REVIEW

The evolution of flight in bats: a novel hypothesis

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ABSTRACT

1. Bats (order Chiroptera) are the only mammals capable of powered flight, and this may be an important factor behind their rapid diversification into the over 1400 species that exist today – around a quarter of all mammalian species. Though flight in bats has been extensively studied, the evolutionary history of the ability to fly in the chiropterans remains unclear.

2. We provide an updated synthesis of current understanding of the mechanics of flight in bats (from skeleton to metabolism), its relation to echolocation, and where previously articulated evolutionary hypotheses for the development of flight in bats stand following recent empirical advances. We consider the gliding model, and the echolocation-first, flight-first, tandem development, and diurnal frugivore hypotheses. In the light of the recently published description of the web-winged dinosaur *Ambopteryx longibrachium*, we draw together all the current evidence into a novel hypothesis.

3. We present the interdigital webbing hypothesis: the ancestral bat exhibited interdigital webbing prior to powered flight ability, and the Yangochiroptera, Pteropodidae, and Rhinolophoidea evolved into their current forms along parallel trajectories from this common ancestor. Thus, we suggest that powered flight may have evolved multiple times within the Chiroptera and that similarity in wing morphology in different lineages is driven by convergence from a common ancestor with interdigital webbing.

INTRODUCTION

Powered flight has evolved in four animal groups independently – insects, pterosaurs, birds, and bats – potentially with more than one origin of flight in each of these groups. The first group to develop the ability was the insects, during the mid-Devonian period. It is likely that this ability originated in controlled aerial descent by the wingless archaeognathans (basal insects; Dudley & Yanoviak 2011), which is also observed in some extant ant taxa (Formicidae; Yanoviak et al. 2005). Due to a gap in the fossil record, intermediate stages between this controlled aerial descent and winged flight are unknown, but around 400 million years ago (mya), we see the first known winged insect, *Rhyniognatha hirsti* (Grimaldi & Engel 2004). The small body mass of insects may have allowed them to take advantage of gusts of wind to become airborne, much like lift-enhanced seed dispersal in some plants (Dudley & Yanoviak 2011), but vertebrates cannot afford this advantage. It was not until around 228 mya

that the first winged vertebrate occurs in the fossil record – the basal pterosaur, *Preondactylus* (Barrett et al. 2008). Unlike insects, whose wings are formed by cuticle membranes (Dudley et al. 2007), pterosaur wings were formed by skin membranes known as patagia extending from highly derived forelimbs, along with patagia which extended towards the neck, and between the hindlimbs. Much of the characteristic anatomy of pterosaurs is present in their sister group, the Protosauria, and it is likely that proto-pterosaurs possessed a wing precursor in the form of an actinopatagium – a membrane extending from digit IV to the body wall (Peters 2001). This membrane is believed to have been used for display purposes prior to being recruited as flight apparatus, meaning that the wings of pterosaurs would have originated at the distal end of the limb and developed proximally later (Peters 2001). Pterosaurs are not the only animals believed to have had wing precursors used for display rather than aerial movement. The early pre-bird avian dinosaurs are

likely to have possessed feathered forelimbs that may have had display functions, given evidence of high melanosome diversity in the preserved feathers of these animals that suggests elaborately coloured wings (Li et al. 2014). From there, animals such as *Archaeopteryx* emerged around 150 mya, with full-feathered wings potentially capable of primitive flapping flight (Senter 2006, Voeten et al. 2018). The insects, pterosaurs, and birds ruled the skies until the Cretaceous–Paleogene extinction event around 66 mya, when the pterosaurs and non-avian dinosaurs became extinct, and mammals entered their age of dominance (Raia et al. 2013).

Chiropterans (bats) are unique in being the only mammals known to be capable of powered flight. Though powered flight is a highly complex trait to evolve, it gives access to a valuable aerial niche, and this probably played a role in the success of ancestral chiropterans. Even in the early Eocene, when bats are believed to have appeared, they were geographically widespread: fossils are known from every continent except Antarctica (Amador et al. 2019).

Besides flight, the other most notable characteristic of bats is their (often highly developed) echolocation ability. Echolocation is the process by which bats emit sound and are able to interpret the returning signals that bounce off the environment to produce a three-dimensional internal map of their surroundings, thus allowing the bats to orientate themselves in their immediate physical environment in the dark (Voigt et al. 2017). Though echolocation can take several forms in chiropterans, the group can be broadly split into those that are capable of laryngeal echolocation (echolocation via vocalisation from the larynx) and those that are incapable of it (the Pteropodidae, which echolocate via tongue clicks, if at all; Jones & Teeling 2006). In fact, echolocation ability is used to define phylogenetic groups within the Chiroptera. Prior to the 2000s, the order Chiroptera was divided into the Microchiroptera (capable of laryngeal echolocation) and the Megachiroptera (the Pteropodidae, incapable of laryngeal echolocation). The Microchiroptera were further subdivided into the Yinochiroptera (with moveable or absent premaxillaries) and the Yangochiroptera (with fused premaxillaries; summarised by Jones & Teeling 2006). However, the Microchiroptera appear to be paraphyletic, and the Rhinolophoidea are placed closer to Pteropodidae than to their fellow microchiropterans by molecular studies (de Jong et al. 2002). This has led to the reclassification of bats into Yinpterochiroptera (Pteropodidae and Rhinolophoidea) and Yangochiroptera (Microchiroptera excluding Rhinolophoidea; Jones & Teeling 2006; Fig. 1). In broader phylogenetic studies, the order Chiroptera has now confidently been arranged as monophyletic and placed within the clade Laurasiatheria (Madsen et al. 2001) along with the order Eulipotyphla (hedgehogs – Erinaceidae, shrews – Soricidae, moles – Talpidae, etc.).

Given the apparently idiosyncratic combination of laryngeal echolocation and powered flight present only within the Chiroptera, understanding the evolution of powered flight in the group is inherently linked to understanding
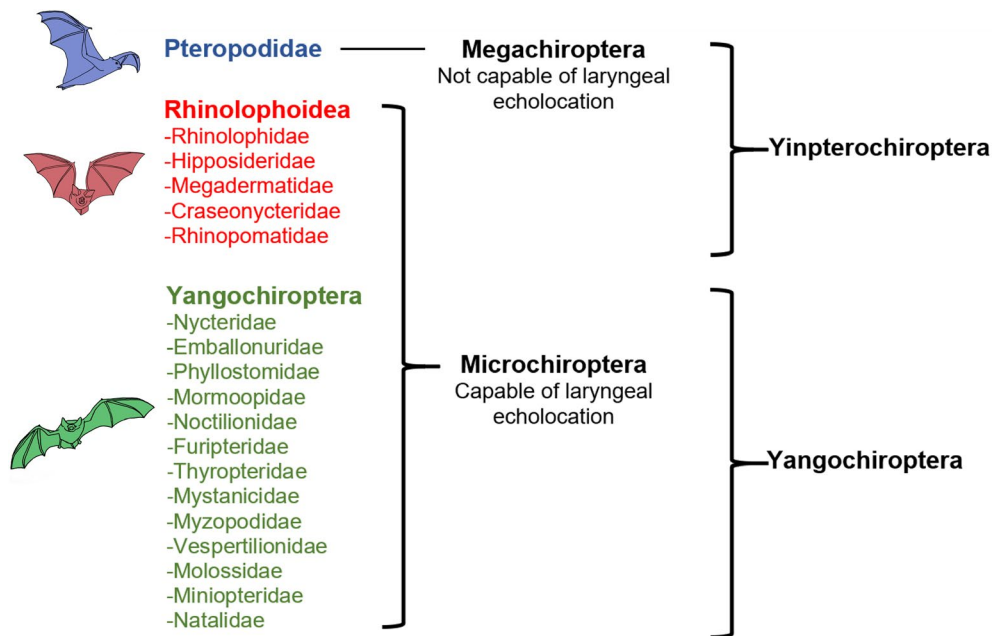

Fig. 1. Phylogenetic groupings of chiropterans, showing the relevant subdivisions of the Chiroptera into the Megachiroptera/Microchiroptera and the Yinpterochiroptera/Yangochiroptera.

the evolution of laryngeal echolocation. This forms the basis for many hypotheses and questions, such as: which came first, echolocation or flight? In 2001, Speakman presented a review of the main hypotheses regarding the evolution of flight in bats (Speakman 2001), adding his own novel hypothesis which challenged assumptions about the ancestral bat being a nocturnal insectivore, and in 2008, Bishop went on to reassess the different hypotheses (Bishop 2008), concluding that the "fundamental differences between gliding and flapping flight should not necessarily be seen as evidence that this transition could not occur". Since then, advances in our understanding of ecology, genetics, and comparative morphology have allowed new insights into bats' impressive abilities, and fossil discoveries (such as that of *Onychonycteris finneyi*, Simmons et al. 2008) have revealed more about the ancestral bats of the early Eocene. Now, with the recent publication of the discovery of the winged theropod, *Ambopteryx longibrachium* (Wang et al. 2019), the stage is set for a re-examination of the story of the evolution of flight in bats.

We present a synthesis of the developments that can inform our understanding of the evolution of powered flight in the chiropterans. Current understanding and evidence do not offer conclusive support for any single previously articulated hypothesis. Thus, we present a novel hypothesis that we believe offers a good fit to the available evidence from diverse sources: that the ancestral bat exhibited interdigital webbing and that the Yangochiroptera, Pteropodidae, and Rhinolophoidea evolved into their current forms along parallel trajectories from this common ancestor.

CHIROPTERAN FLIGHT AND ECHOLOCATION – MORPHOLOGY, MECHANICS, AND METABOLISM

Skeletal morphology and mechanics of flight

Birds and bats, being the only extant vertebrates capable of powered flight, have developed highly specialised morphologies to achieve it. It is, perhaps, surprising how much the skeletal anatomy and flight mechanics of birds and bats differ.

The bat wing (patagium) is formed by a series of skin membranes extending between elongated fingers of the forelimb (the dactylopatagium, or 'hand wing'), from the fifth digit to the ankle, where it attaches to a piece of bone or cartilage known as the calcar, and between the ankles and the tail (an uropatagium) in many species. The dactylopatagium is the product of retention of interdigital skin during embryonic development (Sears 2007). The wing is highly deformable – more so than a bird's – as the finger 'struts' allow very fine control of the

aerofoil mid-flight, leading to high flight efficiency in different conditions (Voigt et al. 2017). This high level of control means that there is considerable variation in exact forelimb movements of individuals during flight in similar conditions. Some bats are able to produce stable leading-edge vortices during slow flight, which prevents stall, and some can even produce this effect on the upstroke as well as the downstroke (Muijres et al. 2008, Muijres et al. 2014, Voigt et al. 2017).

Bats possess a unique forelimb morphology which is more complex than that of birds, with a clavicle that passes dorsally over the shoulder from its articulation with the sternum, to articulate with the acromion of a highly mobile scapula. The intricate musculature of the shoulder allows the bat to take full advantage of five degrees of freedom of movement at the shoulder (Bahlman et al. 2013). The elbow and wrist joint allow folding and expansion of the wing during wingbeat cycles, and thus, in total, bats have up to 25 actively controlled joints in their forelimbs, which provide 34 degrees of freedom of movement (Bahlman et al. 2013). It is this large number of joints that allow fine-scale dynamic control of wing shape during flight.

In order to reduce weight at the wing tip, muscles are concentrated proximally, and tendons extend distally outwards (an arrangement also seen in fast-moving cursorial quadrupeds such as equids; Amador et al. 2018). With tendons extending along the full length of the phalanges and across the many joints of the hand, the risk of tendon slipping would be high, especially given the force placed on the wing during wingbeat cycles. The bats' solution to this is sesamoids: skeletal elements found within the soft tissues passing over a joint or bony process, and although they are commonly ossified, they can be made of fibrocartilage (Amador et al. 2018). Three main functions are proposed for sesamoids: 1) protection of tendons as they pass over bony processes; 2) increasing surface area for muscle attachment at joints, and 3) redirecting the pull of tendons to direct force efficiently. An example of a sesamoid in humans is the patella – the knee cap. The forelimb equivalent – the ulnar patella – is present in no mammals other than bats. This is not the only sesamoid present in bats: 46 individual sesamoids or sets of sesamoids have been identified in several bat taxa, with up to 23 per bat species (Amador et al. 2018). These sesamoids are heavily concentrated in the joints of the forelimb, allowing bats to execute minute and delicate wing movements without risk of tendon damage.

The composition and structure of the bones is unique to bats, as well. Birds have lightweight skeletons thanks to pneumatisation of the postcranial bones (Benson et al. 2012). The postcranial bones of bats are not pneumatised, so how is the skeleton light enough to allow flight? The

answer may lie in the cross-sectional geometry of the long bones. The bones of the forelimbs in bats have very thin cortical walls, with values similar to those of birds (Swartz et al. 1992), and adult bats show high levels of mineralisation of the cortical in forelimbs, which increases distally towards the fingertips (Swartz & Middleton 2007). This reduced cortical thickness of the forelimb bones in bats and birds may contribute more to flight capability than pneumatisation (Swartz et al. 1992). The cranium, humerus and femur of bats, while less dense than those of birds, are more dense than those of rodents (Dumont 2010). Since density is related to bone strength, the relatively high bone density of bats may contribute to maximising strength while minimising weight.

Echolocation and the skeleton

Most echolocating bats produce ultrasound signals in the larynx (via laryngeal echolocation), but a few species within the otherwise non-echolocating Pteropodidae can echolocate via tongue clicks (Veselka et al. 2010). The specialised skeletal morphology of laryngeal echolocating bats includes articulation of the stylohyal bone and the tympanic bone (Veselka et al. 2010). This means that the ability to perform laryngeal echolocation can be identified from skeletal or fossil remains. This led Veselka et al. to suggest that *Onychonycteris finneyi* (the oldest known bat, from the early Eocene) was capable of laryngeal echolocation, based on apparent articulation between the stylohyal and tympanic bones – though they do comment that the crushing of the skull during fossilisation makes it impossible to establish the exact morphology (Veselka et al. 2010). This interpretation goes against the previous hypothesis that the species could not echolocate based on its relatively small cochlea (Simmons et al. 2008).

However, several mammal taxa possess stylohyal-tympanic articulation (known as the tympanohyal articulation) but do not echolocate, including felids, canids, and equids. This indicates that tympanohyal articulation may be necessary, but not sufficient, to allow laryngeal echolocation. If this is the case, what else is necessary to allow laryngeal echolocation? The hyoid morphology relates to the sound production for echolocation, but there must also be specialisation involved in sound perception and processing to allow construction of a virtual map of the environment. There is evidence of a connection between increased relative cochlear size and echolocation ability (Simmons et al. 2008). The structure of the pinna (the external ear) allows perception and processing of sound for echolocation (in the big brown bat *Eptesicus fuscus*, at least; Lawrence & Simmons 1982). Since the pinna is soft tissue, it is unlikely to be preserved in fossils or skeletal specimens. Some members of the Eulipotyphla (the shrews *Sorex* and *Blarina*) are capable of echolocation via laryngeally produced sound (Thomas & Jalili 2004), but they have small pinnae which are barely visible externally (Merriam 1895), so large pinnae are clearly not necessary to allow laryngeal echolocation.

If large cochlear size and tympanohyal articulation are necessary to allow laryngeal echolocation, then the relatively small cochlea of *Onychonycteris finneyi* suggests that it was unable to echolocate laryngeally. However, the animal's cochlear size does not fall entirely outside the size range in extant echolocating bats (Simmons et al. 2008), so no definitive answer emerges.

There are suggestions that the Eulipotyphla and Chiroptera share a common ancestor in the Laurasiatheria and that laryngeal echolocation evolved in the common ancestor and then was retained in specific Eulipotyphla and Chiroptera (de Jong et al. 2002). This leads to the expectation that this common ancestor would have had a relatively large cochlea and that the cochlea was secondarily reduced in size in *Onychonycteris finneyi*. The search for morphological characteristics that can define a laryngeal echolocator requires further attention before it is possible to ascertain the echolocation capability of an extinct species from only fossil remains. A very useful line of evidence in this regard would be a comparative analysis of relative cochlea size in relation to use of echolocation within the Eulipotyphla.

Metabolism of flight

Not only are bats the only mammals capable of powered flight, they are the only synapsids capable of the feat; other synapsids are capable only of gliding at most. Both birds and pterosaurs are members of the Sauropsida, the amniote clade that diverged from the Synapsida approximately 310 mya (Kemp 2005), leaving the question: why is powered flight more common in the Sauropsida than in the Synapsida? Powered flight is metabolically costly, and this may provide the answer: powered flight often requires 3–10 times the basal metabolic rate, whereas gliding flight requires 1–3 times the basal metabolic rate (Duriez et al. 2014). A respiratory system that functions via unidirectional airflow (often referred to as 'an avian lung system') is highly efficient and may have appeared as early as 250 mya in the Archosauria (a clade within the Sauropsida; Farmer & Sanders 2010, Schachner et al. 2013). The Archosauria includes the birds and the pterosaurs, both of which possessed this unidirectional airflow respiratory system (Claessens et al. 2009). Synapsids like bats, however, possess the less efficient tidal, biphasic airflow system; this relatively inefficient respiratory system may have prevented most members of the Synapsida from developing the energetically costly ability to fly, and yet bats have done just that.

Bats have the fastest recorded flight speed of any vertebrate (McCracken et al. 2016) and have particularly high metabolic requirements for flight, as their flight trajectories are usually curved and shifting while they navigate their environment to chase insect prey (Voigt et al. 2017). It is likely that they meet their high metabolic requirements via oxidative phosphorylation, as evidenced by genome analysis that suggests selection favouring this metabolic pathway (Zhu et al. 2010). The by-products of this pathway are toxic, resulting in DNA damage, but bats are able to cope with this due to selection for a high proportion of genes involved in the DNA damage checkpoint – DNA repair pathway (Zhang et al. 2013), essentially allowing correction of damage facilitated by oxidative phosphorylation metabolism.

Despite these adaptations, it may be the intrinsic inefficiency of tidal respiration that has limited the body size (and thus the range of ecological niches) of bats compared to both birds and pterosaurs. Flying becomes more energetically challenging with increasing size, since mass increases faster than the surface area of wings that generate the lift needed to counterbalance the increased effect of the force of gravity. Despite their diversity, there have never been bats substantially larger than extant flying foxes (the largest of which is the giant golden-crowned flying fox, *Acerodon jubatus*, with an average mass of just 1 kg; Hutcheon & Garland 2004), whereas different lineages of flight-capable birds and pterosaurs reached mass orders of magnitude larger than this.

Onychonycteris finneyi: the oldest bat

The oldest known bat species, *Onychonycteris finneyi*, is represented by the holotype of an almost complete fossil skeleton that dates back to the early Eocene of around 52.5 mya (Simmons et al. 2008). As this species is believed to be the basal chiropteran, understanding its ecology may reveal much about the evolution of bats. Though the skeleton is remarkably similar to those of extant bats (including the presence of the calcar), there are distinct differences – notably, the animal possessed claws on all forelimb digits, which extant bats do not (Simmons et al. 2008), indicating that it was an agile climber (Amador et al. 2019). The specimen's dentition indicates that it was insectivorous, but little else can be determined about its ecology.

Based on the fossil remains, Amador et al. (2019) modelled the aerofoil and aerodynamics of *Onychonycteris finneyi* via simulation and showed that the species had low aerodynamic efficiency, falling just outside the morphospace of extant bats and close to the morphospace of extant gliders (Amador et al. 2019). In order to produce sufficient lift, *Onychonycteris finneyi* would have had to fly at high speed, with high metabolic cost and a trade-off resulting in reduced manoeuvrability. This is suggested as a reason for other ancestral bat species outcompeting *Onychonycteris finneyi* (Amador et al. 2019). Models were produced with the dactylopatagium (similar to modern bats) and without the dactylopatagium (such that a membrane was present only between the wrist and ankle, not spanning the spaces between forelimb digits). In simulations, the presence of the dactylopatagium resulted in greatly enhanced aerodynamic efficiency (Amador et al. 2019). This demonstrates how important the development of the dactylopatagium was in allowing bats to achieve powered flight.

HYPOTHESES FOR THE EVOLUTION OF FLIGHT IN CHIROPTERANS

Gliding model

It is likely that bats evolved true flight from an ancestral gliding state (the aerodynamics of this have been subject to detailed theoretical modelling; Norberg 1985, Hedenstrom & Johansson 2015 and references therein). A full evolutionary pathway from gliding to powered flight in bats begins with an ancestral gliding stage via a forelimb-to-hindlimb patagium, which is followed by the development of flapping and the dactylopatagium, and then by the abandonment of gliding entirely (Bishop 2008). However, the question of exactly how and why a flapping motion originated from gliding remains unexplained. Bishop (2008) posits several potential explanations, notably that the musculature strain of controlled gliding resulted in the development of pectoral muscles capable of generating a powerful flapping motion or that other ecological factors resulted in a morphological change that favoured a structure that was more aerodynamic during flapping than during gliding. The development of sufficient metabolism for flight remains unexplained in this model and is assumed to have occurred during the transition. Despite questions still existing within Bishop's (2008) gliding model and the existence of several alternative models (e.g. Padian 1982), the gliding model is generally assumed to describe the sequence of events. Given that echolocation is critical to the ecology of most bats and is physiologically coupled with powered flight, the next aspect to address is the order in which flight and echolocation developed, as this forms the basis for much of the uncertainty in the existing models. Below, we consider a number of alternative hypotheses that have been posited.

Echolocation-first hypothesis

The echolocation-first hypothesis proposes that nocturnal pre-bats used a reach-hunting technique to capture flying

insect prey. This technique involves reaching out with the forelimbs from a stationary perch and is likely to have involved a complex sensory system to calculate and predict prey movements. Forelimbs would already be elongated to adapt to an arboreal lifestyle (Cartmill 1972), and it is possible that ultrasound (used for communication) could have become modified into primitive echolocation to aid in prey capture. Over time, the echolocation would have become more sophisticated and the forelimbs would extend further and include an interdigital membrane to improve prey capture while the pre-bat remained perched, by creating a larger 'net'. Gliding and then flight would have developed later, as the pre-bats leapt from their perch to reach insects further away, and echolocation would have been secondarily lost in pteropodids (Speakman 2001). The hypothesis is often attributed to Fenton et al. (1995), though he actually suggests that echolocation evolved prior to powered flight and that the animals were gliders before evolving echolocation capabilities.

A point in favour of the echolocation-first hypothesis is the fact that some other mammals (notably the shrew genera *Sorex* and *Blarina*) echolocate without any flight ability (Thomas & Jalili 2004), though echolocation in the order Eulipotyphla appears to be understudied and may yield illuminating examples. Coupled with this, since Chiroptera and Eulipotyphla are sister taxa, it is possible that their common ancestor had echolocation without flight capability (de Jong et al. 2002).

If the common ancestor of Eulipotyphla and Chiroptera was capable of echolocation, then the ability was secondarily lost in Pteropodidae (Teeling et al. 2000). If the common ancestor could not echolocate, there is morphological evidence suggesting convergent evolution of laryngeal echolocation in rhinolophoids and other microchiropterans, with the proposed ancestor of Vespertilioniformes (non-rhinolphoid microchiropterans) emitting echolocation calls orally and the ancestor of Rhinolophoidea emitting echolocation calls nasally (Eick et al. 2005). This is based on the fact that the Rhinolophoidea exhibit ossification in the first costal cartilage, fusing the first rib and manubrium, which is not seen in any other microchiropterans. This may be an adaptation that decreases the energetic costs of stationary echolocation (while perched, rather than while flying; Eick et al. 2005). It may seem unlikely that a complex trait such as echolocation could develop independently and convergently in different taxa, but echolocation is highly flexible and is often shaped more by ecology than by phylogeny (Jones & Teeling 2006). The exact process by which ultrasonic calls transition to echolocation ability is unclear. De Jong et al. (2002) proposed that the common ancestor of the Chiroptera exhibited primitive low-frequency echolocation for environmental detection, and the enlargement of the cochlea by the time

of *Hassianycteris* and *Palaeochiropteryx* in the middle Eocene (40.4–37.2 mya) allowed more sophisticated sound detection and processing, to facilitate echolocation for prey capture.

The echolocation-first hypothesis relies heavily on reach-hunting in the ancestral bat. In captivity, *Pteropus livingstonii* and *Pteropus rodricensis* (primarily frugivorous bats that supplement their protein intake with insects) were observed to capture insects via reach-hunting using their wings (Courts 1997). While Courts (1997) posits that the behaviour is not a captivity artefact because it was spontaneous and observed in bats that had never been exposed to insects previously, no reach-hunting has been observed in wild bats. However, wild *Rhinolophus* bats have been observed perch-hunting (remaining stationary on a perch until prey is detected nearby, then taking off from the perch to ambush in a short sallying flight), and, due to the unique morphology of Rhinolophoids, this hunting style is energetically efficient (Voigt et al. 2010). This may not be reach-hunting, but it is possible that the ancestral pre-bat was a glider that developed echolocation and captured prey via perch-hunting. However, without the skeletal morphology of Rhinolophoids, stationary echolocation and perch-hunting seem an energetically inefficient strategy, according to modelling by Speakman (1999).

Flight-first hypothesis

The flight-first hypothesis proposes that the ancestors of bats developed gliding flight while jumping between trees, and then, gliding was replaced by flapping flight since it allowed greater control and manoeuvrability. This is where the divergence between pteropodids and microchiropterans would have occurred, with pteropodids feeding on fruit and microchiropterans feeding on insects, and then developing echolocation to capture this prey more effectively (Speakman 2001). This hypothesis is often attributed to Norberg (1994), though, in fact, Norberg emphasised an ecological link between echolocation and flight and did not indicate that flight had to have evolved prior to echolocation.

Other animals are capable of flight without having ever evolved echolocation. The evolution of flight in birds, though not entirely understood, is unlikely to have involved a gliding stage (Kurochkin & Bogdanovich 2010) – the morphology required to allow gliding is completely different from that of the wings of birds during development and in terms of aerodynamics. While many extant birds are capable of gliding, it is unlikely that their ancestors with only feathered forelimbs would have been. So, given the distinct difference between the evolution of flight in birds and bats, the lack of echolocation prior to flight in birds may not provide evidence for the flight-first

hypothesis. Gliders such as flying squirrels (Pteromyini) are not capable of powered flight, but they have evolved to glide without ever developing the capability to echolocate while exploiting nocturnal niches. Chiropterans are believed to have developed powered flight from gliding flight (Norberg 1985, Bishop 2008, Hedenstrom & Johansson 2015), but it is clear that echolocation was not a pre-requisite to this.

The main piece of evidence in favour of the flight-first hypothesis is the energetic coupling of flight and echolocation in bats. Common pipistrelles, *Pipistrellus pipistrellus*, expend around 0.067 joules per echolocation pulse while stationary (Speakman & Racey 1989), which is 9.5 times basal metabolic rate, but expend no additional energy if echolocating during flight (Speakman & Racey 1991). During flight, sound production from the larynx is synchronised with exhalation and the upstroke of the wingbeat cycle – the point when the abdominal muscles contract and exert pressure on the diaphragm (Lancaster 1995). Although some bat species have adapted to reduce its cost, echolocating while stationary remains energetically expensive (Lancaster & Speakman 2001). This suggests that, in order for echolocation to be energetically advantageous rather than detrimental, flight capability must have been present prior to echolocation evolution.

The flight-first hypothesis does, however, face justifiable criticism. As Speakman (2001) put it, this hypothesis requires a literal 'leap in the dark' – since the ancestral pre-bat is usually assumed to have been nocturnal, early bats would have been leaping to glide from one perch to another in the darkness without echolocation. If bats were indeed gliding before they evolved echolocation, they must have possessed some other advanced sensory modality, such as highly developed nocturnal vision (Speakman 2001) – the implication being that this was maintained in pteropodids and later replaced by echolocation in microchiropterans. However, Speakman argued, if microchiropterans underwent a sensory modality switch from advanced vision to echolocation, an intermediate form that possessed reduced visual capabilities and not fully developed echolocation – a state with no selective advantage which surely would not have arisen via natural selection – must have existed during this evolution (Speakman 2001). However, Nummela et al. (2013) found a strong correlation between increased eye size and increased cochlear size across mammals – a strong indicator of cooperation between vision and hearing. It is very possible that the ancestral bat possessed both advanced vision and hearing, and subsequent descendants refined either their vision or their hearing further to become the Pteropodidae and Microchiroptera, without the need for a sensory modality switch.

Tandem development hypothesis

Following logically from the unresolved echolocation-first and flight-first hypotheses is the tandem development hypothesis. This hypothesis proposes the idea that an echolocation system developed in tandem with flapping flight, such that the length of leaps between branches would increase as echolocation became more sophisticated. This is supported by the energetic coupling of powered flight and laryngeal echolocation without the 'leap in the dark'.

As in the echolocation-first hypothesis, presumably echolocation was secondarily lost in pteropodids (Speakman 2001); this was suggested to require an unlikely sensory modality switch, this time from echolocation to visual acuity in pteropodids. However, as we have argued above, hearing and vision are often cooperative, so this need not be contradictory to the hypothesis. Avoiding this issue entirely, the logical modification to the hypothesis was that powered flight in microchiropterans evolved in tandem with laryngeal echolocation and that powered flight in pteropodids evolved in tandem with increased visual acuity, without the ability to echolocate (Speakman 2001). This suggests diphyly – that flight evolved twice independently in Chiroptera – which requires parallel development of the highly specialised dactylopatagium. Diphyly does not explain the unique morphology and phylogeny of the rhinolophoids, or that extant pteropodids retain features associated with laryngeal echolocation, such as an enlarged auditory brain region (Thiagavel et al. 2018) and enlarged cochleae in some species (de Jong et al. 2002). This is highly suggestive of secondary loss of laryngeal echolocation, rather than of flight developing in tandem with increased visual acuity.

Diurnal frugivore hypothesis

Speakman (2001) proposed that the ancestral bat may not have been a nocturnal insectivore, as is often assumed; it could have been a diurnal frugivore. Angiosperm proliferation in the Cretaceous may have meant that there was a large quantity and diversity of fruit available (Speakman 2001 from Collinson et al., 1993); this hypothesis suggests that the pre-bat would glide from branch to branch, using diurnal vision, to reach fruit. Due to the low nitrogen content of a frugivorous diet, these animals may have supplemented their protein intake by consuming insects – a behaviour observed in extant pteropodids (Courts 1998, Bôlla et al. 2017). Since there were no aerial insectivorous birds at the time (Rydell & Speakman 1995), there was little competition for bats to develop aerial insectivory. As bird species began to radiate into the aerial diurnal niches and became a threat to bats (as predators

and as competition), the bats may have moved into nocturnal niches where echolocation or nocturnal vision developed (Speakman 2001). Competition and predation risk from mainly diurnal birds might then have kept bats in this nocturnal niche (Speakman 2001).

Bôlla et al. (2017) observed both omnivorous (*Phyllostomus* sp.) and frugivorous (*Elanoides forficatus* and *Dermanura* sp.) bat species flying and feeding during the day (between 09:45 and 17:55 h) in the Brazilian Amazon. This was suggested as a strategy to avoid overheating in roosts and to replenish water lost due to overheating, but predation risk and interspecific competition are greater during the day, so this behaviour must be considered a trade-off (Bôlla et al. 2017). Diurnal flight could be seen as evidence of an adaptability and flexibility within the circadian rhythms of chiropterans, which may add support to Speakman's (2001) diurnal frugivore hypothesis.

The diurnal frugivore hypothesis is essentially a diurnal version of the flight-first hypothesis. One unclear area in the proposed scenario is the evolution of the rhinolophoids. According to this hypothesis, the skeletal morphology of rhinolophoids that makes echolocation metabolically viable without flight would have developed after flight. But why would the rhinolophoids secondarily develop the ability to echolocate while stationary if they were already able to fly? And why is stationary echolocation not observed as an adaptively preferred behaviour in extant rhinolophoids? Additionally, once birds dominated the diurnal skies, pushing bats into the nocturnal niche, why did predatory hawks (Accipitridae; which had been preying on the bats) not develop into the nocturnal niche and develop echolocation to follow their prey? It is possible that the predatory birds were not reliant enough on bats as a food source to warrant an ecological shift or that they were somehow physiologically incapable of developing echolocation. It is also possible that laryngeal echolocation is inefficient for capturing fast-moving vertebrate prey such as bats. Echolocating bats are able to track and capture insects because their relatively slower movement allows time for the ultrasonic calls to travel, return and be interpreted before the prey moves outside the sensory 'field of view' (which can be as short as 2.4 m; Stilz & Schnitzler 2012), but fast-moving vertebrate prey would escape this range too quickly to make echolocation an efficient prey-tracking strategy. Bats have been recorded being predated by owls, but do not generally seem to be a major dietary component (Fenton & Fleming 1976).

Introducing the interdigital webbing hypothesis

Given the clear evidence of morphological, behavioural and phylogenetic distinctions between the Pteropodidae,

Yangochiroptera, and Rhinolophoidea, it is possible and perhaps likely that these three groups developed their respective flight and echolocation abilities independently from one another. The weakness of this idea is that, while each group differs in their echolocation characteristics, they all apparently share the same derived flight adaptations. If they had all evolved independently, this would mean proposing the convergent evolution of the highly specialised dactylopatagium wing arrangement in three different groups; but what if, contradictory to the gliding model, the dactylopatagium was present in the common ancestor in the form of interdigital webbing, much like the proposed actinopatagium of proto-pterosaurs (Peters 2001)? This hypothetical common ancestor would have been nocturnal (at the time of the nocturnal bottleneck, until 66 mya, the majority of mammals were nocturnal; Walls 1942, Foster et al. 2013) or crepuscular, and used ultrasonic calls for communication. As an adaptation to nocturnal life, it would have had highly developed hearing, explaining the large auditory region still present in both pteropodids and microchiropterans (Thiagavel et al. 2018). The animal would have been arboreal, with elongated digits (Cartmill 1972) and interdigital webbing much like that seen in the amphibian genus *Rhacophorus* (flying frogs), in the mammalian order Dermoptera (colugos), and in felids such as the arboreal *Pardofelis marmorata* (the marbled cat; Pocock 1932).

According to phylogenetic analyses, the Yangochiroptera and Yinpterochiroptera diverged prior to the divergence of the Pteropodidae and Rhinolophoidea within the Yinpterochiroptera (de Jong et al. 2002, Jones & Teeling 2006). While little can be said about the characteristics of the groups leading to their divergence, we propose that ancestral Rhinolophoidea were the first group to develop laryngeal echolocation and that this was used to aid perch-hunting (given the ability of rhinolophoids to echolocate while stationary with minimal energy expenditure). Interdigital webbing could have provided an advantage in insect capture, preventing insects from escaping between the elongated fingers of the animal, as hinted by Speakman in his summary of the echolocation-first hypothesis (Speakman 2001). The rhinolophoid ancestors developed further specialised gliding apparatus proximally and then developed powered flight as part of improved perch-hunting. We propose that meanwhile, based on the evidence of echolocation-flight coupling in non-rhinolophoid microchiropterans, powered flight and echolocation developed in tandem in the Yangochiroptera. Lastly, we propose that flight developed in tandem with visual acuity in Pteropodidae. It is possible that only the pteropodids have been able to reach larger body sizes due to the body size constraints of terrestrial echolocation. Due to the inertia associated with large ossicle mass, large animals may have

sensitive hearing at lower frequencies than smaller animals (Nummela et al. 2013). Thus, the body mass of microchiropterans may be constrained by the necessity of hearing higher frequencies for echolocation.

Interdigital webbing is likely to have been present prior to a forelimb-to-hindlimb patagium in the common ancestor. Developmentally speaking, interdigital webbing can arise via a relatively simple mutation during embryonic development. Interdigital membranes in bats are retained throughout embryonic development via the upregulation of fibroblast growth factor and downregulation of bone morphogenetic proteins (Weatherbee et al. 2006), resulting in the prevention of apoptosis (which, in amniotes without webbing, results in separation and sculpting of the individual digits; Sears 2007). Though there is no conserved mechanism for the retention of interdigital webbing in amniotes (Weatherbee et al. 2006), downregulation of bone morphogenetic proteins in the distal part of the limbs during embryonic development commonly results in interdigital webbing mutations in animals usually lacking webbing (Zou & Niswander 1996). Interdigital webbing (syndactyly) is one of the most common limb malformations in humans (Malik 2012), and the retention of interdigital webbing is generally not detrimental to the animal. Interdigital webbing is present in all amniote limbs during development and has to be lost during embryonic development to form individual fingers, whereas a forelimb-to-hindlimb patagium extending from the body is an entirely novel feature. An ancestor of bats could have exhibited interdigital webbing, survived, thrived, reproduced and passed on the trait, even if the mutation did not actively confer an advantage. If the mutation was retained in future generations, it may have developed over time into a more specialised structure that conferred advantages in the context of a bat's ecology (for example, by aiding insect capture).

The key factor that may have allowed ancestral bats to utilise interdigital webbing for aerial movement is their relatively small size. No vertebrate species weighing more than approximately 34 g (the weight of female Helen's tree frogs *Rhacophorus helenae*; Rowley et al. 2012) is known to be able to glide using only interdigital webbing. The mass of *Onychonycteris finneyi* has been estimated at around 40 g (Amador et al. 2019), and bats today, with the aid of fully developed wings, remain among the smaller mammals capable of aerial locomotion, with the largest only reaching around 1 kg in mass (Hutcheon & Garland 2004). Some of the largest gliders are much heavier (e.g. Verreaux's sifaka *Propithecus verreauxi* can reach a mass of 7 kg; Nowak et al. 1999). If a mammal weighing less than ca. 40 g develops interdigital webbing without a forelimb-to-hindlimb patagium, there is evidence to suggest that this mutation could provide at least some benefit

for parachuting. Secondarily developing a forelimb-to-hindlimb patagium could then provide an advantage as gliding apparatus with increased efficiency. If a mammal weighing >40 g develops interdigital webbing without a forelimb-to-hindlimb patagium, it is unlikely to confer aerial advantage. Thus, larger gliders have developed the forelimb-to-hindlimb patagium as gliding apparatus preferentially over interdigital webbing alone. Though interdigital webbing is a common mutation, gliders (excluding Dermoptera) have not developed it secondarily as part of their patagium. This may be due to the inherent stress placed on the digits of the limbs during aerial movement if the hand itself becomes involved in lift. Bats possess sesamoids and highly specialised anatomy to cope with this, which may have been present in their early ancestors. The long limbs of Dermoptera ensure that the highest levels of force are accommodated close to the body, while the digits of *Rhacophorus* frogs are splayed widely to reduce pressure on any individual part of the hand or foot. Unfortunately, the ontogenic development of chiropterans provides little insight into the developmental chain of events, as interdigital webbing, the forelimb-to-hindlimb patagium and the uropatagium (hindlimb-to-tail) are all present from the same embryonic stage (Wang et al. 2010).

Another important aspect suggests that the chiropteran membrane arrangement did not evolve from an animal with only a forelimb-to-hindlimb patagium like that of flying squirrels. In other mammals with a forelimb-to-hindlimb patagium, the membrane extends from the wrist to the ankle, whereas in bats, this section of the membrane extends from the outer edge of digit V to the ankle. If chiropterans originally had a patagium like flying squirrels, the attachment point of the membrane to the forelimb would have had to move as the dactylopatagium developed. It is more likely that the ancestor had interdigital webbing and that the webbing evolved to extend from the outer edge of digit V towards the ankle, thus forming the forelimb-to-hindlimb patagium.

Not only does the development of interdigital webbing prior to a forelimb-to-hindlimb patagium make developmental sense, it makes ecological sense. This interdigital webbing morphology would have been advantageous to pre-bats, eventually to facilitate gliding between perches, but also in a sensory capacity – the increased tactile surface area provided by the interdigital skin would allow the animal to detect fine-scale information about its substrate, allowing better grip in darkness and perhaps even allowing the animal to detect vibrations produced by the movement of predators or prey along the substrate. Star-nosed moles, *Condylura cristata*, provide striking examples of tactile sensitivity associated with increased surface area (Gould et al. 1993). They also possess structures known as Eimer's

organs which increase tactile sensitivity and are present in other members of the Talpidae (Catania 2000) – eulipotyphlans sharing a common ancestor with chiropterans. Given the shared common ancestor, early bats may have possessed Eimer's organs or structures that were functionally similar. In addition, many extant chiropterans have derived epidermal ridges or scales on the thumb pad, associated with adhesion to the substrate and enhanced tactile sensitivity (Hamrick 2003).

Interdigital webbing makes so much sense in arboreal animals that the Dermoptera exhibit interdigital webbing and, as a result, their particular mode of gliding is known as 'mitten gliding', though the majority of lift is provided by a forelimb-to-hindlimb patagium. It is possible that this was the ancestral mode of gliding in chiropterans, and it does not necessarily need to be the case that the interdigital webbing developed prior to the rest of the patagium. Though colugos are relatively distantly related to chiropterans (the Chiroptera being part of the Laurasiatheria, and the Dermoptera being part of the Euarchontoglires), they represent the only other known example of a mammal with interdigital webbing as an adaptation for aerial manoeuvrability. Since Chiroptera and Dermoptera do not share a common ancestor since the divergence of the Euarchontoglires and Laurasiatheria, the interdigital webbing and patagium combination is likely to have evolved convergently, which requires the convergent evolution of many complex characteristics. The Dermoptera
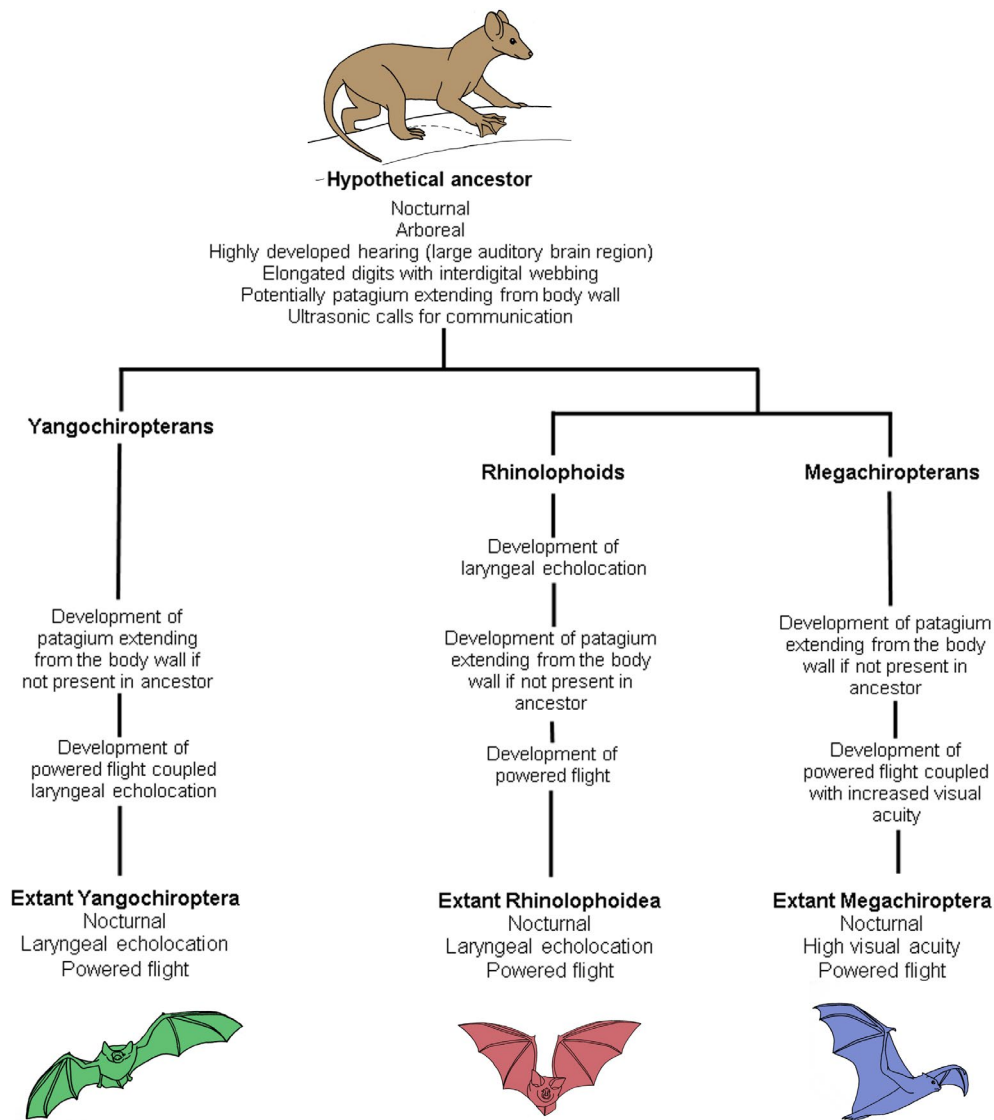

Fig. 2. Summary of the interdigital webbing hypothesis, showing the proposed evolutionary trajectories of the Yangochiroptera, Rhinolophoidea and Megachiroptera.

even share similar carpal morphology with the Chiroptera, both exhibiting fusion of the scaphoid, central and lunate bones into the scaphocentralolunate (Stafford & Thorington 1998). There is evidence in the fossil record that the ancestor of Dermoptera, *Dermotherium*, coexisted with pteropodid bats (Marivaux et al. 2006). It is possible that the ancestors of chiropterans were the first to develop mitten gliding, but their transition to powered flight left the niche available to be exploited by the *Dermotherium*.

The discovery of interdigital webbing in the non-avian dinosaur *Ambopteryx longibrachium* (Wang et al. 2019) confirms the unusual morphological characteristics first observed in the closely related species *Yi qi* (Xu et al. 2015) – these members of the arboreal dinosaur family Scansoriopterygidae are unique in being the only non-avian dinosaurs potentially capable of flight. Evidence of a membrane extending between the digits of the manus in both fossils suggests flight apparatus similar to that of the Chiroptera. It is unclear if *Ambopteryx* and *Yi* were capable of powered flight, but it is believed that they were gliders due to a lack of evidence of the musculature necessary to control powered flight (Xu et al. 2015). These scansoriopterygids are unique among dinosaurs in possessing a styliform element (a rod-like bone extending from the distal end of the ulna) which is likely to have supported the gliding membrane (Wang et al. 2019). Reconstructions of both *Ambopteryx* and *Yi* show interdigital webbing and a patagium extending from the styliform element to contact the body wall without attaching to the ankles (as is seen in Chiroptera and Dermoptera). Though the exact morphology of the membrane cannot be reconstructed accurately, all the proposed models indicate interdigital webbing without a forelimb-to-hindlimb patagium which, if correct, supports the idea of interdigital webbing evolving prior to a forelimb-to-hindlimb membrane as sufficient apparatus for gliding.

Our proposed interdigital webbing hypothesis (summarised in Fig. 2) is falsifiable, however. Evidence of a forelimb-to-hindlimb patagium prior to interdigital webbing in Dermoptera, a reconsideration of the membrane morphology in *Ambopteryx* and *Yi*, or evidence of a species that transitioned from gliding via a forelimb-to-hindlimb patagium to powered flight with the addition of interdigital webbing could all contradict the hypothesis.

CONCLUSION

The ability of some vertebrates to take flight has been studied in a range of scientific disciplines, and yet the evolutionary journey of chiropterans from small arboreal mammals to the adept flyers we know today has never been laid out definitively. The story is inherently more complex than that of other vertebrate flyers such as birds, thanks to the close

coupling of flight and echolocation in many bat species, and the evolution of flight in bats cannot be uncovered without taking this into account. With advances in molecular analyses, the phylogenetic tree of chiropterans is becoming clearer; the Rhinolophoidea is emerging as unique, not only in morphology and behaviour, but also in phylogeny.

Many hypotheses for the evolution of flight in bats remain viable, but we present a novel hypothesis which synthesises current understanding of chiropteran flight, phylogeny and evolution: that the ancestral bat exhibited interdigital webbing, and that the Yangochiroptera, Pteropodidae, and Rhinolophoidea evolved into their current forms along parallel trajectories from this common ancestor. Drawing on comparisons from the vertebrates, and in the light of the recently published description of the membrane-winged dinosaur *Ambopteryx longibrachium*, this interdigital webbing hypothesis provides a biologically satisfying narrative for the evolution of flight in bats, from arboreal mammals to the fastest-flying vertebrates that we know of. In comparison with some previous hypotheses, this novel hypothesis may be less parsimonious, but we feel it offers the best fit to currently available empirical evidence. Further evidence could strengthen support for this hypothesis, or falsify it.

ACKNOWLEDGEMENTS

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