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Palaeoatmosphere facilitates a gliding transition to powered flight in Eocene bats

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Abstract

Bats are the only flying mammals but their transition to flight remains poorly understood and controversial. We applied aerodynamic modeling to reconstruct flight in the oldest complete fossil bat, the archaic *Onychonycteris finneyi* from the early Eocene of North America, under paleo-atmospheric conditions. Results indicate that *Onychonycteris* was capable of both gliding and powered flight either in a standard normodense aerial medium or in a hyperdense atmosphere estimated for the Eocene from two independent paleogeochemical proxies. Aerodynamic continuity across a morphological gradient is demonstrated by modeled intermediate forms with increasing aspect ratio (AR) produced by gradual digital elongation, such as indicated by chiropteran developmental data. Here a performance gradient emerged of decreasing sink rate with increasing AR that eventually allowed available muscle power to achieve level flight using flapping, a process greatly facilitated under elevated atmospheric densities. This gradient strongly supports a gliding (trees-down) transition to powered flight in bats.

Keywords: Bats, Flight evolution, Gliding, Aerodynamics, Eocene
Powered flight is the most demanding mode of animal locomotion, and the three independent origins of powered flight in vertebrates are among the major macroevolutionary transitions of the Phanerozoic. These events were widely spaced in geologic time: pterosaurs first evolved powered flight in the Late Triassic, dinosaurs (birds) in the Late Jurassic, and mammals (bats) in the Early Eocene. Our understanding of the origins of bat flight is precarious. First advanced by Darwin in his 1859 *Origin of Species*, the current gliding hypothesis of bat flight rests on the evolution of a webbed and elongated handwing integrated into a preceding gliding bauplan. Gliding is thought to have evolved independently at least seven times in mammals. These gliders possess up to three separate skin membranes between the body and legs, the pro-, plagio- and uro-patagium, that together act as an aerofoil; these are all present in bats, in addition to the handwing, or dactylopatagium (Supplementary Figure 1). The dactylopatagium is a retention into adulthood of embryonic interdigital tissue, a developmental process controlled by a regulatory circuit involving expression of the genes *Bmp2*, *Gre*, *Fgf8* and *Shh* that prevents the programmed cell death (apoptosis) that otherwise produces separate digits in terrestrial mammals. Digital elongation in the wing involves *Bmp2* gene expression upregulated by c. 30% as compared to a mouse model, which keeps cartilage growing in epiphyses of hand digits 2-to-5. Remarkably, bat feet are neither webbed nor elongated, so this regulatory configuration is unique to the hand, as well as to bats as a group, and constitutes the developmental foundation of the bat handwing evolution.

In birds, gliding is a derived locomotion mode; all gliding birds can also fly, and these birds possess mid-to-high-AR wings that operate at low angles of attack. By contrast, gliding mammals lack a significant handwing contribution to the aerofoil, thereby operating low-aspect-ratio wings (AR ≤ 2) at steep angles of attack, while extant bats fly high-AR (≥ 6) wings capable of low-angle-of-attack performance. Thus, gliding and flying seem aerodynamically divergent in mammals, each locomotion mode with its own set of optimal aerodynamic parameters such that a wide morpho-functional gap exists between powered fliers (just bats) and all extant or fossil mammalian gliders. Alternative hypotheses of bat flight evolution have rejected climbing-and-
gliding intermediates (trees-down) and chiefly favor a vertical (ground-up) take-off scenario\textsuperscript{17-19}. However, the latter has been questioned on aerodynamic grounds as it requires the initial capability of a particularly demanding mode of flight, both in terms of power and kinematic complexity\textsuperscript{20}. Thus, the origin of bat flight remains obscure, with currently no theory satisfactorily explaining its early evolution.

While extant bats exhibit spectacular adaptations to flight\textsuperscript{5,21}, truly intermediate forms are lacking in the fossil record\textsuperscript{3}. The oldest fossil bats date from the early Eocene, and key among these forms is \textit{Onychonycteris finneyi}, a 52.5 Ma old North American species known from two complete skeletons\textsuperscript{3}. \textit{Onychonycteris} was a small mammal (estimated mean 40 g)\textsuperscript{22}, but still larger than most modern bats (with median at 12 g)\textsuperscript{16}. Although its morphology suggests that it was capable of powered flight\textsuperscript{3}, this hypothesis has yet to be tested, which is of considerable importance given that the postcranium of \textit{Onychonycteris} is less derived than that of any other known bat\textsuperscript{3}. Our aim is to investigate flight performance of \textit{Onychonycteris} and model intermediate forms under the conditions that we infer here for the Eocene atmosphere in order to establish the mechanisms involved in the evolution of powered flight in mammals.

Evolution of flapping flight in diverse organisms may have generally occurred in hyperdense paleo-atmosphere\textsuperscript{23}. This may have been the case in bats, and other biological phenomena, such as the appearance of giant soaring pelagornithid birds\textsuperscript{24}, also point to the presence of a denser flight medium during the critical initial phase of bat flight evolution—the early Eocene\textsuperscript{3}. We tested the possible hyperdense atmospheric conditions of the Eocene\textsuperscript{23} (23) by using two independent proxies, reconciliation of marine\textsuperscript{25} vs. terrestrial\textsuperscript{26} $pCO_2$ decoupling, and fractionation of Carbon isotopes\textsuperscript{27} in fossil amber\textsuperscript{28}. Then, we took a specimen-based approach to investigate aerodynamics of reconstructed \textit{Onychonycteris} and intermediate models based on its anatomy in both normodense and estimated hyperdense atmosphere applying the well-established program Flight v. 1.25\textsuperscript{13}, an aerodynamic reconstruction program successfully used with fossil taxa\textsuperscript{1,29}. We demonstrate flapping and gliding capabilities in \textit{Onychonycteris}, and confirm aerodynamic continuity, and hence evolvability, between gliding and flapping in
intermediate models, thereby strongly supporting a gliding transition to flapping flight in bats, which is especially likely under inferred hyperdense atmosphere.

Results

Flight in normodense versus hyperdense conditions. Our simulations using Flight 1.25, first run with air density at standard 1.225 kg/m3 or atmospheric pressure (PATM) of about 1 bar (= 100 kPa), yielded a climb rate (vertical component of airspeed during flight) of +0.27 m/s (Supplementary Table 1). A climb rate ≥ 0 demonstrates that *Onychonycteris*, as reconstructed here, was capable of sustaining level flight with available muscle power. However, flight costs (Supplementary Table 1) were high: Power was 46% higher than in extant bats of comparable mass, with myofibril work and wingbeat frequency also relatively high (Supplementary Table 1). In addition, flight conditions were dangerous in terms of collision risk: cruising speed was 22% higher (Supplementary Table 1) than horizontal velocities seen in extant bats in a body mass range widely inclusive (e.g., mean 4.98 m/s in 30-300 g pteropodid bats) of that estimated for *Onychonycteris*.

Both approaches used to estimate air density in the early-middle Eocene (see Methods) converge on a maximum upper constraint of c. 1.6 bar (= 160 kPa), i.e., hyperdense atmosphere. Then, Flight 1.25 was set to calculate flight parameters with this PATM. All aerodynamic parameters improved in this hyperdense flight medium, making flight less costly and also safer with regard to collision risk. Flight parameters approached values calculated for modern bats flying at 1 bar, including a power decrease of 22% to 0.36 W, airspeed decrease of 28%, and a climb rate increase of 26% (Supplementary Table 1).

In parallel, a sensitivity test using a heavier model with an extra 10% weight at 44 g exhibited generally poorer flight parameters: power was an additional 17% higher, myofibrils work and wingbeat frequency higher, while climb rate was lower. However, this penalized model also greatly improved performance under hyperdense conditions (Supplementary Table 1).
Intermediate models. Investigating flight performance with models has been successfully applied in fossils\(^1,^2\), as well as in situations when animal structure is challenging from an aerodynamic perspective, as in five-winged feathered dromaeosaurids\(^3\), membrane-winged scansoriopterygid theropods\(^2\), giant pelagornithid birds\(^3\), and flying fish\(^3\). Here we modeled intermediate forms based on the observation that bodily proportions of  Onychonycteris  depart from those seen in terrestrial mammals\(^3\) but are remarkably comparable to those of specialized gliding mammals (including the colugo, Dermoptera). Thus, we were able to preserve the overall anatomical structure of  Onychonycteris  while varying only the contribution of the handwing to the aerofoil, in line with the requirement of the current gliding theory of bat flight origins. We considered four cases of webbed handwing elongation beginning with minor elongation (Model 1) and progressing to elongation approaching that seen in bats (Model 4; Supplementary Figure 1). Simulations with Models 1 and 2 did not indicate any thrust or lift produced by flapping; Model 3 produced little effective lift but required myofibrils muscle work that exceeded a theoretical maximum of 57 J/kg\(^1\), so flapping flight was thus deemed unattainable. Model 4 (wingspan 0.24 m, AR 3.9) did respond to the flapping simulations, suggesting that a mechanical threshold is reached at about this wingspan or AR for this morphology. However, flight costs and airspeed risks were all high and it did not achieve level flight in normodense conditions with climb rate at -0.36 m/s (Supplementary Table 2). Flight parameters of Model 4 greatly improved under hyperdense atmosphere (Supplementary Table 2), reducing power requirement, myofibrils work, flight speed, and wingbeat frequency, while nearly achieving level flight with climb rate at just -0.06 m/s (Supplementary Table 2). Thus, hyperdense conditions would have allowed sustained flapping flight for a model with AR effectively intermediate between mammalian gliders (maximum AR = 2) and  Onychonycteris  (AR = 5).

Gliding. We also used Flight 1.25\(^1\) to simulate gliding performance for the all the models outlined above, including the full-winged reconstruction of  Onychonycteris . Gliding starts after
sufficient speed is gained from gravity, with glides long enough as to disregard losses due to the
initial drop; i.e., standard steady-state gliding following a climbing phase to gain height and store
potential energy to be released to the air during gliding\textsuperscript{15}. Vertical climbing in trees in these
models was deemed possible given the small body size and the sharp claws preserved on all five
digits of the \textit{Onychonycteris} hand\textsuperscript{3}.

Under normodense conditions, gliding generally improved as AR increased across the
models: glide ratio and maneuverability increased, and collision risk was reduced through a
decreasing best-glide speed (Supplementary Table 3). Most significantly, sink rate (negative
vertical component of velocity) decreased with increased AR, with the actual full-winged fossil
performing better at gliding than any of the intermediate models (Fig. 2). Specifically, gliding
performance improved with wingspan from the AR 2.6 Model 1 sinking at 2.19 m/s, to the AR
5.14 full-winged fossil model sinking at 0.88 m/s.

Combining the vertical velocities of sink rate from gliding and climb rate from flapping in a
single frame of comparison (Fig. 2), we show that muscle power of the full-winged model was
already available (to allow the observed positive climb rate) to overcome sink by switching to
flapping mode (vertical dotted arrow in Fig. 2), using about 3 seconds of flapping to recover the
sink from each second spent gliding. These combined results strongly support a gliding transition
to flapping flight under normodense conditions.

Under hyperdense conditions, sink rates and airspeeds decreased for all models tested,
making gliding safer (slower) and more maneuverable in terms of tighter turning ability
(Supplementary Table 3). Moreover, the muscle power needed to switch from gliding to flapping
also was already available in Model 4, with a climb rate nearing level flight (at -0.06 m/s). This key
result in the estimated hyperdense medium makes the morphological transition from gliding to
flapping shorter by -24% in AR in comparison to \textit{Onychonycteris} flying in normodense
atmosphere (Fig. 2), calling for an earlier transition to powered flight in the Eocene atmosphere.

Flapping in Model 4 was highly costly at 0.61 W but still within the theoretical limit of myofibrils
work (at 51.5 J/kg at minimum power speed) and was 20% less costly than flight of this model at 1 bar (0.77 W; see Supplementary Table 2).

**Discussion**

Our reconstructions illuminate the origins of mammalian flight. We show that the key fossil bat *Onychonycteris finneyi* was capable of both gliding and flapping, whereas modeled intermediate forms demonstrate a gliding performance gradient of decreasing sink rate with increasing AR; eventually, flapping becomes viable with available muscle power to sustain level flight (Fig. 2). This continuity supports the current gliding hypothesis of mammalian flight origins on aerodynamic grounds.

Under normodense conditions, gliding must be employed until the model handwing extends the aerofoil to $AR \approx 5$ for an ancestral bat similar in size and anatomy to *Onychonycteris*, placing the actual fossil at the very beginning of flapping flight. But this morpho-functional transition is greatly facilitated in a denser flight medium, as level powered flight is within reach with AR as low as 3.9 at the estimated maximum of 1.6 bar in the Eocene atmosphere, implying an earlier evolutionary switch to a flapping regime (Fig. 2). This latter scenario of an earlier transition of a more primitive form is more likely also from the perspective of clade age, as bat origins have been dated 61.5-57.4 Ma\textsuperscript{34} or slightly older\textsuperscript{35}, while the actual age of *Onychonycteris* is younger at 52.5 Ma\textsuperscript{3}.

The adequacy of *Onychonycteris* as model for the gliding transition is easily seen in several features of gliding mammals that are present in *Onychonycteris*. These include joints rotated such that limbs extend laterally in aerial locomotion\textsuperscript{6}; the relatively long limbs\textsuperscript{3} that characterize all gliders despite other anatomical differences\textsuperscript{36}; and particularly, limb segment differences that suggest distal elongation of the arm, as measured by the dimensionless brachial index (BI: radius-to-humerus length ratio). In *Onychonycteris*, BI is 1.25-1.30\textsuperscript{3}, whereas in most gliding mammals BI varies from 0.88 to 1.29, extending into the range of 1.36-1.43 in colugos\textsuperscript{6},
the latter, arguably, the most capable mammalian gliders\textsuperscript{7}. Therefore, limb structure in
Onychonycteris can be assimilated to that of specialized mammalian gliders, making this fossil an
adequate glider model with the handwing removed, as in our Model 1. The adequacy of our
model is further reflected in principal parameters like the calculated glide ratio of 2.93 in Model 1
(Supplementary, Table 3) which is extremely close to the glide ratio of 2.85 observed in some
extant gliders such as the sciurid flying squirrel Pettaurista\textsuperscript{37}.

Significantly, the performance gradient shown here between gliding and flapping depends
only on extending the handwing, an evolutionary modification strongly supported by
developmental data. Rapid evolution of increasing wingspan in bats, and hence AR and
concomitant gliding and flapping capabilities, is suggested by a unique molecular regulatory
circuit that determines the elongation of a webbed handwing\textsuperscript{10,11,38}. This is a key factor in the
evolution of mammalian powered flight as the gliding theory on the origin of bat flight requires that
a fully functional gliding \textit{bauplan} precedes the evolutionary addition of the handwing\textsuperscript{5}.

Our modeling not only supports a gliding transition to flapping flight in paleogene bats; it
also compromises key aspects of alternative hypotheses, particularly direct take-off (ground-up)
or parachuting proposals (see Introduction). Adding to the fact that limb structure of reconstructed
intermediate forms resembles that of gliders, so alternatives like a cursorial scenario become
improbable, we have shown via our models that no useful lift to sustain level flight by flapping is
produced unless a relatively well-developed handwing is present (Supplementary Table 2).
However, the handwing alone is not enough, given that a handgliding parachuting model with
only distal-arm dactylopatagium and lacking other wing membranes\textsuperscript{39} has been demonstrated
inferior to a standard gliding \textit{bauplan}\textsuperscript{40}. Therefore, our models demonstrated gliding \textit{and} flapping
capabilities in intermediate forms, and the performance gradient that they show, stand out as
indicative of the more likely transition leading to powered flight in bats.

Early theoretical work\textsuperscript{15,20} as well as more recent experimental\textsuperscript{41} and robotic\textsuperscript{42}
approaches, suggest that low-amplitude wing oscillations significantly aid gliding performance, for
instance by improving lift:drag ratio, although these models were based solely on aerodynamic
principles, and estimated under standard PATM. Here we quantitatively demonstrate a gliding transition based on the actual features of a key fossil bat with the least derived flight apparatus\(^3\), in the estimated hyperdense atmospheric conditions of its actual geologic time of occurrence. We suggest that evolutionary responses to high atmospheric density may have been key in the evolution of powered flight\(^{13,23}\), as has been suggested for Permian griffinflies (Protodonata)\(^{43}\), early Mesozoic\(^{44}\) and gigantic Miocene\(^{45}\) birds, and as shown here for Eocene bats.

As originally proposed by Darwin\(^4\), and advanced further more recently\(^{5,46-48}\), the hypothesis of a gliding origin of bat flight as evaluated here represents a case of incremental evolution through intermediate forms of changing function, which may be critical in functionally demanding transitions like the evolution of powered flight in vertebrates\(^1\). This transitions may be greatly facilitated by favorable extrinsic conditions, such as those palaeoatmosphere conditions that we infer for the period of evolution of the unique bat handwing. While the origin of pterosaur flight remains obscure, although it may be related to scansorial habits\(^2\), a gliding transition to flight in bats stands in striking contrast with the cursorial-dominated transition inferred for birds\(^1,49\). This highlights the fact that disparate mechanisms and diverse macroevolutionary pathways have been used by vertebrates for the conquest of the aerial medium.

**Methods**

**Species and Specimens**

*Onychonycteris finneyi* (Chiroptera: Onychonycteridae) is a fossil bat species known from two nearly-complete skeletons from the Fossil Butte Member of the Green River Formation in Wyoming (~52.5 Ma\(^3\)). Phylogenetic analyses including both extant species and other Eocene fossil bats indicated that *Onychonycteris* is on a basal branch of archaic bats\(^{50}\). *Onychonycteris* represents the most primitive of all known bats, retaining relatively plesiomorphic limb proportions as well as claws on all forelimb digits, unlike any other fossil or living bats\(^3\). This bat species also exhibits relatively primitive features of the ear region that suggest that it was not capable of echolocation\(^3\). We examined and measured both the holotype (Royal Ontario Museum ROM
55351A) and paratype (American Museum of Natural History AMNH 142467) of *Onychonycteris finneyi* to reconstruct body mass and patagial proportions. The two specimens are extraordinarily similar in both bodily proportions (Fig. 1) and weight estimations, having a body mass range of 38-41 g, total aerofoil surface range 0.016-0.018 m², wing loading (WL) range 21.5-24.0 Pa, wingspan of 0.28-0.32 m, and aspect ratio (AR) range of 4.75-5.32. Other important available wing data (see ref.16), such as tip shape index, are not directly used in the aerodynamic model (see below).

**Aerofoil reconstruction**

The skeletal frame of the wing was reconstructed by placing the wrist level with the shoulder, keeping the elbow joint flexed at 90° between the humerus and the proximal half of the radius shaft; digits were extended following the anatomical configuration of their joints, which are similar to that of modern bats3,16; the vertebral column was straightened and the hind leg was stretched following joint morphology. Patagia were inserted in that skeletal frame of stretched arms and legs, and were reconstructed as seen in modern bats including a uropatagium (tail membrane) extended from tip of calcar as preserved in the holotype3 to tip of tail (Supplementary Figure 1).

In addition, we constructed models based on the anatomical structure observed in *Onychonycteris* by changing the contribution of the handwing to the aerofoil. Flapping flight and gliding was simulated by changing the extension of the handwing as supported by developmental data9-11,38,51-58, first with the handwing reduced to a minimum (no handwing contribution to the aerofoil). Such form was similar to gliding rodent species in the genus *Glaucomys* (flying squirrels; Sciuridae), and diprotodontian marsupials in the genus *Petaurus* (sugar gliders; Petauridae)7, but maintaining limb proportions as in the fossil bats—a hallmark of bat anatomy as the most preeminent forelimb-dominated mammals3 and known to be controlled by differential gene expression between embryonic hand- and footplates that are maintained along all development stages9. A subsequent form was modeled on the same skeletal frame but assuming a hand with slightly elongated fingers enclosed in the patagium; extant colugos (dermopterans in
the genera *Cynocephalus* and *Galeopterus*; *Cynocephalidae*) exhibit this feature. Wingspan was thus increased to about 20 cm with an estimated AR of 3.3 (Supplementary Figure 1). Further digital extensions that increase each wing/forelimb and dactylopatagium (= handwing) length by 1 cm per side (i.e. previous wingspan + 2 cm to yield 0.22 m and AR 3.73), termed Model 3, and then again by another 1 cm per side (previous wingspan + 4 cm to yield 0.24 m with AR 3.9), termed Model 4. These changes gave the outlines shown in Supplementary Figure 1, with extended forearm, legs stretched as in gliding mammals (see ref. 7), and with a tail membrane as reconstructed in the fossil3,16. In these reconstructions, all bodily proportions were held constant as for the full-winged fossil, such that head and body, fore- and hind-limbs, pro-, plagio- and uropatagium, were invariant across models; therefore, only the dactylopatagium was modified. The basic aerodynamic parameters of wing area, wing span and aspect ratio are given in Supplementary Table 4 for all four models and the fossil.

### Flight parameters

Bat flight can be exceedingly complex in natural conditions59, but the simulation model used can be applied to bats13 to accurately calculate parameters with variables measurable in fossils (e.g. refs.1,29). The basic model input data were taken as averages between the two *Onychonycteris* specimens (Fig. 1). The model setup uses input data with no pay-load (i.e. no prey or fetus being carried) and a body drag coefficient of 0.25, based on the values for the extant *Phyllostomus discolor* of similar mass and size60. The frontal area factor (which considers the aerodynamic form of the head and for most birds is taken as unity) is here increased to 1.3 (see ref.60). The flight muscle fraction was found to be on average 9.13% of total body mass in extant bats, with a minimum value of 7.8% for Emballonuridae (a 24 g *Taphozous australis*)61. Thus, a modeled value of 8% has been adopted, which takes into account the extra hind limb mass and robust nature of *Onychonycteris finneyi* (see ref.3); this is slightly lower than the 10% value used for an
evaluation of basal gliding or flying theropod dinosaurs. To give a wingbeat similar to medium-sized extant bats, a factor of 0.5 is used, which results in wingbeat of >6 Hz at 1 bar Patm values which agree with the scaling relationship of wingbeat and mass for extant bats. These bats have a reduction factor of 0.68 in relation to birds; however, with this higher factor the model tends to overestimate wingbeat frequency (7-8 Hz) in relation to extant values as the wing length is shorter in Onychonycteris and the models tested. With these specifications, Flight 1.25 was set to calculate power curves and the flapping flight parameters of mechanical power (W), maximum rate of climb (m/s), specific work in myofibrils (J/kg), wingbeat frequency (Hz), minimum power speed (m/s), and maximum range speed (m/s).

Given the relatively longer legs and more robust and archaic nature of the fossils, a sensitivity test was made by increasing the average estimated mass of 40 g by 10% to 44 g. Note that this larger model imposes a significant penalty on the potential ability to generate lift and trust. Flapping flight simulations were thus carried out independently for both mass values (40 and 44 g) and for varying air densities, from 1 bar (present low altitude) to a maximum constraint of 1.6 bar estimated to be the air pressure during the early Eocene (see below).

**Glide parameters**

The Glide Polar feature of Flight 1.25 can reproduce the glide performance of extant mammals, as well as large soaring birds and ultra-light gliders. The same input data as above were used to calculate Glide Polars in this program. We report the output parameters Glide ratio, best glide speed (m/s), sink rate (m/s), impact speed (m/s), and turn radius (m, at 24° bank). A higher-than-default Lift Coefficient (L) of 3 was introduced, to reflect the high camber of the bat wing membrane, and considering that the head generates less drag and lift at airspeeds of around 5 m/s.

Mammalian gliding differs from bird gliding in that the aerofoil has a very low AR and operates at a high angle of attack. Thus, the dimensionless wing profile drag coefficient adopted by the model has to be modified to account for these characteristics. To adjust this, the
following sources were considered. The airfoil NACA0012, utilized in applications such as Mini-
Unmanned Aerial Vehicles (UAVs), flies at low velocity and small scale in a low Reynolds number
regime; wind tunnel experiments at 13.1 m/s and air density of 1.225 kg/m³ (normodense)
showed that the drag coefficient jumped sharply from about 0.1 to 0.2 at an attack angle of 20
degrees, reaching about 0.3 for angles of attack of about 30 degrees in which lift was highest
Similar results were found for a UAV low-speed wing with functional constraints, the fluent
program indicating that the wing drag coefficient goes from 0.1 at an angle of attack of 14
degrees (Glide Ratio, GR > 4) to 0.2 at 20 degrees (GR < 2.75). Also, for a high AR, bat-inspired
membrane wing profile, the wing drag coefficient was not dependent on flapping frequency or AR
(2.5 to 4.5), but did depend on amplitude angle (sweep and flap). With little wing movement, this
coefficient was found to be about 0.24 for both the downstroke and upstroke. As the angle of
attack for mammalian gliders has been found to be greater than 40 degrees, this suggests that
the wing profile drag coefficient would be at least 0.2. This value reproduces squirrel flight and
was used in the initial simulation model tests (see below).

Most organisms can withstand impacts at 4.4 m/s but impacts at greater speeds can be fatal. Average woodland speeds of bats were found to be 4.8 m/s and maximum modeled
speed of Rhinolophidae was taken as 6 m/s. In our simulations this speed was thus taken as a
practical limiting constraint. Better gliding performance can be obtained by lowering the angle of
attack, but this increases airspeed above this limit. However, for the larger AR models in higher
density air it was possible to simulate gliding with a lower angle of attack (to less than 20
degrees) with a Wing Drag Coefficient of 0.1 and still remain within airspeed limits.

Aerodynamic model validation
We validated the aerodynamic model by comparing empirical parameters measured in both
powered-flying bats and gliding mammals, with the respective output of the model. A mammal
glide set up, based on the Indian giant flying squirrel Petaurista philippensis (Sciuridae), gave an
air speed of 5.6-8.6 m/s and a glide ratio of 2.30-2.85 with a Lift Coefficient of 1.78, compatible
with the observed data (mean glide ratio of 2.32, air speed of 7.51 m/s)\(^ {37}\), indicating that the Flight 1.25 model\(^ {13}\) effectively reproduces the gliding mechanics of mammals. A further test was carried out by simulating the glide of the smaller N American squirrel, *Glaucomys sabrinus* (Sciuridae) based on published data\(^ {68}\) with average AR\(^ {62}\). The very steep angle of glide and thus angle of attack was simulated by increasing the wing profile drag coefficient to 0.3. The results indicate a glide speed of 7.1 m/s (best glide) and glide ratio of 1.8 to 2.1, values that match the observed\(^ {68}\) average glide speed of 7.2 m/s and glide ratio of 1.98.

Testing the model with the flight of extant bats is more complex as aerodynamic theory suggests that minimum power and thus preferred flight speed should increase with mass\(^ {21,59}\). Bats can modify the shape of their wings\(^ {21}\) and large bats can adopt higher lift coefficients or modify wingbeat and angle of attack. Test flights in corridors and wind tunnels are also artificial environments that might affect bat speed. The Flight 1.25\(^ {13}\) model can reproduce bat as well as bird flight, and using the parameters for extant bats of: wingbeat reduction factor of 0.68, body drag coefficient of 0.25, frontal area coefficient of 1.3, and muscle mass of 9%, simulations were carried out for the bat species *Rousettus aegyptiacus*, *Cynopterus brachyotis* (Pteropodidae), *Glossophaga soricina* (Phyllostomidae) and *Tadarida brasiliensis* (Molossidae; Supplementary Table 5). The measured values of airspeed, with Lift Coefficients (L) around the normal flight value of less than 1\(^ {30}\), can then be compared with the minimum power airspeed (VmP) simulated by Flight 1.25, as well as maximum range airspeed (Vmr).

The simulated value of wind tunnel speed is slightly lower than the average for *Rousettus aegyptiacus*, a commuting bat\(^ {69}\); it is also slightly lower for *Glossophaga soricina* and *Cynopterus brachyotis*, while it was clearly lower for *Tadarida brasiliensis*. Thus, VmP as determined by the Flight program\(^ {13}\) tends to be on the conservative side for airspeeds, but still within the observed Vmp-to-Vmr range of speeds, so the overall model is generally validated, only with some caveat for highly specialized bats, such as *Tadarida brasiliensis*—an open-space, high-altitude flight specialist\(^ {69}\). The horizontal velocities of pteropodid bats\(^ {30}\) concentrate around 4.98 m/s, with non-
wind tunnel data being slightly mass dependent; thus, simulation values greater than 6 m/s would indicate airspeeds higher than levels in extant species, putting the animal at risk from collisions.

**Estimation of possible Eocene Air Densities**

Composition of paleo-atmosphere is extremely difficult to determine in any direct way; thus proxies are typically used to estimate properties of past atmosphere. Traditional models of estimating the mass of these gases from bulk rock calculations, such as Geocarbsulf (GCS) and related models, assume a constant mass of nitrogen over geologic time, thus the derived mass of atmospheric components such as oxygen and carbon dioxide are normally given as partial pressures ($p_{O_2}$ and $p_{CO_2}$). However, this assumption may not be valid. In view of the variable nature of atmospheric nitrogen, it could also be expected that PATM has both increased and decreased many times in the geological past. The assumption that atmospheric mass should be constant over Earth’s history is not an inherent property of the planet. In fact, analysis of two independent proxies, as outlined below, strongly suggests elevated PATM and consequently higher air densities for the Eocene. In the following, air pressure, air density and atmospheric mass are taken to scale at approximately the same values over the variations being considered, hence an increase of, for instance, 30% in standard air density; PATM in bar; and atmospheric mass of 1 atmosphere; are all represented as being equivalent to 1.3 bar.

**Marine versus Terrestrial Derived pCO2.** Boron isotopes in foraminifera have been used to record seawater pH and, consequently, the partial pressure of atmospheric CO$_2$ in equilibrium with this water. Low pH values of between 7.8 (40 Ma) and 7.6 (53 Ma) have been found for the Eocene, from which $pCO_2$ of about 1400 ppm (parts per million) has been derived. This technique suffers from some limitations, such as the influence of “vital effects” and size of the foraminifera; thus an attempt to resolve the discrepancy between these high CO$_2$ levels and terrestrial data suggested a basic calcite-derived CO$_2$ level of 800 ppm for the Middle Eocene.
Marine nahcolite and boron data also indicate CO$_2$ levels at c. 800 ppm or higher in marine environments by ~50 Ma$^{25,76,77}$. In contrast to this, Eocene CO$_2$ terrestrial levels from fossil plant-leaf stomata sources in New Zealand and Australia indicate levels closer to 500 ppm for the period covering 38 Ma to 53 Ma$^{78}$, which agree with many other global stomatal studies$^{25,78-85}$. The difference in derived Eocene CO$_2$ from marine and terrestrial realms has been termed 'contradictory'$^{86}$, and is also seen in the Miocene, where 'conditions are difficult to reconcile with present climate models'$.^{87}$ However, these Eocene values can be reconciled by including air pressure as a variable. The sea absorbs a large amount of CO$_2$ due to the relatively high solubility of this gas in seawater, the dissolved CO$_2$ participating in chemical and biological processes while being circulated around the global oceans. The solubility of CO$_2$ in seawater is expressed by Henry's Constant (KH) as [mol (kg H$_2$O)$^{-1}$ atm$^{-1}$]; this is approximately linear over the range 0 °C to 50 °C, and directly proportional to partial pressure$^{88}$, but highly responsive to air pressure—about 55 times greater than that of N$_2$ at 20 °C. Hence, CO$_2$ solubility in seawater is highly dependent on atmospheric pressure. CO$_2$ solubility in seawater, examined from a constant flow of gas mix (2% CO$_2$, 98% N$_2$) at 1 and 2 bar and over several constant temperatures, indicated that at 25 °C and 1 bar, solubility was 70 (CO$_2$ concentration in ppm); at 2 bar, it rose to 550 ppm$^{89}$. Assuming a reasonable linear difference given that CO$_2$ solubility in seawater from 0.1 bar to 0.9 bar is almost linear$^{89}$, this gives a gradient of about 48 ppm per 0.1 bar increase. This relation can therefore be used to match the observed terrestrial-derived and boron (seawater) derived $p$CO$_2$ such that:

Marine $p$CO$_2$ (800 ppm) = Terrestrial $p$CO$_2$ (500 ppm) + P (300 ppm)

where P approximates the extra density component derived from PATM. Thus, the difference of 300 ppm based on the CO$_2$ gradient of 48 ppm per 0.1 bar from data on CO$_2$ solubility in seawater$^{89}$ suggests an extra component of 0.63 bar, giving a paleo PATM estimate of c. 1.63 bar for the Eocene (c. 50 Ma).
Carbon Isotopes in Amber. Resins have chemical properties that make them particularly suitable as proxies of environmental changes over geological time, as these properties have not changed significantly with plant evolution\(^{28,90}\). Thus, for profuse resin producers, it can be assumed that the metabolized CO\(_2\) was sourced from isotopically undisturbed air that had a δ\(^{13}\)C composition approximating a global atmospheric average. An evaluation of the effect of a variable \(p\)O\(_2\) on amber isotopes, using experimental work on the isotopic fractionation in C3 plants and partial pressure of oxygen, revealed that the fractionation of carbon during photosynthesis was found to increase when \(p\)O\(_2\) in the ambient air is significantly higher than modern values, resulting in depleted δ\(^{13}\)C plant mass\(^{91}\). The opposite effect has also been observed under lower-than-modern \(p\)O\(_2\) in ambient air\(^{92}\). From these observations, a direct relationship is a reasonable assumption for moderate \(p\)O\(_2\) levels, provided that major physiological adaptations of plants are not involved\(^{28}\). In this empirical model, paleo-\(p\)O\(_2\) at the time of resin formation may have been as low as 13% in the Eocene - a value starkly at variance with all versions of the Geocarbsulf and Geoacarbsulfor models which predict similar \(p\)O\(_2\) levels for the past 50 Ma in relation to the c. 21% value at present\(^{70}\).

Low \(p\)O\(_2\) for the Eocene presents some apparent problems. Fire activity is effectively "switched off" at \(p\)O\(_2\) < 16%, but was greatly enhanced at 22%\(^{93}\) so it has been suggested that the low \(p\)O\(_2\) values derived from amber are incompatible with wildfire data\(^{94}\). However, these data can also be reconciled by considering that PATM may have been higher and that this empirical relationship with wildfires should therefore be reinterpreted. At higher pressure, low levels of \(p\)O\(_2\) not only sustain biological processes, but are in fact essential to avoid oxygen poisoning. A modern example of this is deep sea diving: in order to work at 130 m depth in the northern sector of the North Sea oil field, for example, the breathing mixture used only contains 10% oxygen; on the deepest working dives, at depths greater than 600 m, divers breath gas mixtures containing only 2% oxygen to avoid acute oxygen toxicity – although a lung full of gas containing 2% oxygen at 600 m contains about six times as many molecules of oxygen as a lung full of air at sea level\(^{95}\).
Thus, the mass estimates of O\textsubscript{2} based on the Geocarbsulf model data\textsuperscript{26,78} and on the pO\textsubscript{2} derived from resin/amber data can be reconciled by varying the PATM values (air density) of the resin model such that the O\textsubscript{2} mol m\textsuperscript{-3} are similar, essentially by increasing the atmospheric mass by the relevant factor. Thus for any given period:

Paleo Patm = (pO\textsubscript{2} GCS / pO\textsubscript{2} AMB) bar

where pO\textsubscript{2} GCS is the value estimated from the geocarbsulf model (21%) and pO\textsubscript{2} AMB is from amber data (averaged 13% from above sources). These factors suggest estimates of PATM (in bar) of between 1.44 and 1.64 for the Eocene (c. 50 Ma). Recent Eocene amber data\textsuperscript{96} suggest a sharp drop in PATM during the Eocene to Oligocene Transition, thus at about 50 Ma, possible levels of PATM were between 1.54 and 1.6 bar. Limited experiments at varying pressures indicate that the pO\textsubscript{2} minimum for fire is a function of the product of pO\textsubscript{2} and Patm\textsuperscript{97,98}, such that these low values would be sufficient for the wildfire propagation seen in the record. These low values are also seen in air trapped in Eocene halite and derived from a revised pyrite proxy suggesting that this could have been a period of higher air density\textsuperscript{99}.

**Data availability**

All data generated for this study are available in the Main Text and the Supplementary Information

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The authors declare no competing interest.

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Figure 1. Reconstructed aerofoil of the two existing *Onychonycteris finneyi* specimens. Half wingspan is indicated on top. Insets: dorsal view of holotype ROM 55351A, ventral view of paratype AMNH 142467, and selected parameter values.
Figure 2. Performance space for the gliding to flapping transition in bats. Positive (climb rate) or negative (sink rate) variation in vertical velocities as function of aspect ratio. Level flight is achieved at 0 m/s vertical speed (16). Intermediate models with varying aspect ratio (AR) are indicated as Gm1-to-4. Full-winged Onychonycteris finneyi fossil is indicated as Of. For the 40 g analysis (see text), variation is shown by dots representing models joined by a full line of increasing AR and decreasing sink rate under normodense (1.0 bar) and hyperdense conditions (1.6 bar). For the 44 g analysis (see text), variation is shown by black (normodense) or gray dots (hyperdense). Decreasing sink rate as AR increases depicts a positive performance gradient (gray arrow) up to the point in which a model responds to flapping, achieving level flight (dotted arrows). This scenario is intermediate between gliding (AR ≤ 2) and flapping (AR ≥ 5) regimes.
Supplementary Files

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