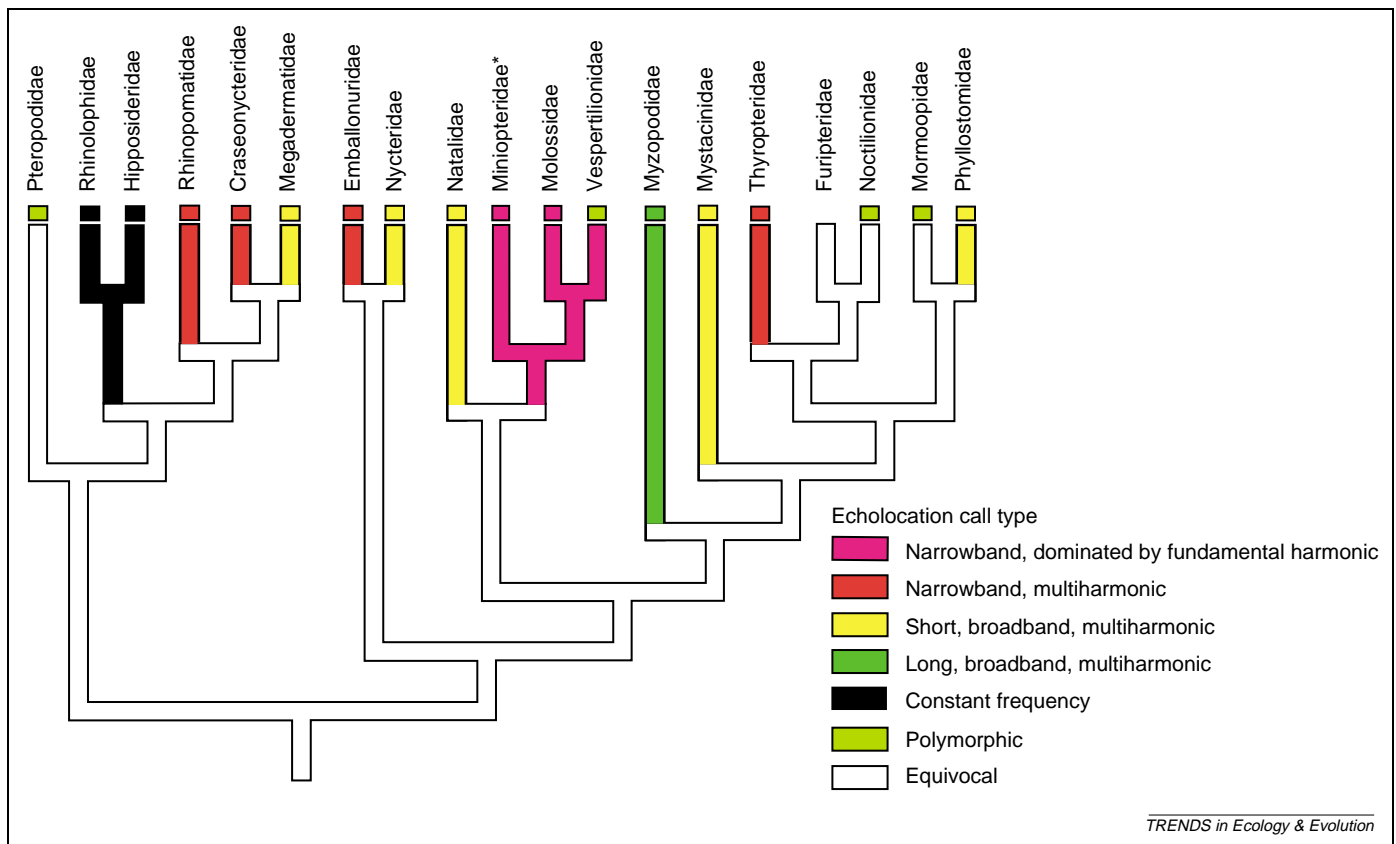
Pure constant frequency signals with DSC are arguably the most sophisticated echolocation signals used by any animal, and it is remarkable that such signals and processing mechanisms evolved independently within Yinpterochiroptera (Rhinolophidae) and Yangochiroptera (*P. parnellii*, Mormoopidae). Interestingly, whereas rhinolophid and hipposiderid bats emit long constant frequency signals through their nostrils, *P. parnellii* is an oral emitter. Both sets of bats show remarkable convergence in their auditory physiology, including expanded frequency representation in the cochlear basilar membrane and narrow tuning of peripheral or central nuclei in the auditory pathways. However, substantial differences in cochlear responses suggest that the functional mechanisms responsible for the acoustic fovea differ in horseshoe bats and *P. parnellii* [62]. Major differences also occur in the organization of the auditory cortex in these two specialized echolocators [63].

### Mapping call structure onto phylogeny highlights the presence of convergence

Attempts to map echolocation call structure onto phylogeny can be informative and have shown, for example, that the single clicks used by cave swiftlets have evolved from double clicks at least twice [64]. However, the large

variation in call diversity within and between bat families renders the evolutionary reconstruction of signal types unclear (Figure 1). Overall, our perspective on the evolution of echolocation is clouded by the diversity and plasticity of signals that we see in extant bats, suggesting that the animal's habitat is often more important in shaping its call design than is its evolutionary history.

The Vespertilionidae is the largest family of bats (> 300 species), with bats in this family tending to use echolocation signals that are dominated by the fundamental harmonic. However, the most frequently recorded echolocation signals documented in extant bats are not necessarily ancestral for that group. When we view the diversity of echolocation signals at the family level, it is evident that multiharmonic signals are both widespread and present in some of the more basal families in the bat phylogeny. Indeed, the 'cleaner' signals dominated by the fundamental harmonic as used by bats in Vespertilionidae and Molossidae might be recent evolutionary innovations. Although bats in these families can also produce multiharmonic calls facultatively (e.g. during the late stages of prey capture), bats that use multiharmonic signals when searching for prey seem unable to produce more filtered calls, lending support to the argument that calls dominated by the fundamental harmonic are derived. Schnitzler *et al.* [65] argued that the first echolocating bats produced signals that were tonal, low-intensity, short, multiharmonic and broadband. Low-intensity



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**Figure 1.** Ancestral reconstructions of the eight categories of echolocation call types mapped onto the molecular tree using methods described in [6] using the family-level echolocation character states identified and classified in Table 1. The phylogenetic position for Miniopertidae is taken from [27] and is indicated by an asterisk. The large variation in call diversity and signal design among bat families makes it impossible to define any ancestral echolocation call type in bats. The ancestor of vespertilionids, molossids and miniopertids might have used a call dominated by the fundamental harmonic. All other call types show signs of convergent evolution across the entire tree.

(‘whispering’) echolocation is present in at least six lineages of extant bats, although Eick *et al.* [27] proposed that high intensity signals were in fact ancestral [27].

Nasal emission has also arisen independently in nycterids and phyllostomids within Yangochiroptera. A further independent evolution of nasal emission occurred in Vespertilionidae, with Rafinesque’s big-eared bat *Corynorhinus rafinesquii* emitting similar signals (although of lower intensity) when its mouth was covered compared with when the covering was removed [1]. Nasal echolocation enables bats to call and chew at the same time, an adaptation that might be especially important when eating large prey items such as moths.

The new phylogenies also enable a better understanding of how DSC echolocation evolved. Several bat species in Yinpterochiroptera emit long narrowband multiharmonic signals (e.g. *Craseonycteris* [45] and *Rhinopoma* [46,66]). *Rhinopoma* also has a prominent sensitivity peak in its audiogram that is tuned to the frequency of the dominant second harmonic [66]. Although it is unable to use DSC [66], it has been argued that *Rhinopoma* is in the process of evolving an acoustic fovea [62], and might therefore retain features that were found in ancestral horseshoe bats.

### Conclusions and future directions

It is important that echolocation calls are recorded from some little studied species (e.g. those in Furipteridae, Thyropteridae and Natalidae) to complete our understanding of call diversity in bats. Recording the low-intensity echolocation calls produced by many of these bats in nature remains a challenge. Field studies are essential because familiarity with surroundings might influence how the bat uses echolocation under laboratory conditions [67]. Clearly, many of the diverse echolocation call designs used by extant bats evolved independently on several occasions. Echolocation, similar to morphology, is a flexible character that is often shaped more by ecological demands than by phylogeny. Although echolocation provides some remarkable examples of convergent evolution within bats, this same convergence makes reconstruction of ancestral call types problematic. Using coarser subdivisions of call types and/or multiple characters with fewer character states per character helps to resolve the evolutionary histories of specific features of echolocation, such as nasal emission of calls [27]. We need further evidence to determine whether laryngeal echolocation evolved once or at least twice in bats; detailed comparative genomic studies that investigate the molecular mechanisms of audition could facilitate this. The discovery of additional fossil bats together with careful examination of their morphology might help calibrate divergence times of taxa better and assist in studies that incorporate molecular scaffolds. The new phylogenies enable examination of call type in an evolutionary framework that has hitherto been misleading because previous relationships were based partly on convergent morphological characters that had little phylogenetic signal.

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### Supplementary data

Supplementary data associated with this article can be found at doi:10.1016/j.tree.2006.01.001

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