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Evolutionary neuroscience

Ear anatomy traces a family tree for bats

M. Brock Fenton

How should the bat family tree be arranged? Analysis of bats' inner ear anatomy supports a previously proposed arrangement that was based on DNA analysis. The findings also shed light on the evolution of echolocation. **See p.449**

Echolocating animals, including most species of bat and echolocators such as dolphins, obtain information about their surroundings from the differences between outgoing signals that they emit and the echoes returning to them. Some blind people orient by echolocation using tongue clicks. Signals emitted by animals for echolocation can be used for orientation and communication, and the ability to echolocate allows animals to operate in the dark or under conditions of unpredictable lighting. Echolocation also provides evidence of bats' evolutionary history, as portrayed by their family tree. On page 449, Sulser *et al.*[1] present neuroanatomical evidence from an examination of canals in bats' inner ears. The data aid our understanding of bat evolution and the importance of echolocation.

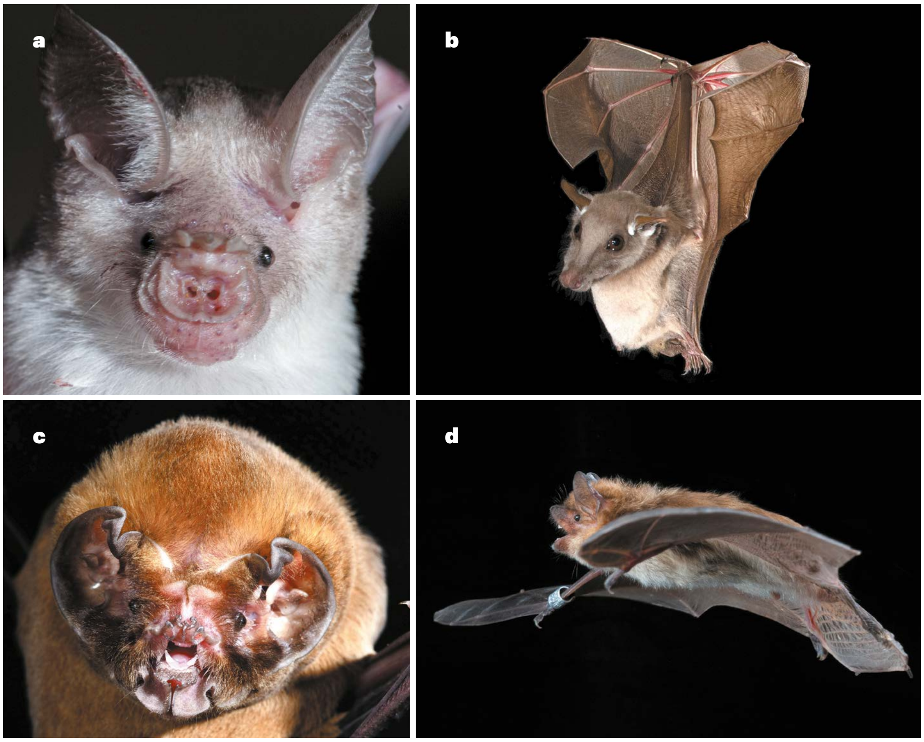
The options for bat classification and our understanding of the evolutionary relationships between them have changed greatly since 2000. Bats were previously classified into one of two suborders. Megachiroptera included the comparatively large species, mostly non-echolocating fruit bats of the Old World (Africa, Europe and Asia). All other bats are echolocators, and were placed in the suborder Microchiroptera. But a study[2] published in 2000 used DNA evidence to challenge this arrangement, and assembled families into two other suborders – Yinpterochiroptera and Yangochiroptera (Fig. 1).

Yinpterochiroptera (410 species belonging to 7 families) occur only in the Old World. This group includes Old World fruit bats (family Pteropodidae), which are mainly non-echolocating fruit bats, as well as six families of echolocating insectivores. Yangochiroptera (938 species belonging to 14 families) are echolocators, and occur anywhere there are bats[3]. These two groupings are not based on whether there is echolocation. Sulser and colleagues present anatomical evidence obtained from 39 species (19 of 21 families of living bats). The authors' findings support the Yinpterochiroptera and Yangochiroptera classification.

Sulser *et al.* describe previously unknown neuroanatomical features of Rosenthal's canals, structures in bat inner ears that are associated with hearing. Specifically, the authors report that Rosenthal's canals are thick-walled in Yinpterochiroptera and wall-less in Yangochiroptera. Thick-walled Rosenthal's canals are typical of most 'modern' mammals (eutherians, such as humans and elephants). Wall-less canals are known only from Yangochiroptera.

The wall-less condition accommodates more neuronal structures (a larger spiral ganglion and a higher innervation density of nerve cells) compared with the walled version. These wall-less features might coincide with a higher capacity for echolocation, such as better resolution of target details. Variations in these features among species suggest interspecific variation in the capacity for echolocation. The findings will give those who study echolocation new ideas to test in bats. Such work could demonstrate specific consequences of having a larger spiral ganglion and a higher innervation density of nerve cells.

The first known complete fossils of bats[4] are from the early Eocene (approximately



SHERRI & BROCK FENTON

Figure 1 | Bat classification. A version of the bat family tree proposed[2] in 2000 used DNA analysis to assign animals to groups called Yinpterochiroptera, which includes the species *Asellia tridens* (**a**) and *Epomophorus wahlbergi* (**b**), and Yangochiroptera, represented here by the species *Mormoops megalophylla* (**c**) and *Eptesicus fuscus* (**d**). However, previously, there were no known anatomical characteristics that offered a way to distinguish between Yinpterochiroptera and Yangochiroptera. Now, Sulser *et al.*[1] present evidence that a structure in the inner ear called Rosenthal's canal is walled in Yinpterochiroptera and wall-less in Yangochiroptera.

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52 million years ago). Bat shoulder skeletons indicate that, by this time, the animals could fly. Whether they could echolocate is a topic of ongoing discussion[5].

Did the immediate ancestor of bats echolocate? Wings and flight capacity are common to all of the more than 1,400 living species of bat; however, in addition to the fact that not all bats echolocate, variations in echolocation behaviour contribute to bat diversity. Furthermore, Sulser and colleagues suggest that the wall-less Rosenthal's canals of Yangochiroptera are derived through evolutionary transformations from walled canals characteristic of Yinpterochiroptera. This interpretation supports the Yinpterochiroptera and Yangochiroptera classification and the view that echolocation is ancestral to bats (and lost in some Yinpterochiroptera).

Echolocation underlies the diversification of bats in both Yinpterochiroptera and Yangochiroptera. Interestingly, although yinpterochiropterans occur only in the Old World, yangochiropterans have flourished almost everywhere there are bats. There are astonishing evolutionary convergences that have driven echolocation in yinpterochiropterans and yangochiropterans.

In either proposed classification scheme (Megachiroptera and Microchiroptera or Yinpterochiroptera and Yangochiroptera), echolocation looms as a notable feature. Most species of the pteropodid family of bats do not echolocate, and the few that do use tongue clicks as echolocation signals, rather than chirps produced in the larynx (laryngeal echolocation is the echolocation mode of most bats). Sulser and colleagues' findings support the view[3] that pteropodid bats are yinpterochiropterans that lost their capacity for laryngeal echolocation during the course of evolution. A study[6] reporting patterns of growth of the ear structure known as the cochlea provided evidence that pteropodids lost their capacity for laryngeal echolocation. Another investigation[7] of bat embryological development proposed that laryngeal-mediated echolocation evolved independently in Yangochiroptera and Yinpterochiroptera. The samples from that study lacked species of three families of Yinpterochiroptera (Craseonycteridae, Rhinopomatidae and Megadermatidae) that were part of the samples assessed by Sulser and colleagues. Sulser *et al.* have used a combination of a large sample size and the presentation of previously unreported neuroanatomy to sharpen our view of the family tree of bats.

Arguably, flight combined with echolocation gave the ancestors of bats a competitive advantage over other animals, such as nocturnal birds — namely, access to nocturnal flying insects as food. Bats in both yinpterochiropteran and yangochiropteran suborders show an astonishing variation in their echolocation tactics, from the signals used to the specializations for broadcasting signals and receiving echoes, and the patterns of sound emissions.

Some bats produce very strong signals (to maximize range), whereas others generate quiet signals. Outgoing pulses are much stronger than returning echoes, so most echolocators avoid deafening themselves by separating pulse and echo in time. Simply put, they cannot broadcast and receive simultaneously.

However, using a phenomenon called a Doppler shift to separate pulse and echo in frequency allows some bats to simultaneously broadcast and receive. Some species in both suborders also use Doppler shifts to detect the flutter of the wings of a flying insect. In bats, flutter detection is much more prevalent among yinpterochiropterans (3 families and approximately 210 species) than among yangochiropterans (one family, and approximately 3 out of 12 species)[3]. The success of this approach in detecting flying insects by echolocation is central to the diversity of yinpterochiropterans. Sulser and colleagues have provided insights that also give us a fresh perspective on how bats diversified (their adaptive radiation).

Using neuroanatomical data, the authors provide robust support for the molecularly based classification of Yinpterochiroptera and Yangochiroptera, and have opened up new avenues for bat research. These extend from understanding the details of how bats use echolocation, to investigating the community structure of groups of bats (bat assemblages). Echolocation continues to be a gift that keeps on giving.

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Virology

The human and mosquito receptors for alphaviruses

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Alphaviruses are transmitted by mosquitoes to many species, and can be fatal to humans. The identification of virus receptors that are evolutionarily conserved between mosquitoes and humans might explain the wide range of viral hosts. **See p.475**

The group of viruses called alphaviruses can cause severe disease, including inflammation of the brain (encephalitis) and of joints (arthritis). Despite the high disease potential of these viruses, which can cause fatal illness, there are currently no licensed vaccines or antiviral therapeutics available to tackle human alphavirus infections. On page 475, Clark *et al.*[1] now pinpoint key targets that enable several of these viruses to infect cells (Fig. 1).

In general, alphaviruses can infect many different types of animal host, including mosquitoes, which act as a vector to transmit the viruses to humans, birds, horses and other vertebrates. To successfully infect a host cell, an alphavirus — which is surrounded by a membrane envelope — needs to deliver its genome through the cell's membrane into the cytoplasm. This pathway involves the virus binding to specific proteins on the cell surface called virus receptors, which are key determinants of infection of hosts and tissues.

After an alphavirus binds to a receptor, the virus is internalized into the cell inside a membrane-bound structure called a vesicle. As the vesicle and its alphavirus cargo are transported, the vesicle becomes increasingly acidic, which triggers the fusion of the virus's membrane envelope with the vesicle membrane[2]. This releases the viral genome into the cytoplasm. These stages of alphavirus entry have been extensively studied using Semliki Forest virus (SFV) as a model system, and many other alphaviruses have been shown to have similar entry properties. However, the specific cell-entry receptors for SFV and for eastern equine encephalitis virus (EEEV), an alphavirus associated with lethal human disease, have remained elusive until now.

The arduous process of identifying receptors for a virus of interest has been revolutionized by the introduction of methods that

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