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Aerodynamic reconstruction of the primitive fossil bat *Onychonycteris finneyi* (Mammalia: Chiroptera)

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Bats are the only mammals capable of powered flight. One of the oldest bats known from a complete skeleton is *Onychonycteris finneyi* from the Early Eocene (Green River Formation, Wyoming, 52.5 Ma). Estimated to weigh approximately 40 g, *Onychonycteris* exhibits the most primitive combination of characters thus far known for bats. Here, we reconstructed the aerofoil of the two known specimens, calculated basic aerodynamic variables and compared them with those of extant bats and gliding mammals. *Onychonycteris* appears in the edges of the morphospace for bats, underscoring the primitive conformation of its flight apparatus. Low aerodynamic efficiency is inferred for this extinct species as compared to any extant bat. When we estimated aerofoil variables in a model of *Onychonycteris* excluding the handwing, it closely approached the morphospace of extant gliding mammals. Addition of a handwing to the model lacking this structure results in a 2.3-fold increase in aspect ratio and a 28% decrease in wing loading, thus greatly enhancing aerodynamics. In the context of these models, the rapid evolution of the chiropteran handwing via genetically mediated developmental changes appears to have been a key transformation in the hypothesized transition from gliding to flapping in early bats.

1. Introduction

Bats represent one of the most diverse lineages of mammals with nearly 1,400 currently recognized extant species [1]. The rapid diversification of bats likely reflects their capacity for flapping flight, a trait unique among mammals [2]. With Early Eocene fossils known from all continents except Antarctica, bats were the first truly cosmopolitan mammalian clade [3,4]. Among the earliest chiropteran fossils, *Onychonycteris finneyi* from the Early Eocene (52.5 Ma) of the Green River Formation, Wyoming, has been recovered as sister to all bats in phylogenetic analyses [5]. Known from two well-preserved complete skeletons, *Onychonycteris* was clearly capable of powered flight and its general wing shape has been hypothesized to indicate an undulating gliding-fluttering flight style [5]. Limb proportions and presence of claws in all wing digits suggest that *Onychonycteris* may have been a more agile climber than any other known bat [5]. The basal phylogenetic position of *Onychonycteris*, and lack of clear morphological signatures of echolocation in this bat, led Simmons *et al.* [5,6; cf. 7] to favour the flight-first hypothesis for bats over echolocation-first or tandem evolution hypotheses. Evaluating the flight adaptations and capabilities of *Onychonycteris* is thus paramount for understanding the origins of mammalian flight.

Simmons *et al.* [5] suggested rather poor flight performance in *Onychonycteris* based on a proxy of aspect ratio that is lowest among known bats.

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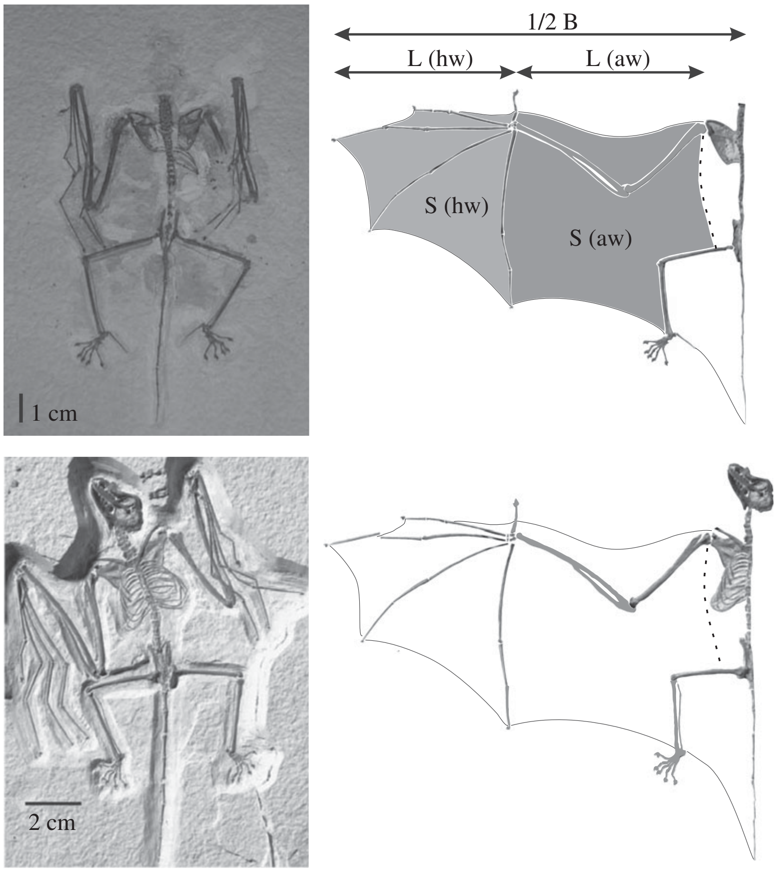

Figure 1. Holotype (ROM 55351A, upper left) and paratype (AMNH FM-142467, lower left) of *Onychonycteris finneyi*, and the reconstructions of their aerofoils (right). Aerodynamic measurements following Norberg & Rayner [15] are indicated. B, wingspan; S, surface; L, length; aw, armwing; hw, handwing.

However, that was the extent of their reconstruction and those authors did not attempt any detailed aerodynamic evaluations. In this study, we estimated basic aerodynamic features of carefully reconstructed aerofoils of the two known specimens of *Onychonycteris finneyi* and compared these with a wide sample of extant bats. Next, we manipulated aerofoil structure by removing the handwing, a key evolutionary innovation of bats [8–11]. This allowed us to evaluate the handwing's contribution to various aerodynamic variables, and to compare *Onychonycteris* with gliding mammals in which the hand contribution to the aerofoil is negligible. We predicted that *Onychonycteris* would compare poorly with other bats in terms of basic aerodynamic variables, and that removing the handwing from the reconstructed aerofoil would bring *Onychonycteris* close to the aerodynamic morphospace of gliding mammals. We evaluate the contribution of these morpho-functional findings to the gliding hypothesis of bat flight origins.

2. Material and methods

We examined the two known specimens of *Onychonycteris*: the holotype ROM 55351A (Royal Ontario Museum) and the paratype AMNH FM-142467 (American Museum of Natural History). We digitally reconstructed the aerofoil extended in a standard position as in living bats (figure 1). We estimated basic aerodynamic variables from aerofoil reconstructions of both specimens (details in electronic supplementary material, appendix S1). Wing area S (m^2) and wingspan B (m) were estimated using ImageJ software [12]. S included both wings, the body in between and the uropatagium. S and B were also measured without the handwing (patagial tracts between digits I–V; i.e. dactylopatagium plus propatagium brevis) [13]. Body mass for each specimen was taken from Giannini *et al*. [14], who reverse-estimated mass from the least mid-shaft diameter of the humerus. A sensitivity analysis was applied to these measurements (see electronic supplementary material, appendix S1). Three traditional aerodynamic variables were calculated [15]: wing loading WL (Pa), aspect ratio AR (adimensional) and tip shape index I_{tip} (adimensional). WL relates body mass (BM), gravity force (g) and wing area, and is defined as the ratio between body weight and wing area. WL varies with the square of velocity V^2 (ms^{-1}); hence, high WL requires fast flight to generate enough lift [16]. AR (B^2/S) describes the overall wing shape and reflects aerodynamic efficiency: the higher the AR, the lower the total flight power and cost of transport [16,17]. The tip shape index (the proportion between the handwing and the armwing) describes the wingtip shape defined as $I_{\mathrm{tip}} = T_{\mathrm{s}}/(T_{\mathrm{l}} - T_{\mathrm{s}})$, where T_{s} is the tip area ratio between handwing and armwing ($S_{\mathrm{hw}}/S_{\mathrm{aw}}$), and T_{l} is the tip length ratio ($L_{\mathrm{hw}}/L_{\mathrm{aw}}$; figure 1). High values of I_{tip} indicate rounded to nearly square wingtips; $I_{\mathrm{tip}} \approx 1$ corresponds with triangular wingtips; $I_{\mathrm{tip}} < 1$ indicates tapering wingtips as in high-flying bats using open spaces [15,16].

The aerodynamic variables described above are known to be only rough estimators of wing aerodynamics [18]. Nonetheless, these variables are intended to be used as approximations, are generally recognized to contain a considerable comparative value, and can be estimated with repeatability in both fossil and extant specimens. As such they are useful for interpreting general flight abilities in taxa for which biomechanical studies are lacking. The variables AR and WL were estimated for both the complete aerofoil of *Onychonycteris* and for its aerofoil excluding the handwing. These values were contrasted with aerodynamic measurements compiled from the literature for 474

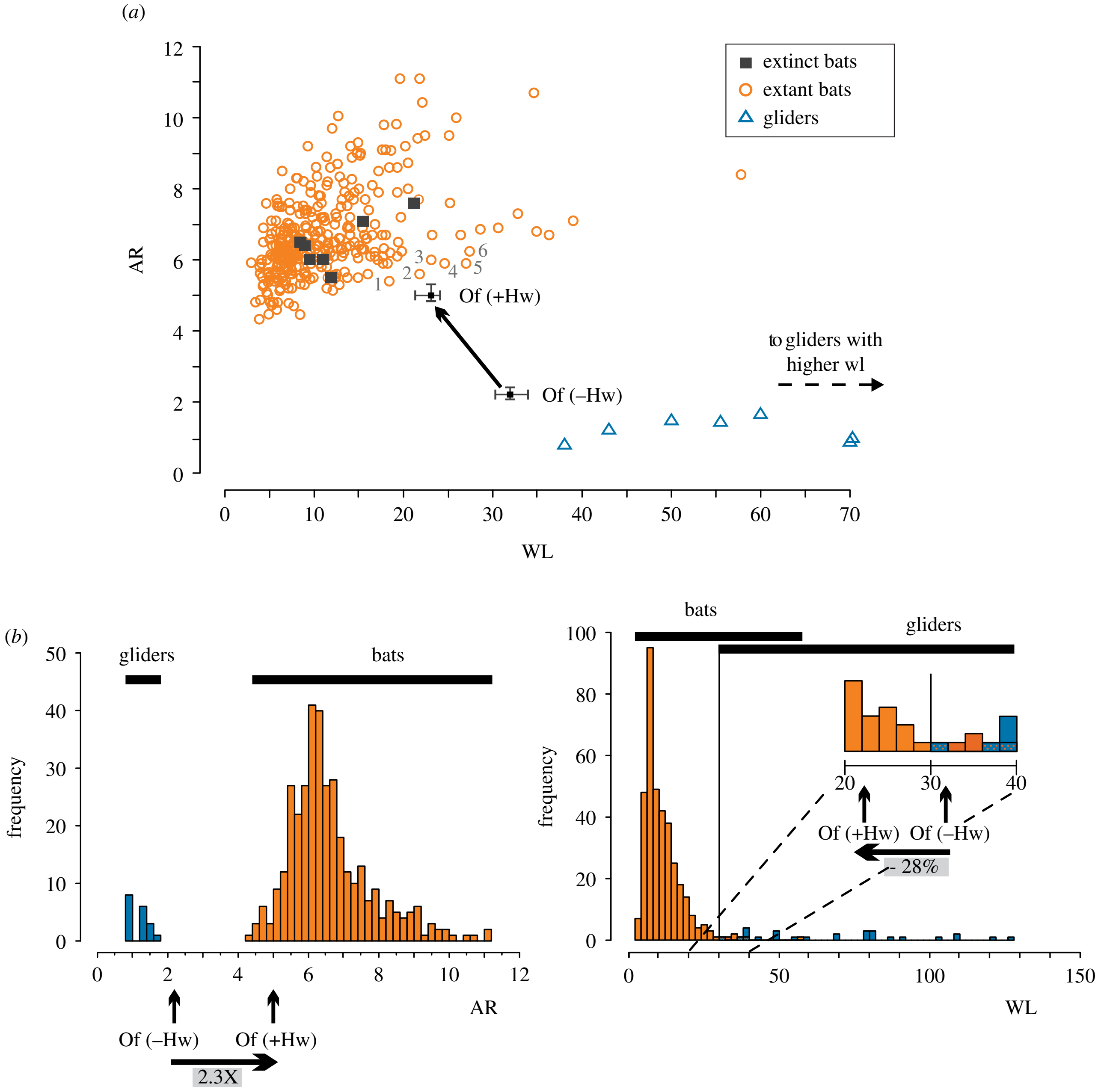

Figure 2. Comparison of wing loading (WL) and aspect ratio (AR) values estimated for *Onychonycteris finneyi* (Of), both with and without the handwing (+Hw, −Hw), to values compiled for extant bats and mammalian gliders. (*a*) Bivariate AR–WL plot showing the relative position of *Onychonycteris*; other Eocene bat species belonging to *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* are added for comparison. 1. *Vampyrum spectrum*; 2. *Stenonycteris lanosus*; 3. *Rousettus leschenaultii*; 4. *Rousettus aegyptiacus*; 5. *Epomophorus gambianus*; 6. *Epomophorus minor*. (*b*) Histograms of AR and WL showing the effect on these aerodynamic variables of the addition of the handwing on a gliding bat ancestor similar to *Onychonycteris* but lacking this structure. (Online version in colour.)

extant bat species and 28 species of gliding mammals (electronic supplementary material, table S1). We also included in the comparison previous estimates of seven selected Early Eocene bat species (those with preserved complete skeleton) in four genera (figure 2*a*; electronic supplementary material, table S1). We compared *Onychonycteris* to extant bats with a bootstrap simulation (see electronic supplementary material, appendix S2).

3. Results

The aerodynamic data calculated for *Onychonycteris finneyi* are shown in table 1. The estimated AR value was 5.0 for both the holotype and the paratype. This estimate is 22% less than the median calculated for extant bats (AR median: 6.4; AR mean: 6.7) and is among the lowest known in bats (4.3–14.3) [15]. Extant bats with similarly low AR include *Nycteris* spp. (AR = 4.8–5.5; Nycteridae), *Lavia frons* (AR = 5.4; Megadermatidae), *Chrotopterus auritus* (AR = 5.5; Phyllostomidae) and *Vampyrum spectrum* (AR = 5.4; Phyllostomidae) [15]. In *Onychonycteris*, WL was calculated to be 23.1 and 22.4 Pa (holotype and paratype, respectively), far exceeding the extant bat median (at 9.2 Pa) and mean (11.1 Pa). Extant bats with WL exceeding 20 Pa include mid-to-large sized Old World fruit bats (Pteropodidae: 21.8–57.8 Pa); *Taphozous melanopogon* (Emballonuridae: 25.9 Pa); and *Tadarida fulminans*, *Chaerephon plicatus* and *Promops nasutus* (Molossidae: 20.2 Pa, 21.8 Pa and 24.7 Pa, respectively). Wingtip descriptors were the same for both *Onychonycteris* specimens (table 1); wingtips were rounded in shape ($I_{tip} = 1.54$, a value very close to the extant bat median at 1.51).

Figure 2*a* shows the position of *Onychonycteris* when compared with extant bats, seven additional extinct bat species,

Table 1. Aerodynamic variables estimated for both known specimens of *Onychonycteris*, holotype (ROM 55351A) and paratype (AMNH FM-142467), considering both the complete wing and reconstructions excluding the handwing. See §2 for formulae used to calculate variables. Extreme values are indicated in parentheses (electronic supplementary material, appendix S1).

	holotype		paratype	
aerodynamic variables	**excluding handwing**	**complete wing**	**excluding handwing**	**complete wing**
BM: body mass (g)	39 (38.6–39.4)	39 (38.6–39.4)	41 (40.6–41.4)	41 (40.6–41.4)
S: wing area (m^2)	0.0118 (0.0112–0.0124)	0.0166 (0.0158–0.0174)	0.0128 (0.0122–0.0134)	0.018 (0.171–0189)
B: wingspan (m)	0.16 (0.152–0.168)	0.29 (0.276–0.305)	0.17 (0.162–0.179)	0.30 (0.285–0.315)
AR: aspect ratio	2.2 (2.06–2.28)	5.0 (4.81–5.32)	2.2 (2.14–2.37)	5.0 (4.75–5.25)
WL: wing loading (Pa)	32.4 (31.19–33.79)	23.1 (22.17–24.02)	31.4 (30.23–32.75)	22.4 (21.46–23.29)
Tl: tip length ratio	—	0.94	—	0.94
Ts: tip area ratio	—	0.57	—	0.57
I_{tip}: tip shape index	—	1.54	—	1.54

and mammalian gliders, in a bivariate AR–WL plot. All the extinct taxa fell within the realized morphospace of extant bats; *Onychonycteris* was placed in the lower boundary of this space. The species closest to *Onychonycteris* are the extant fruit bats *Stenonycteris lanosus* and *Rousettus leschenaultii*. Only 4.6% of all bat species equalled or exceeded the distance of *Onychonycteris* from the bat centroid (bootstrap $p = 0.045$).

Figure 2*a* also shows the position of *Onychonycteris* reconstructed without the handwing. Here, AR was 2.2 for both the holotype and paratype; WL was 32.4 Pa and 31.4 Pa, respectively (table 1). Without the handwing, *Onychonycteris* appeared very close to mammalian gliders in the AR–WL space (figure 2); all gliders exhibited $\text{AR} \leq 2$ (electronic supplementary material, table S1).

4. Discussion

Our reconstruction of the aerofoil of *Onychonycteris* suggests that it has no modern or fossil aerodynamic equivalent. *Onychonycteris* exhibits a unique, comparatively inefficient combination of very low AR and very high WL for its estimated weight (39–41 g). We interpret this aerofoil structure as primitive, in keeping with the plesiomorphic states of many discrete morphological characters in this species (e.g. presence of claws on all wing digits) and its basal (nearest to the root) phylogenetic position in the chiropteran tree [5]. *Onychonycteris* would have had to fly very fast in order to generate enough lift for its weight, at very high metabolic cost, as inferred from very low AR and the concomitant high profile drag [15]. Estimated on the basis of Rayner's vortex model [17], the power required by *Onychonycteris* to sustain level flight would have been *ca* 25% greater than a similar-sized extant bat of $\text{AR} = 6$ (*ca* 0.5 W versus 0.4 W, respectively) ([17]: fig. 20]). Fast flight typically compromises manoeuvrability, but in *Onychonycteris* the rounded shape of the wingtips might have ameliorated this effect to some extent, as expected in low AR wings [15]. However, Norberg & Rayner ([15], p. 359) warned that 'low aspect ratio acts against rapid changes of direction unless […] it is linked with low wing loading, when it becomes an adaptation for turning in slow flapping flight'. Because manoeuvrability is inversely proportional to WL [15], and in our reconstruction, *Onychonycteris* had very high WL, we conclude that this bat was not capable of manoeuvrable flight involving sharp turns. From comparison with other bats, we infer that manoeuvrable flight evolved in the bat lineages that superseded *Onychonycteris* in the Eocene skies. *Onychonycteris* most probably used flight for (necessarily fast) commuting between roosting points and foraging sites; in fact, its position in AR–WL space is closest to extant species that evolved commuting flight as a derived adaptation ([19]: fig. 1.16).

Without the handwing, WL of *Onychonycteris* is 31.4–32.4 Pa, thus roughly comparable to the minimum values observed in mammalian gliders (range 30–130 Pa; figure 2*b*), and AR is 2.2, only slightly larger than the upper boundary for gliders (range 0.8–1.7, figure 2*b*). This places our model very close to the realized morphospace of extant gliding mammals. We speculate that, other variables being equal, evolving the handwing in a lineage with an ancestor similar to our *Onychonycteris* model would have caused an important decrease in WL (*ca* 28% in our reconstruction) with respect to a gliding *bauplan*. Concomitantly, addition of the handwing would have produced a dramatic increase in AR (2.3X in our reconstruction) from AR in the upper boundary of gliders to one within the lower limit seen in extant bats (figure 2*b*). Addition of the handwing thus bridges the AR-gap between gliders and bats (figure 2). From a developmental perspective, evolution of the handwing in bats is thought to have occurred through retention of the embryonic interdigital membrane and the lengthening of wing digits [9–11,20]. In the latter process, altered expression of protein BMP2 during embryonic development promotes proliferation and retards maturation of chondrocytes in epiphyseal cartilages of digital joints. BMP2-expression in the bat hand is 30% upregulated as compared to a mouse model, thereby explaining the rapid lengthening of embryonic wing digits in bats [9–11,20]. This developmental mechanism might have provided a direct mechanism for evolving the bat handwing from an ancestral form lacking this structure but already possessing membranes and gliding capabilities.

Onychonycteris might have had an undulating flight style involving alternating flapping and gliding [5], a type of flight in which much energy can potentially be saved during the gliding phase. During gliding, an animal typically speeds up while losing altitude [21,22]; intermittent flapping then helps recover level flight, also reducing velocity [21,23,24]. From the perspective of the gliding hypothesis of the origin of bat flight [14,17,21,25,26], this type of flight provides a plausible transition model in the sense that, as predicted from vortex models [17], incipient flapping is energetically possible for a bat near the size of *Onychonycteris* with $AR \geq 2.5$. Evolution of the handwing thus would have served to slow down flight and to reduce the cost of transport during commuting [21], thereby facilitating subsequent evolution of level (0° gliding angle) flight.

Our reconstructions of the aerofoil of the aerodynamically unique bat *Onychonycteris finneyi*, and of a model based on this key fossil without its handwing, contribute significantly to shape the gliding hypothesis of the origin of bat flight, first advanced by Darwin [27]. We propose that evolution of the handwing by a developmental mechanism promoting digit lengthening would have enabled a gliding bat ancestor to reduce WL, thus decreasing velocity while gaining manoeuvrability, and to increase AR, enhancing aerodynamic efficiency, thereby reducing the cost of transport. Our reconstruction thus provides a morpho-functional link between the aerofoil of mammalian gliders and the flapping aerofoil of bats.

Ethics. Fossil specimens were examined with permission from corresponding authorities.

Data accessibility. All morphometric data are available from electronic supplementary material, table S1 and from Dryad Digital Repository: https://doi.org/10.5061/dryad.0ks22bg [28].

Authors' contributions. L.I.A. and N.P.G. conceived the study and performed the statistical data analysis. N.P.G. and N.B.S. examined the specimens. N.B.S. provided the images. L.I.A. estimated the measurements from images, collected literature data and processed the information. All authors interpreted the data, drafted and revised the manuscript, gave final approval for publication and agree to be held accountable for the work performed therein.

Competing interests. We have no competing interests.

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