

An Integrative Perspective on Bat Evolution

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Keywords

Chiroptera, flight, echolocation, diet, longevity, immunity

Abstract

Bats are one of the most widespread, species-rich, ecologically and morphologically diverse mammal lineages, and the only mammals capable of powered flight. Due to their evolution within the constraints of a mammalian template, bats represent an important and unique system in which to investigate the factors and mechanisms associated with mammalian phenotypic evolution and diversification. Here we review key traits and functions associated with bat diversification: powered flight, specialized senses, diverse diets, and exceptional longevity and immunity. We also highlight the roles of bats in driving the evolution of other species and their importance to global ecosystems. We integrate information across the fields of paleontology, developmental biology, functional morphology, biomechanics, genomics, physiology, and ecology to piece together the complex processes underlying bat evolution and diversification.

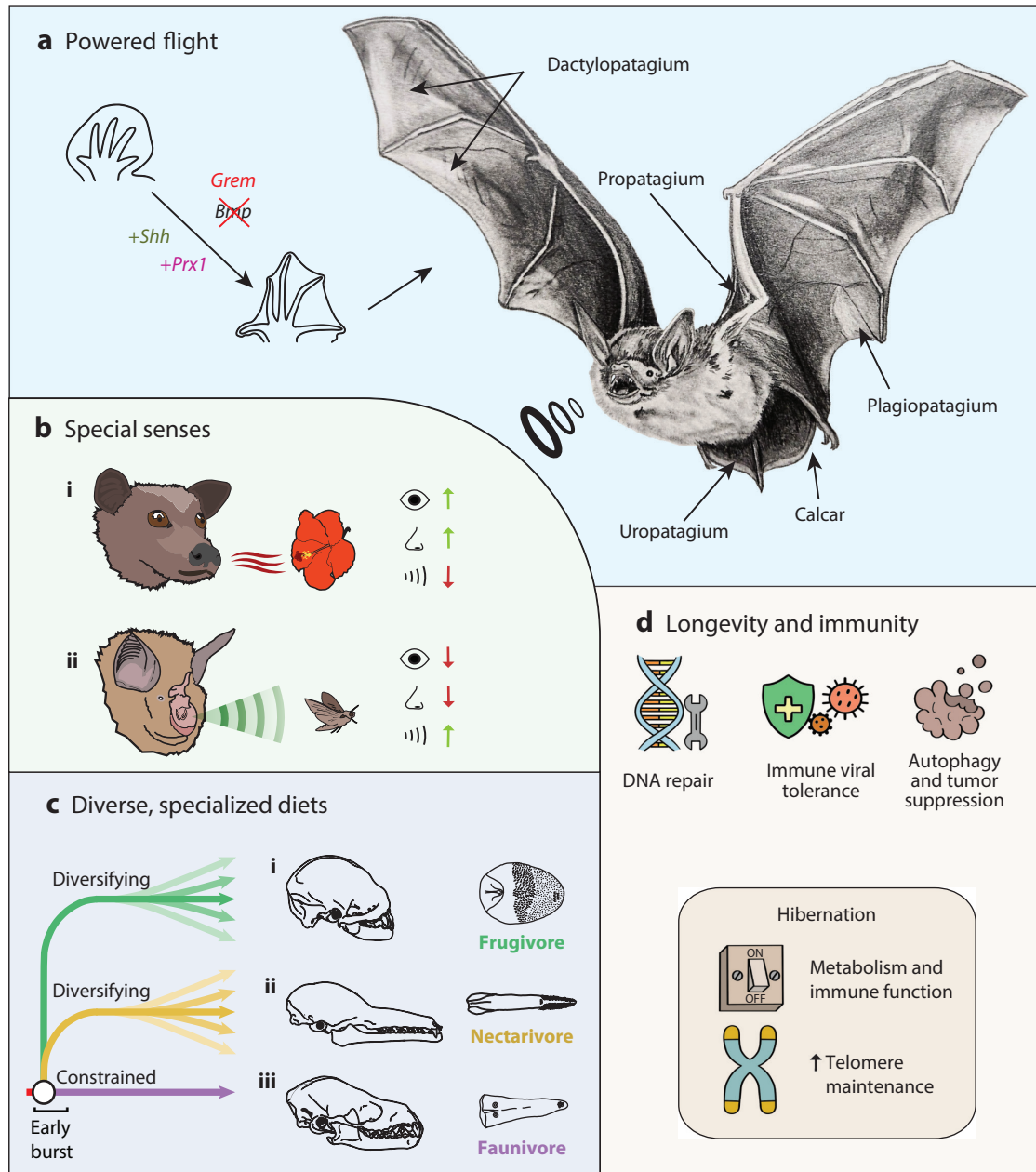
INTRODUCTION

Bats (order Chiroptera) have a remarkably high level of species and phenotypic diversity. With origins dating back to at least the early Eocene (56–54.5 Mya) (Jones et al. 2021, 2024), bats have since diversified to more than 1,400 species across 21 extant families. They represent over 20% of all extant mammals, occupy a wide range of ecological niches, and inhabit all continents except Antarctica. As the only mammals capable of powered flight, bats evolved wings and specialized body plans as a major synapomorphy (Amador et al. 2019, Sears et al. 2006, Vaughan 1970) and are one of two mammalian orders that uses specialized echolocation for foraging and navigation. Together, powered flight and echolocation released bats from life-history constraints and allowed them to exploit ecological opportunities within the nocturnal aerial niche, which in turn facilitated the vast ecological and phenotypic diversity found in the clade today. This diversity is best exemplified by their dietary ecology, as bats exhibit the greatest range of dietary specializations across all mammals—from insectivory to carnivory, piscivory, frugivory and granivory, nectarivory and palynivory, and sanguinivory. In turn, bat evolution has also impacted the species with which they interact mutualistically or antagonistically, leading to cospecialization or coevolution with plants and arms races with insects. In this review, we explore the major traits associated with and stemming from bat diversification (powered flight, specialized senses, and diverse diets) (**Figure 1a–c**) and highlight life-history and physiological adaptations stemming from their unique evolutionary path (**Figure 1d**).

POWERED FLIGHT

Wings capable of powered flight are the most distinctive feature of the bat body plan (**Figure 1a**). Unlike the wings of other extant flying organisms, bat wings are multi-jointed structures embedded in thin, flexible skin (patagia) covered in receptors that facilitate environmental sensing for flight adjustment. The evolutionary origin of bat wings remains elusive due to the lack of postcranial fossil evidence (Brown et al. 2019). Despite a fossil record of over 70 extinct bat species extending to the earliest Eocene, 56–54.5 Mya (Jones et al. 2021, 2024), relatively complete postcranial skeletons are rare. Fossils with preserved wing skeletons suggest that early bats were already capable of powered flight (Amador et al. 2019, Simmons et al. 2008). Despite the lack of transitional fossils, bat flight is thought to have evolved through a trees-down transition, with the ancestors of bats evolving from tree-dwellers to gliders and eventually achieving powered flight (Bishop 2008, Simmons et al. 2008). According to this hypothesis, bat ancestors (70–60 Mya) (Teeling et al. 2000, Upham et al. 2019) underwent evolutionary changes that resulted in elongated limbs, followed by the development of membranes on the armwing that facilitated gliding and, later, wing membranes on the handwing that enabled controlled, powered flight (**Figure 1a**). The 52.5-million-year-old *Onychonycteris finneyi* from North America exemplifies these adaptations: It had wings similar to those of modern vespertilionid bats but retained claws on multiple digits, potentially indicating enhanced climbing ability compared to modern bats (Simmons & Jones 2024, Simmons et al. 2008). Further supporting the trees-down transition, *O. finneyi* is thought to have been capable of both gliding and powered flight, which were greatly facilitated in the hyperdense atmosphere of the Eocene (Giannini et al. 2024). Recent phylogenetic comparative studies modeling adaptive evolution of limb bones in bats and other terrestrial mammals also support this hypothesis (Burtner et al. 2024). Specifically, bats appear to have evolved under selection for increased length (greater Ornstein–Uhlenbeck optima) in all forelimb bones compared to the forelimb bones of mammals with other locomotor modes (Burtner et al. 2024) (**Figure 2**).

Selection for elongation appears to have been particularly high in the hand bones (metacarpals and phalanges), which contributed to the development of the handwing—a key innovation thought to have catalyzed the bat adaptive radiation (Amador et al. 2019, Sears et al. 2006, Vaughan 1970). Handwing bones are less mineralized and have thicker cortices, reducing stiffness and increasing resistance to bending failure during wing deformation (Papadimitriou et al. 1996, Swartz et al. 1992). Selective pressures also led to relatively wider humeri and metacarpals



(Caption for Figure 1 appears on following page)

Figure 1 (Figure appears on preceding page)

Evolutionary innovations and adaptations in bats. (a) Powered flight. The evolution of bat wings enabled powered flight and involved bone elongation and the development of specialized wing membranes; these are the results of modifications to several developmental pathways, including prolonged and intensified *Sbb* signaling, which leads to extended digit growth, and an antagonistic effect of *Grem* on *Bmp* that results in the preservation of the interdigital webbing that ultimately forms the wing membranes. The resulting handwing is composed of the metacarpals, phalanges, and the dactylopatagium (finger membranes), and the armwing is composed of the humerus, radius, and ulna. The propatagium forms the leading edge, and the plagiopatagium connects the body to the fifth digit; the uropatagium (tail membrane), together with the calcar, aids in stability and maneuverability. (b) Special senses. Bats exhibit unique sensory adaptations that vary across ecological niches. (i) Frugivorous bats (e.g., genus *Pteropus*) rely on enhanced (↑) olfaction and visual acuity while exhibiting reduced (↓) reliance on auditory specialization. (ii) In contrast, echolocating bats (e.g., genus *Rhinolophus*) have auditory systems highly specialized for echolocation, with reduced reliance on vision and olfaction. (c) Diverse, specialized diets. The diversification of bats into various ecological niches is best exemplified by the dietary adaptive radiation of phyllostomid bats, which includes (i) frugivory (e.g., *Centurio senex*), (ii) nectarivory (e.g., *Choeronycteris mexicana*), and (iii) faunivory (e.g., *Macrotus waterhousii*), among other diets. Phyllostomids underwent an early burst of diversification, where frugivorous and nectarivorous species broadly diversified in craniodental and soft tissue morphologies, whereas faunivorous species maintained more constrained morphologies. Bat tongue illustrations show dietary specialization and correspond to the same species as the skull illustrations. Subpanel c adapted from Grossnickle et al. (2024). Tongues redrawn from (i) Arellano et al. (2004) and (ii and iii) Griffiths (1982). Drawings are not to scale. (d) Longevity & immunity. Bats exhibit exceptional longevity and immune function, underpinned by molecular mechanisms such as enhanced DNA repair, viral tolerance, and autophagy-mediated tumor suppression. Hibernation further regulates metabolism and immune function, promoting telomere maintenance and supporting an extended lifespan with reduced aging-related decline.

in bats compared to mammals with other locomotor modes (Burtner et al. 2024, Swartz & Middleton 2007). These evolutionary trends in forelimb morphology likely resulted in changes that increased patagial surface area for greater lift and improved resistance to bone bending and torsion during flapping flight (Burtner et al. 2024, Giannini et al. 2024, Papadimitriou et al. 1996, Swartz & Middleton 2007, Swartz et al. 1992). Bat hindlimbs are rotated 180° and serve as attachment points for the plagiopatagium and uropatagium (if present), thereby playing a role in modulating lift, drag, and pitch (Cheney et al. 2014, Jackson & Thorington 2012, Swartz et al. 2006). Consistent with the trees-down hypothesis (Burtner et al. 2024), bats evolved more gracile hindlimb bones, but these were not as long as those found in gliders. These different evolutionary patterns demonstrate the locomotor differences between bats and modern gliders: In bats, the hindlimb, specifically the ankle, serves as an anchor to the wing membrane (Cheney et al. 2014), whereas in gliders, relatively longer hindlimbs are needed to increase the surface area of the patagium in tandem with relatively longer forelimbs to generate lift during gliding (Thorington & Heaney 1981). These differences suggest that modern gliders are evolutionary and morphologically distinct from the gliding ancestors of bats.

From an evolutionary developmental biology perspective, small changes in gene regulation are associated with major phenotypic innovations in bats. Bat skin membranes—the propatagium, plagiopatagium, uropatagium, and dactylopatagium (**Figure 1a**)—together create an airfoil that enables powered flight. The evolution of these flight membranes involved the redeployment of conserved developmental toolkit genes that are critical in regulating limb development across vertebrates. These include fibroblast growth factor (*Fgf*), Sonic hedgehog (*Sbb*), bone morphogenetic protein (*Bmp*), and gremlin (*Grem*). The dactylopatagium, in particular, results from a unique retention of embryonic interdigital tissue that is achieved through a regulatory network that balances high levels of *Fgf8* signaling with inhibition of *Bmp* signaling, together with modulation by *Grem* to sustain the wing structure (Cretekos et al. 2007, Hockman et al. 2008, Sears et al. 2006, Weatherbee et al. 2006). *Fgf8* plays a key role in cell proliferation and tissue patterning during embryonic development, while *Bmp* regulates cartilage and bone formation, as well as apoptosis (programmed cell death) in developing tissues (Cretekos et al. 2007, Sears et al. 2006, Weatherbee et al. 2006). *Grem*, by antagonizing *Bmp*, is critical in fine-tuning apoptosis and preserving the interdigital webbing that is essential for creating the wing membrane (**Figure 1a**)

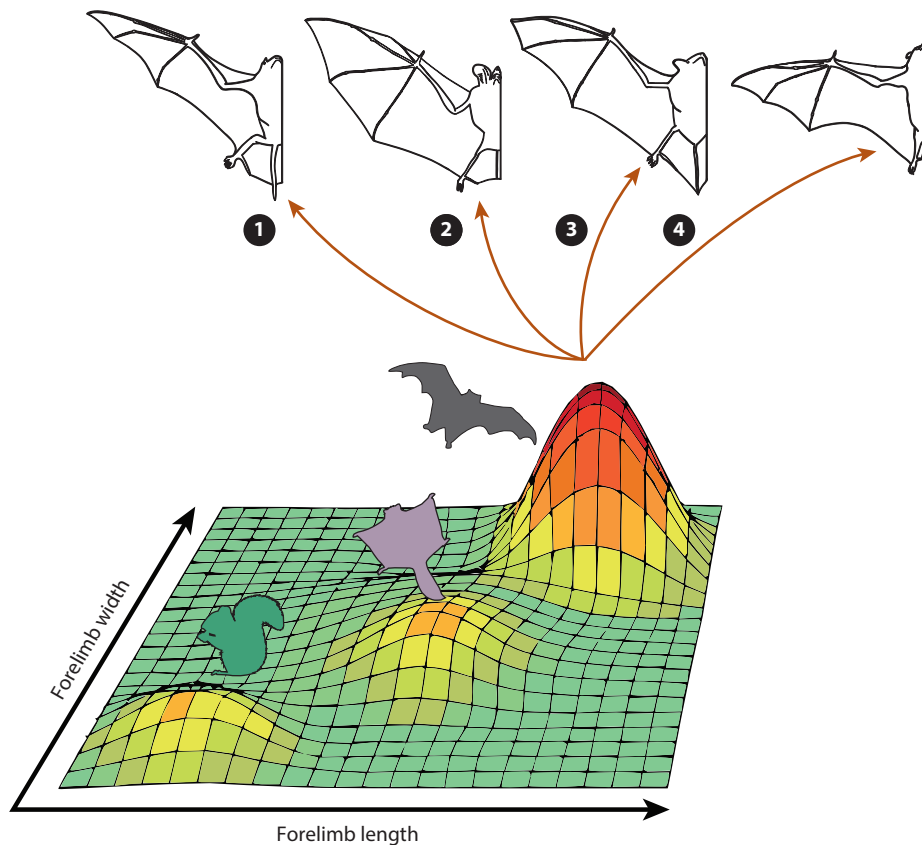


Figure 2

A hypothetical adaptive landscape of forelimb evolution illustrates fitness peaks for arboreal mammals, gliding mammals, and bats, reflecting skeletal trait optima in forelimb length and width. Bats occupy a steep adaptive peak at greater length and width optima, reflecting wing morphology. Diverse wing shapes and high variation in limb proportions subsequently evolved in bats, influencing flight performance; this variation is exemplified by the wings of (①) *Molossus rufus*, (②) *Trachops cirrhosus*, (③) *Myotis nigricans*, and (④) *Pteropus* sp. Figure adapted from Burtner et al. (2024). Wing outlines were traced from (①–③) Louzada (2020) and (④) a photo by Ken Griffiths (<https://www.dreamstime.com/little-red-flying-fox-flight-little-red-flying-image192131948>).

(Hockman et al. 2008). *Sbb* signaling is also intensified and prolonged in the bat forelimb, guiding the extended growth of digits and establishing the digit identity and polarity needed for flight adaptation (Figure 1a) (Hockman et al. 2008). Together, these interactions result in the retention of interdigital webbing and elongation of forelimb bones, whereas hindlimbs undergo normal interdigital apoptosis, resulting in freed digits (Sears 2007, Weatherbee et al. 2006). Additionally, transgenic experiments in mice, where a bat-specific *Prx1* enhancer was introduced, show that this enhancer drives forelimb bone growth (Cretokos et al. 2008), highlighting how modifications in noncoding regulatory elements play a crucial role in the phenotypic evolution of bat limbs (Sears 2007). Integrating insights from evolutionary developmental biology into comparative morphological studies offers a promising avenue for elucidating the evolution of wing shape diversity in bats (Figure 2).

The evolution of the bat wing is accompanied by the evolution of large pectoral and back muscles, skin muscles and connective tissues, and the calcar, all of which represent major innovations enabling powered flight. Bats have an architecturally unique muscle complex called the occipito-pollicalis that extends along the anterior wing membrane (propatagium) and is necessary for powered flight (Thewissen & Babcock 1992, Tokita et al. 2012). Specialized structures within the wing membrane additionally reflect evolutionary modifications from ancestral mammalian traits, providing new functional capacities. For example, the plagiopatagiales proprii muscles adjust wing-membrane stiffness throughout the wingbeat cycle, acting to reduce passive deformation and enhance aerodynamic control (Cheney et al. 2014). These muscles likely evolved from skin-associated muscles in other mammals, are an autapomorphy of bats, and exhibit notable variation across the radiation of phyllostomid bats (Conceição-da-Silva et al. 2024). In this group, larger bats with higher wing loading exhibit larger plagiopatagiales proprii muscles to counterbalance greater curvature and drag experienced during flight. This positive evolutionary allometry suggests that muscle development in larger bats reflects adaptive responses to maintain membrane tension and reduce aerodynamic drag. Elastin fibers derived from general mammalian connective tissue fibers give bat wings their distinctive wrinkles and extreme extensibility. These fibers facilitate self-folding and self-packing of the membrane, enabling gust resistance and flutter prevention during flight (Cheney et al. 2015). Furthermore, sensory adaptations, such as the development of wing hairs that monitor airflow, reflect the integration of sensorimotor control into the bat wing (Sterbing-D'Angelo et al. 2011). For example, Merkel cells and hair receptors allow for rapid, precise adjustments that enhance controlled, agile flight and support complex behaviors like climbing and foraging (Marshall et al. 2015).

The calcar—a small skeletal element associated with the interfemoral membrane—is a bat synapomorphy first noted in the bat fossil record alongside wings (Simmons et al. 2008). It exhibits considerable diversification across bat lineages in its size, shape, and tissue composition, reflecting specialization for different flight mechanics and ecological niches (Stanchak et al. 2019). In all bats with a calcar, two muscles attach to it—the calcaneocutaneous and the depressor ossis styliformis—emphasizing its active control and functional role in uropatagium support (Stanchak & Santana 2018). Many bat species use the uropatagium for foraging (Simmons & Jones 2024); for instance, bats that hunt using aerial hawking can scoop prey from the air, while gleaning bats employ the membrane to catch prey from surfaces or water. The calcar itself is hypothesized to have developed within existing connective tissue in the hindlimb membrane via metaplasia, where connective tissue transforms into cartilage or bone under stress (Stanchak et al. 2019). This could explain its plasticity and diversification and highlights how evolutionary novelties like the calcar can arise from preexisting structures and shape bats' unique flight capabilities.

The high metabolic demands of powered flight have driven evolutionary changes beyond morphology. Mitochondrial and nuclear-encoded oxidative phosphorylation genes in bats have undergone adaptive evolution, ensuring the high ATP production necessary for sustained flight (Shen et al. 2010). In parallel, the significant energy requirements of flight have driven bat wing morphology to balance surface area for efficient thermoregulation with an optimal surface-to-mass ratio, reducing both energy expenditure and heat loss (Rubalcaba et al. 2022). This balance is especially adaptive to climate—with colder environments selecting for wing morphologies that limit heat loss and warmer climates allowing greater wing shape diversity—and reflects environmental constraints on wing evolution (Rubalcaba et al. 2022). Furthermore, wing morphology influences flight performance and energetic costs. For instance, wing traits in *Carollia perspicillata* explain 7–10% of flight energy expenditure, with certain morphologies enabling energy savings of up to 30% of daily energy requirements (de Oliveira Carneiro et al. 2023). Altogether, the wide variety of wing shapes that have evolved across bats reflect their flight capabilities, environments,

foraging behaviors, and dietary habits, all of which in turn influence their habitat use (Marinello & Bernard 2014, Norberg & Rayner 1987). While the evolutionary history of bat flight reveals adaptations in limb morphology and function, these innovations are part of a broader tapestry of traits—including specialized sensory systems, diverse dietary strategies, and exceptional longevity and immunity—that collectively define the unparalleled diversification of bats.

SPECIAL SENSES

As flying nocturnal mammals, bats evolved a suite of sensory adaptations that allow them to face the unique challenge of navigating and foraging in dark and often cluttered environments. Perhaps the most distinctive and well-studied of these adaptations is echolocation, or the ability to emit high frequency sound pulses and use returning echoes to perceive surrounding objects (Griffin 1944, 1958). Bats use echolocation not only for navigation and orientation but also for detecting, localizing, and differentiating prey items (Fenton 1984, Jones 2005). Most bats produce echolocation pulses from their larynx, with the help of specialized vocal membranes and superfast, hypertrophied muscles supported by reinforced cartilage (Carter 2020, Elemans et al. 2011, Novick & Griffin 1961). However, Old World fruit and nectar bats (family Pteropodidae) (**Figure 3**) are incapable of laryngeal echolocation, and the few echolocating pteropodids rely on tongue or wing clicks to produce echolocation pulses (Boonman et al. 2014, Yovel et al. 2011).

The evolutionary history of laryngeal echolocation in bats has sparked widespread debate, particularly after molecular phylogenetic studies revealed Microchiroptera to be a paraphyletic group (Jones & Teeling 2006, Teeling et al. 2000). Given the currently accepted phylogeny of bats, two pathways have been suggested that describe the evolution of echolocation (**Figure 3**). First, laryngeal echolocation evolved once in the common ancestor of all bats and was subsequently lost in pteropodids (the most parsimonious hypothesis). Second, laryngeal echolocation was absent in the common ancestor and evolved independently in the superfamily Rhinolophoidea and suborder Yangochiroptera (Jones & Teeling 2006). Based on osteological features such as cochlear size, basicranium shape, and stylohyal bone morphology, it has been proposed that many Eocene fossil bats had the capacity for laryngeal echolocation (Habersetzer & Storch 1992, Hand et al. 2023, Simmons & Geisler 1998, Veselka et al. 2010). Because these fossils are from stem groups to all extant chiropterans, it is generally accepted that laryngeal echolocation arose quite early in the evolutionary history of bats and possibly had a single origin (Springer et al. 2001). However, it is still controversial whether one of the earliest Eocene bat fossils, *O. finneyi*, was capable of echolocation. The original description of *O. finneyi* showed that its relative cochlear size overlapped with extant nonecholocating bats and that it lacked many derived features of malleus and stylohyal bone morphology indicative of echolocation (Simmons et al. 2008). However, it has been argued that *O. finneyi* did echolocate because its stylohyal likely articulated with the tympanic bone, a feature that is prevalent across laryngeal echolocators (Veselka et al. 2010, but see Simmons et al. 2010).

Ideally, inferences about echolocation capabilities in fossil bats would be based on the three-dimensional morphology and positioning of ear bones, but these can be hard to precisely determine due to flattening and other preservation artifacts (Hand et al. 2023, Simmons et al. 2010). Recently, the oldest bat fossil with an uncrushed skull, *Vielasia sigei*, was described as the closest known relative of crown bats. *V. sigei*'s three-dimensionally preserved skull enabled more detailed comparisons of skull shape and inner ear morphology with modern bats, revealing that it likely possessed advanced echolocation abilities (Hand et al. 2023). Yet, the prevalence of laryngeal echolocation in these stem lineages still does not rule out the possibility that echolocation evolved multiple times in crown and non-crown bats. The bat fossil record is remarkably scarce, and the absence of transitional fossils with whole skulls (particularly pteropodid fossils)

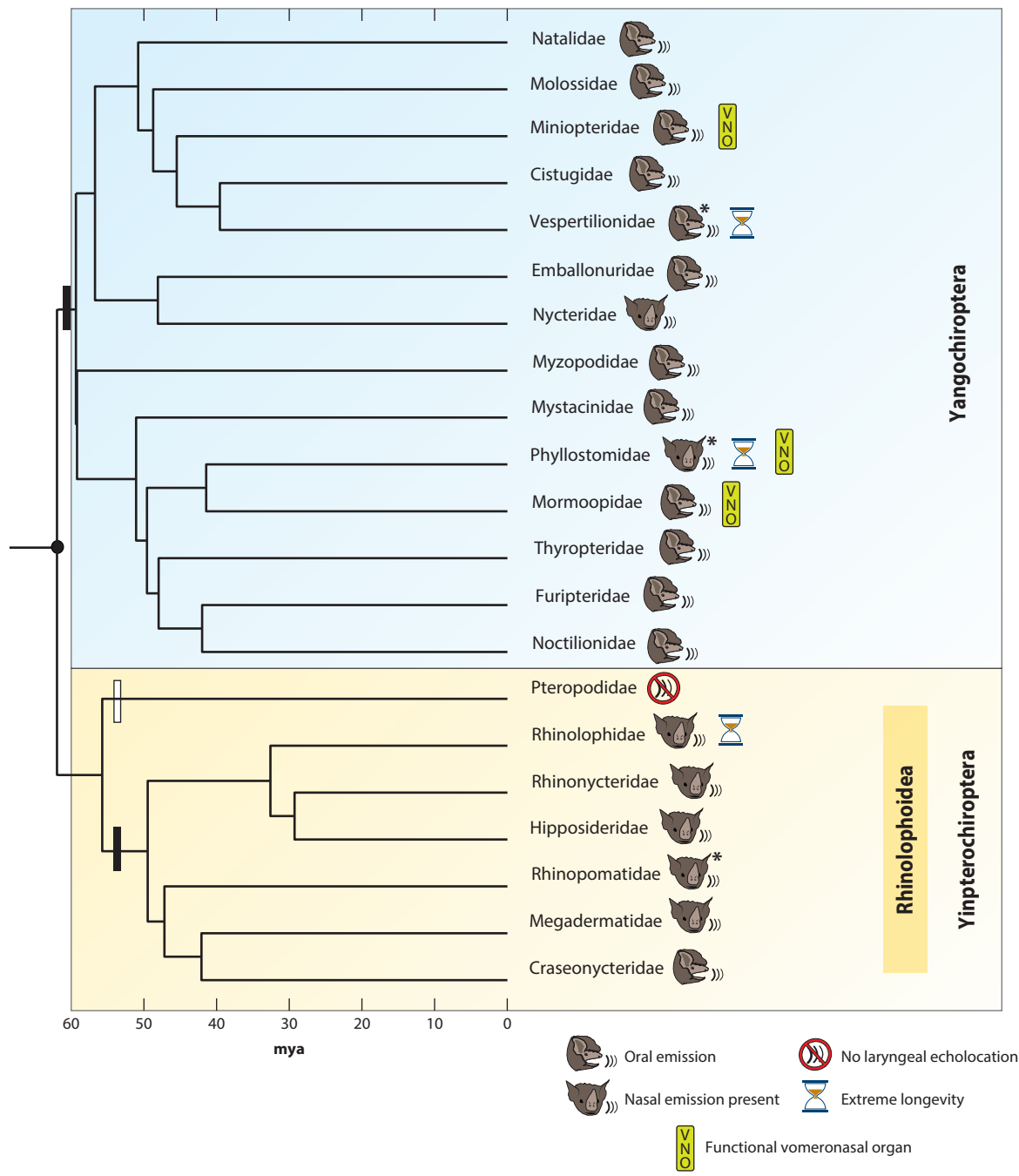


Figure 3

A family-level phylogeny of Chiroptera mapping major clades and key sensory and physiological traits discussed in the text. Black bars represent the independent gain of laryngeal echolocation in Yangochiroptera and Rhinolophoidea (multiple origins hypothesis), while the white bar represents the loss of laryngeal echolocation in Pteropodidae (single origin hypothesis). Asterisks indicate that both nasal and oral emission might be present in the family (Phyllostomidae and Vespertilionidae), or there is insufficient evidence regarding the predominant echolocation mode (Rhinopomatidae). Figure created using data from Upham et al. (2019).

implies that current paleontological evidence remains insufficient to conclusively substantiate the single-origin hypothesis (Brown et al. 2019, Eiting & Gunnell 2009).

In recent years, developmental biology and comparative genomics have contributed to understanding this evolutionary conundrum. An embryological comparison of the hearing apparatus across Chiroptera showed pteropodids possess prenatal cochlea that are relatively smaller than those of other echolocating bats and similar to nonbat mammalian outgroups (Nojiri et al. 2021, but see Wang et al. 2017). Moreover, the laryngeally echolocating clades Yangochiroptera and Rhinolophoidea exhibit heterochrony and heterotopy of their hearing apparatus, specifically the petrosal, stylohyal, and ectotympanic bones (Nojiri et al. 2021). These findings collectively support the multiple origins hypothesis, consistent with inferences from phylogenetic comparative analyses of inner ear morphology in adult bats (Davies et al. 2013). The independent acquisition of laryngeal echolocation in Yangochiroptera and Rhinolophoidea is also indicated by convergence in the laryngeal anatomy of the two groups in the form of distinct musculoskeletal modifications (Usui et al. 2024). However, genes implicated in high-frequency hearing such as *Prestin* and *KCNQ4* exhibit signatures of strong purifying selection in the echolocating lineages and not in Pteropodidae, pointing back toward the single origin hypothesis (Jebb et al. 2020, Li et al. 2008, Zeng et al. 2011).

Among laryngeal echolocating bats, the independent, repeated evolution of nasophonation or the nasal emission of echolocation calls in some taxa (as opposed to oral emission) offers another evolutionary mystery. Despite its wide prevalence in bats, the adaptive significance of nasophonation is not well understood, though it is hypothesized that nasal emission allows bats to navigate and orient while carrying large food items in their mouths (Pedersen & Müller 2013). Additionally, the presence or absence of nasophonation in many taxa is still a debated subject, and it is possible that some bat species can facultatively switch between oral and nasal echolocation modes or emit signals through both the mouth and the nostrils simultaneously (**Figure 3**) (Gessinger et al. 2021, Seibert et al. 2015). The evolution of nasophonation is often accompanied by a range of morphological features (Gessinger et al. 2021, Pedersen & Müller 2013), the most notable of which are diverse fleshy nose-leaves and horseshoes surrounding the nostrils. These structures help in directing and modifying echolocation beams emitted through the nostrils (Hartley & Suthers 1987, Linnenschmidt & Wiegerebe 2016, Vanderelst et al. 2010, Zhuang & Müller 2006), but although their shape diversity has been associated with some ecological correlates [e.g., diet (Leiser-Miller & Santana 2020)], much remains unknown about their functional implications. Nasophonation is also associated with ventral flexion of the basicranium relative to the rostrum and the compensatory rotation of the semicircular canals (Gilley et al. 2025, Pedersen 1993). Some nasophonating families like Rhinolophidae and Hipposideridae possess conspicuous bony rostral inflations, which putatively act as resonating structures that enhance echolocation performance (Ma et al. 2016, Suthers et al. 1988).

In addition to (or instead of, for pteropodids) echolocation, bats are highly reliant on olfaction to find food and engage in social interactions [e.g., distinguishing food from noxious substances, identifying conspecifics and predators, and navigating (Yohe & Brand 2018)], making this sense an important target for natural selection. Processing of environmental chemical signals in mammals is done through two major sensory organs in the nose: (a) the olfactory epithelium, which expresses olfactory receptors (ORs) responsible for binding volatile organic compounds (VOCs) from the environment in the main olfactory system, and (b) the vomeronasal organ, located in the anteroventral region of the rostrum and thought to allow for the detection of primarily nonvolatile chemical cues such as pheromones (Yohe et al. 2018). OR genes are categorized into Class I and Class II families, and their nomenclature reflects the subfamily to which they belong (e.g., subfamily OR5/8/9 is named after receptors 5, 8, and 9, which are clustered closely together on a gene

tree). ORs make up the largest multi-gene family in vertebrates and have undergone rapid rates of evolution, leading to vastly different gene repertoires (functional versus nonfunctional genes) across species (Potter et al. 2021). This high level of genomic variation across taxa is particularly notable in bats, and a species' repertoire is believed to reflect its living environment (Hughes et al. 2018). Frugivorous bats, in particular, rely on olfaction when foraging (Leiser-Miller et al. 2020, Thies et al. 1998), more strongly so when approaching fruits, since the cluttered environments they inhabit present challenges when searching for visually and/or acoustically inconspicuous targets (Thies et al. 1998). As a consequence, frugivorous species in both Yinpterochiroptera and Yangochiroptera evolved larger olfactory structures and different OR gene repertoires compared to their nonfrugivorous relatives, including a greater number of ORs in families 1/3/7 and 2/13 for those in the suborder Yinpterochiroptera (Hayden et al. 2014). Similarly, OR gene diversity differs between frugivorous and nonfrugivorous species within specific families [e.g., Phyllostomidae (Hayden et al. 2010, Yohe et al. 2021)], where a higher number of functional OR genes in families 1/3/7 and 2/13 indicate these receptors could be important for chemosensation in frugivores, whereas a high number of functional genes in OR family 5/8/9 highlights their potential importance to nonfrugivorous species. Contrary to these patterns, the differentiation in OR gene repertoires within Yinpterochiroptera is driven by pseudogenization as opposed to expansion of functional genes, specifically the proportions of pseudogenes in OR subfamilies 11 and 52 (Hayden et al. 2010).

While both the main olfactory system and vomeronasal system play a role in certain social behaviors, the latter is thought to be more specialized for detecting heavier molecular weight molecules that mediate courtship, mating, maternal care, and territoriality. Vomeronasal is of vital importance for survival and reproduction in mammals and so has been lost only in a few groups such as cetaceans, primates, and most bat clades. While loss of this system in cetaceans and primates is believed to have been driven by chemosensory perception under water and greater reliance on visual cues, respectively, the loss of vomeronasal in bats is still poorly understood (Yohe et al. 2019). The vomeronasal organ expresses vomeronasal type-1 and type-2 receptors (V1Rs and V2Rs), which, upon activation by binding to pheromones, activate the transient receptor protein cation channel 2 (*Trpc2*) ion channel. This cascade is necessary so the signal can be processed by the brain (Yohe et al. 2019). However, despite its relevance to fitness in other mammals, most bat species appear to have lost complete function of the vomeronasal system. Exceptions to this include the Phyllostomidae, the genus *Pteronotus*, and Miniopteridae (**Figure 3**) (Smith et al. 2024, Yohe et al. 2018). Complete pseudogenization of *Trpc2* evolved independently at least 13 times across bats—more than three times as many losses as in all other mammals—as opposed to a more parsimonious loss of *Trpc2* function in the ancestor of all bats, with reactivation of the gene in only two families (Yohe et al. 2017). Because bats are the only flying mammals, it is tempting to assume this widespread pseudogenization is due to this trait; however, flight seems unrelated to vomeronasal loss, since airborne pheromonal cues during roosting are still effective in their aerial environment (Yohe et al. 2017). Similar to *Trpc2*, the *V1R* genes exhibit independent loss of function in most bats, with the exception of phyllostomids and miniopterids, who retained function throughout their evolution along with an intact vomeronasal system. Most components of the vomeronasal system likely evolved together, since lineages with intact *V1R* also present intact *Trpc2* genes and a well-developed vomeronasal organ (Yohe et al. 2019, and see Smith et al. 2024).

Differences in OR repertoire and loss (or retention) of *Trpc2* and *V1R* have been attributed to factors such as habitat differences, the evolution of flight, and a shift from diurnal to nocturnal habits. However, several studies have rejected these hypotheses, as all nocturnal primates and several bat species have functional vomeronasal systems (for example, Torres et al. 2023). Additionally,

hypotheses involving sensory trade-offs in echolocating bats have been dismissed, since several echolocating bats still rely on olfaction and vomerolfaction (Thies et al. 1998, Yohe et al. 2017). Why some bat clades have completely lost the function of some OR genes and/or the vomeronasal system while others exhibit strong selection for their functionality remains unknown and thus a potential avenue of study.

Contrary to popular belief, all bats have functional eyes and integrate visual information with echolocation and olfaction to navigate and orient successfully (Danilovich & Yovel 2019). Pteropodids, in particular, have relatively larger eyes and well-developed vision compared to other bats, which presumably compensates for the absence of laryngeal echolocation (Liu et al. 2015, Thiagavel et al. 2018). This sensory trade-off is prevalent across Chiroptera, as bats with less sophisticated echolocation evolved more developed visual capabilities (**Figure 1b**), including relatively larger eyes and functional short-wavelength-sensitive opsin (*SWS1*) genes (Thiagavel et al. 2018). Many bat species are thought to be capable of UV vision, though multiple lineages have independently lost the *SWS1* genes that encode for UV-sensitive pigments (Müller et al. 2009, Winter et al. 2003, Xuan et al. 2012). These losses were thought to be associated with high duty cycle echolocation in laryngeal echolocating bats and cave roosting in pteropodids, but a few exceptions to this rule have been identified since then (Li et al. 2018, Simões et al. 2019, Xuan et al. 2012). Moreover, there are frequent mismatches between the presence of intact opsin genes, transcripts, and proteins, indicating that gene sequences alone may not accurately reflect the presence or absence of UV vision in bats (Sadier et al. 2018). Whether UV sensitivity in bats plays a functional role or is an evolutionary epiphenomenon needs to be investigated in future studies.

The evolution of specialized sensory systems, such as echolocation, olfaction, and vision, has been central to the diversification and ecological success of bats. Echolocation allows bats to navigate and forage in nocturnal environments, with variations in call frequencies and hearing sensitivity facilitating resource partitioning and reducing competition (Griffin 1944, Safi & Siemers 2010). Similarly, the evolution of diverse OR repertoires, particularly in frugivorous species, underscores the importance of olfaction in detecting and selecting food resources in cluttered environments (Hayden et al. 2014, Yohe et al. 2021). Divergence in ecomorphological and sensory traits therefore promotes the coexistence of multiple bat species by reducing competition and allowing them to occupy different ecological niches (Aguirre et al. 2003, Safi & Siemers 2010, Saldaña-Vázquez 2014). Thus, the evolution and specialization of sensory systems in bats has been fundamental to their ability to adapt to diverse ecological challenges, driving their success, diversification, and unique evolutionary trajectory.

DIVERSE, SPECIALIZED DIETS

The earliest bat fossils from the Eocene exhibit dental morphologies consistent with a primarily insectivorous diet (e.g., Hand et al. 2023, Simmons et al. 2008). However, as a whole, early Eocene bat faunas already appear to have evolved ecological diversity within the insectivorous niche, spanning a variety of foraging strategies that persist in modern species—such as perch hunting, aerial hawking, and gleaning—and including species that may have also exploited plant resources (Simmons & Jones 2024). The relatively early divergence of echolocation modalities (e.g., oral and nasal echolocation) likely facilitated further specialization within the insectivorous niche by enabling navigation and foraging within habitats that offered diverse prey resources. Further, sensory evolution and its association with distinct evolutionary trajectories in cranial shape and modularity (Arbour et al. 2021) could have facilitated or constrained the adaptability of the cranium to expand into novel diets (Gilley et al. 2025, Mutumi et al. 2023). For example, oral echolocators exhibit highly modular crania and are largely insectivorous, whereas nasal echolocators have fewer cranial

modules and high dietary diversity; conversely, plant-eating non-echolocators structure their cranial diversity primarily via allometry rather than modularity (Arbour et al. 2021). In all cases, the cranial morphologies resulting from these processes reflect selection on functional traits common to terrestrial mammals, such as a greater mechanical advantage (e.g., shorter faces, greater jaw adductor in-levers) in species that have tougher diets (Dumont et al. 2009; Freeman 1979, 1981; Santana et al. 2010).

Much of the dietary diversity within bats is concentrated within the family Phyllostomidae (**Figures 1c** and **3**), a clade that adaptively radiated into an outstanding array of diets (insectivory, carnivory, frugivory and granivory, nectarivory and palynivory, and sanguinivory) and associated phenotypic adaptations. Biogeographic processes, ecological opportunity, and sensory evolution possibly enabled the first stages of the phyllostomid adaptive radiation (Hall et al. 2021, Mutumi et al. 2023, Rojas et al. 2011, Santana et al. 2024, Villalobos & Arita 2010), followed by intense selection on functional components of cranial morphology within specialized dietary niches (Arbour et al. 2019, Monteiro & Nogueira 2011, Rossoni et al. 2017). This resulted in the most diverse array of cranial morphologies within any mammal family, particularly along the axis of rostral and mandibular elongation (Arbour et al. 2019, Rossoni et al. 2017), with resulting differences in mechanical advantage and bite force (Aguirre et al. 2002, Santana et al. 2010).

The evolution of craniomandibular elongation and foreshortening in phyllostomids also had implications for the gain, loss, and shape of teeth via modification of developmental mechanisms (Sadier et al. 2023). Initial dietary shifts seem to have posed strong selective pressures on the gene networks and processes that control tooth development, as evidenced by novel morphotypes and tooth proportions that are found in phyllostomids but not in other mammals (Sadier et al. 2023). While most phyllostomids have maintained the basic building blocks that make up the mammalian molar, these have been modified by selection into highly divergent shapes specialized for processing varied diets (e.g., dilambdodont molars in insectivores, bunodont molars in frugivores) or reduced or lost in guilds for which mastication is not critical for feeding [e.g., sanguinivores and nectarivores (Freeman 1988, López-Aguirre et al. 2022, Santana et al. 2011)]. Recent evidence stemming from phylogenetic comparative analyses of functional axes of molar shape further suggests that phyllostomids radiated through an early burst process followed by finer-scale partitioning within dietary adaptive zones (**Figure 1c**) (Grossnickle et al. 2024). This, together with the ecomorphological diversification of other traits, makes phyllostomids not only a unique case study of bat ecological diversification but also one of the few demonstrated adaptive radiations within mammals.

In addition to craniomandibular adaptations, soft tissue adaptations—particularly those related to the tongue—reflect the dietary diversification of bats. The tongue plays an important role in feeding because it is involved in food intake, transport, and swallowing. Bat tongues are generally flexible and have papillae and keratinized areas on their dorsal and lateral surfaces (Gregorin & Zanatta 2021), and the high dietary diversity of bats is also reflected in the morphological diversity of their tongues (**Figure 1c**) (Freeman 1995, Griffiths 1978, Park & Hall 1951, Park et al. 1982). Bat tongues vary in size, from very short in some insectivores (e.g., *Lasiurus*) and short-faced frugivores (e.g., *Ametrida*, *Carollia*, *Pygoderma*) to extremely long in nectarivores (Gregorin 2003, Gregorin & Zanatta 2021, Muchhala 2006, Muchhala et al. 2024, Park & Hall 1951, Winter & von Helversen 2003). Tongues can also have few papillae, as in Emballonuridae; many papillae, as in Molossidae; or distinctive and specialized papillae (i.e., hair-like or brush-like papillae), as in nectarivores (Birt et al. 1997; Gonzalez-Terrazas et al. 2012; Harper et al. 2013; Quinche et al. 2023, 2024). Comparative studies indicate that similarities in tongue morphology and microanatomy can be attributed to common ancestry. However, many of these traits also occur in phylogenetically distant taxa, suggesting that diet and feeding ecology may have driven convergent evolution

in tongue morphology (Birt et al. 1997, Gregorin 2003, Gregorin & Zanatta 2021, Park & Hall 1951, Quinche et al. 2023, Winter & von Helversen 2003). Conversely, convergence in nectar feeding can also be achieved through divergent tongue morphologies and nectar extraction behaviors (Quinche et al. 2024, Tschapka et al. 2015). This illustrates the complex interplay between phylogeny and functional adaptation in shaping the diversity of soft-tissue structures among bat species.

The evolution of distinct diets also involved physiological changes related to differential nutrient utilization. Sugars, proteins, and vitamins play different roles in bat physiology based on their dietary specialization, and this is reflected in differences in digestion and assimilation capabilities (Camacho et al. 2024, Mena Canata et al. 2024, Strobel et al. 2013). For example, the evolutionary shift from insectivory to sugar-rich diets—like nectarivory or frugivory—involved intestinal, pancreatic, and renal changes, as well as an increase in the activity of enzymes for sugar digestion and the expression of specific glucose transporters (Camacho et al. 2024, Gordon et al. 2024, Schondube et al. 2001). On the other hand, the shift from insectivory to sanguinivory involved modifications in the gastrointestinal tract of vampire bats, including developing a unique morphology in which the esophagus communicates with both the stomach and the intestine (Park & Hall 1951) and adapting the urinary apparatus to prevent renal damage from excessive protein and iron consumption (Linhares et al. 2021).

Multiple unique genomic changes, including gene losses, have resulted in crucial adaptations to diet in bats (e.g., Blumer et al. 2022). Bat dietary evolution was accompanied by a wide array of molecular adaptations involving the metabolism of carbohydrates, fats, and proteins (Potter et al. 2021), but another important component of this process involves their gut microbiota. Bats microbiomes are different from other mammals' and more similar to those of other flying vertebrates (Lutz et al. 2019). Additionally, although gut microbiome diversity is not predicted by bat phylogeny (Lutz et al. 2019), microbiome metabolic function is linked to bat diet and phylogeny; microbiome functionality can help identify specialized diets among bats and seems to complement their nutritional needs (Ingala et al. 2021). Gut microbiomes are therefore thought to have been coevolving within specific diets in bats.

The dietary diversification of bats is critical to niche partitioning within diverse communities; the morphological, behavioral, and physiological traits that have evolved in tandem with dietary specialization allow bats to exploit specific ecological resources, which in turn help structure bat communities (Aguirre et al. 2002). For example, in frugivorous phyllostomids, dietary specialization is closely associated with body mass, craniodental morphological traits, and digestive capacity, with species showing distinct dietary preferences based on their ability to process certain types of fruit (Saldaña-Vázquez 2014). In addition, bats with different bite-force capabilities can access different food resources, with food hardness directly influencing dietary diversity and niche differentiation (Aguirre et al. 2003, García-Herrera et al. 2021, Giménez et al. 2021, Villalobos-Chaves & Santana 2022). Dietary adaptation—reflected in craniodental, soft-tissue, physiological, and genomic modifications—is therefore a key evolutionary driver of bat phenotypic, species, and ecological diversity.

LONGEVITY AND IMMUNITY

The ability to fly and the evolution of high ecological diversity had an immense impact on bat longevity. Bats have exceptionally long lifespans, living at least three times longer than similarly sized nonflying eutherians (Austad & Fischer 1991). Multiple traits have been linked to the evolution of bat longevity, including flight, low reproductive rates and small litter size, hibernation, and roosting behaviors (Brunet-Rossinni & Austad 2004, Wilkinson & South 2002). The maximum

longevity of wild and captive bats has been documented for over one hundred species and ranges between 4 and 44 years, with presumed underestimation for some species (Tacutu et al. 2018). The longevity record for a captive bat is held by a male Indian flying fox [formerly *Pteropus giganteus*; 1,175 g, 44 years (Tacutu et al. 2018)], while the free-living record was established by a Brandt's bat (*Myotis brandtii*; ~6 g, 41 years) found while hibernating in Russia. This wild *M. brandtii* exhibited the most extreme lifespan among wild and captive mammals, living 9.8 times longer than expected for its body size (Podlutsky et al. 2005).

Ancestral state reconstructions suggest that the ancestral bat could have lived 2.6 times longer than a placental mammal of a similar size, and extreme longevity [i.e., a longevity quotient (i.e., observed longevity/predicted longevity based on body mass) > 4.2] has evolved at least four times across the bat phylogeny (**Figure 3**) (Wilkinson & Adams 2019). The lineages where extreme longevity has evolved include bats from both the suborders Yinpterochiroptera (*Rhinolophus*) and Yangochiroptera [*Desmodus*, *Plecotus*, and some *Myotis* lineages (Wilkinson & Adams 2019)] (**Figure 3**). For temperate species, the evolution of longevity has been associated with hibernation (Wilkinson & Adams 2019), due to its demonstrated impact on biological aging at the individual level via metabolic regulation and immune function suppression (**Figure 1d**) (Sullivan et al. 2022). In these species, longevity also seems to be determined by body mass; cave use, which reduces extrinsic mortality risks; and extreme latitudes, which lead to longer hibernation (Wilkinson & Adams 2019). The non-hibernating lineage that exhibits extreme longevity (the common vampire bat, *Desmodus*) undergoes torpor, has flexible thermoregulation, and exhibits cooperative social behaviors that might have helped enable the extension of their lifespan (Wilkinson & Adams 2019). Neither diet nor number of progeny per year seem to be related to longevity predictions (Wilkinson & Adams 2019); however, the production of multiple pups per gestation is correlated with species longevity (Garbino et al. 2021).

There are many molecular mechanisms underpinning the evolution of long lifespans in bats, and different bat species show specialized or enhanced oxidative metabolism, protein regulation, and stress resistance mechanisms (Lagunas-Rangel 2020). Specifically, bats exhibit a distinctive gene expression pattern related to DNA repair and autophagy (**Figure 1d**) (Huang et al. 2019, 2020), and autophagy-related genes appear to be under positive selection in bats (Kacprzyk et al. 2021). Chromosome maintenance has also been related to lifespan, since telomere shortening has been linked to aging; among bats, hibernators show greater antishortening telomerase activity than non-hibernator lineages (**Figure 1d**) (Wang et al. 2011). Nevertheless, among hibernators, some lineages show age-related telomere shortening (e.g., *Rhinolophus*, *Miniopterus*), while others do not (e.g., long-lived *Myotis*), even when lacking telomerase expression. This points to the evolution of alternative mechanisms to cope with chromosome damage (Foley et al. 2018). Epigenetics also plays a crucial role in bat longevity. The rate of change in DNA methylation at age-related sites is negatively associated with longevity across bat species, and genes near differentially methylated positions associated with longevity are related to tumor suppression and innate immunity genes in both short- and long-lived species from different lineages (**Figure 1d**) (Wilkinson et al. 2021).

Similarly, the evolution of the immune gene repertoire in bats reflects diverse immune strategies, some of which are specific to Chiroptera or lineages within it (Scheben et al. 2023). Bats exhibit a distinct combination of immune adaptations that enhance viral tolerance while minimizing inflammation (**Figure 1d**) (Banerjee et al. 2020). This includes positive selection on antiviral genes, such as APOBEC3 and MHC class I genes, and the loss of proinflammatory genes like those in the PYHIN family (Jebb et al. 2020, Scheben et al. 2023, Tian et al. 2023). The high levels of antiviral activity maintained by bats (particularly through type-I interferon responses), while dampening inflammatory responses, may contribute to their long lifespan and their unique ability to host multiple viruses without clinical disease (Banerjee et al. 2020). Additionally, the

high diversity of endogenized viruses in bat genomes further suggests a historical tolerance to viral infections (Jebb et al. 2020). Comparative genomic analyses have highlighted significant differences in immune gene evolution between bats and other mammals. For instance, system-wide inflammatory gene losses and selection of antiviral immunity genes, including the expansion of the APOBEC3 and MHC class I families, have been detected across 37 bat genomes (Demian et al. 2024). Higher evolution rates in immunity-related genes, resulting in the loss of genes such as *Nlrp1* and duplications of *Pgklyrp1* and *C5ar2*, have also been found in pteropodid bats compared to other bat species (Tian et al. 2023). Additionally, unique structural variants of tetherin genes in fruit bats within the family Pteropodidae and vesper bats further support the differential evolution of antiviral genes, with vesper bats possessing at least five tetherin genes, the most reported in any mammal to date (Hayward et al. 2022). Together, these adaptations illustrate how bat immune systems have evolved through both order-wide and lineage-specific mechanisms, enabling them to thrive during their long lifespans in diverse ecological niches while effectively managing viral infections (Demian et al. 2024).

Studies on the evolution of longevity, immunity, and the extraordinary health span of bats are still in their early stages. Age distributions of more species need to be assessed using recently developed techniques (e.g., Wilkinson et al. 2021), especially for wild bats. Bat maximum lifespans for many species are unknown or have probably been underestimated, since they were based on mark–recapture studies. This limits discoveries on bat longevity evolution and aging. Future research should also expand sampling coverage on short- and long-living bat species from the tropics, where there is greater diversity and bats do not hibernate. This would provide broader insights on how longevity is related to aging and senescence and how it impacts organ deterioration (e.g., skeleton, sensory organs), nutrient processing, and immunity.

BATS AS EVOLUTIONARY FORCES

Bat diversification and specialization have impacted the evolution of the species they feed on, from plant resources such as fruits and flowers to prey animals such as moths and frogs. Several studies have revealed coevolutionary processes in mutualistic and predator–prey relationships with bats. The relationship between plants and bats particularly exemplifies how mutualism influences the evolution of the lineages involved, ultimately leading to diverse types of coevolution (Flores-Abreu et al. 2019, Muchhala et al. 2024). For example, in bat–flower interactions, the presence of similar sulfur-containing compounds in the floral scents of distantly related, bat-pollinated plants suggests convergent evolution influenced by similar bat olfactory biases (Knudsen & Tollsten 1995). The interaction with bats has also driven the evolution of other floral traits, such as nocturnal anthesis and echo-acoustic signaling shapes and surfaces (Fleming et al. 2009; Muchhala et al. 2024; Simon et al. 2011, 2023; Tschapka et al. 1999). In tandem, nectarivorous bats have evolved elongated rostra, reduced dentitions, and specialized long tongues, all reflecting adaptations to their nectar-feeding lifestyle (Dumont 2004, Freeman 1995, Winter & von Helversen 2003). Examples of extreme coevolution include the tube-lipped nectar-feeding bat *Anoura fistulata*, whose long tongue has coevolved with the deep flowers of *Centropogon nigricans* (Muchhala 2006, Muchhala & Thomson 2009). Similarly, in bat–fruit interactions, some traits have evolved within multispecies networks. For example, *Carollia* bats prefer *Piper* fruits that emit specific VOCs, which in turn are produced only by *Piper* species highly consumed by *Carollia* (Leiser-Miller et al. 2020, Santana et al. 2021). This suggests a scenario in which the chemical composition of fruit scents and the OR gene repertoires of bats have undergone coevolutionary changes that facilitate the detection of specific fruit chemical cues and subsequent seed dispersal by bats (Santana et al. 2021, Yohe et al. 2021).

One of the most fascinating examples of coevolution involves bats and moths. Bats use echolocation to detect, locate, and capture prey by emitting ultrasonic pulses and interpreting the returning echoes to navigate and hunt (Conner & Corcoran 2012). This sophisticated sensory system has exerted strong selective pressures leading to the evolution of several defensive adaptations in moths (Barber et al. 2022, Conner & Corcoran 2012, Rubin et al. 2018, ter Hofstede & Ratcliffe 2016). These include longer hindwings and tails, which acoustically deflect bat attacks; thoracic scales that absorb ultrasound within the bat echolocation frequency range (Neil et al. 2020, Shen et al. 2018); and tympanic organs that are sensitive to bat echolocation calls (Jacobs & Bastian 2016). Many moths also produce ultrasonic clicks in response to bat sonar. These clicks serve several purposes: They can startle bats, interfere with their echolocation by creating phantom echoes, and function in acoustic aposematism or mimicry (Barber et al. 2022, Conner & Corcoran 2012). In response to moth defenses, bats have evolved stealth echolocation, in which they use lower-intensity calls to reduce detection by moths (Conner & Corcoran 2012, ter Hofstede & Ratcliffe 2016). For both bat–plant and bat–insect interactions, however, there is a strong need for broad phylogenetic comparisons measuring the influence of other selective pressures and detailed behavioral and ecological studies to generalize coevolutionary patterns across species (Conner & Corcoran 2012, Fleming et al. 2009, Jacobs & Bastian 2016).

BEYOND BATS

After over 52 million years of phenotypic diversification, bats now play an irreplaceable role in maintaining ecosystem stability worldwide through their diverse ecological interactions and resulting ecosystem services [e.g., pest control, pollination, seed dispersal, nutrient cycling (Aguar et al. 2021, Aziz et al. 2021, Castillo-Figueroa 2020, Kunz et al. 2011)]. Insectivorous bats significantly reduce crop damage and reliance on chemical pesticides by preying on nocturnal agricultural pests (Aguar et al. 2021), while nectarivorous and frugivorous bats contribute to forest regeneration and plant diversity by pollinating flowers and dispersing seeds over long distances, supporting the recovery of degraded areas and the reproduction of economically important plants (e.g., Muscarella & Fleming 2007). Therefore, the evolution of key traits (flight, special senses, diverse diets, longevity, and immunity) had profound implications not only for the success and diversification of bats but more broadly for biodiversity and human well-being. To better understand the evolutionary history that has shaped bats' remarkable biodiversity and maintained their critical ecosystem roles, a multidisciplinary approach addressing knowledge gaps is required. Integrating fossil evidence, developmental biology, biomechanics, genomics, physiology, phylogenetics, ecological modeling, and field studies is essential to continue unraveling the processes underlying bat evolution and diversification.

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