



Venditti, C., Baker, J., Benton, M. J., Meade, A., & Humphries, S. (2020). 150 million years of sustained increase in pterosaur flight efficiency. *Nature*, 587, 83-86. <https://doi.org/10.1038/s41586-020-2858-8>

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1 **150 million years of sustained increase in pterosaur flight efficiency**

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11 **Summary**

12 *The long-term accumulation of biodiversity has been punctuated by remarkable*
13 *evolutionary transitions that allowed organisms to exploit new ecological*
14 *opportunities. Mesozoic flying reptiles, the pterosaurs, which dominated the skies for*
15 *over 150 million years (Myr) were the product of one such transition. The ancestors of*
16 *pterosaurs were small and likely bipedal early archosaurs¹, which were certainly well*
17 *adapted to terrestrial locomotion. Pterosaurs diverged from dinosaur ancestors in the*
18 *Early Triassic (~245 Myr ago, Ma), and yet their first fossils come 25 Myr later, in the*
19 *Late Triassic. Thus, in the absence of proto-pterosaur fossils, it is difficult to study*
20 *how flight first evolved in this group. Our aim here is to study the evolutionary*
21 *dynamics of pterosaurs' adaptation to a new locomotory medium. The earliest known*
22 *pterosaurs took flight and subsequently appear to have become capable and efficient*
23 *flyers. However, it seems clear that transitioning between forms of locomotion^{2,3} -*
24 *from terrestrial to volant – challenged early pterosaurs by imposing a steep energetic*
25 *hill to climb, thus requiring flight to provide some offsetting fitness benefits. Using*

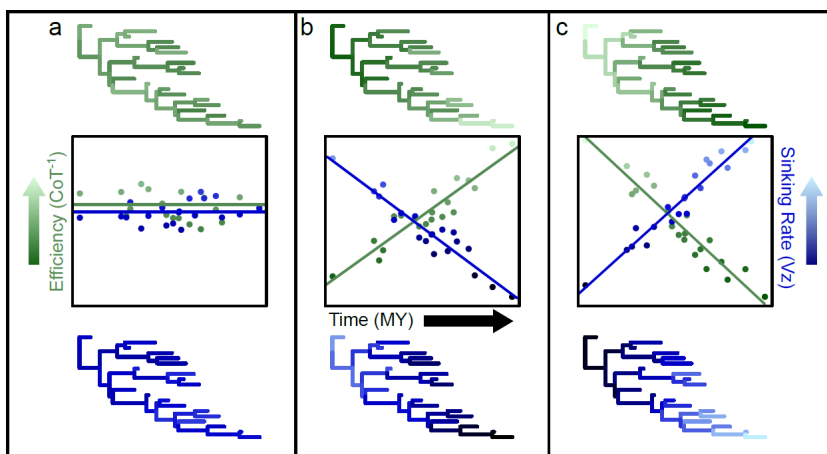
26 ***novel phylogenetic statistical methods and biophysical models combined with***
27 ***information from the fossil record, we detect an evolutionary signal of natural***
28 ***selection acting to increase flight efficiency over millions of years. Our results show***
29 ***that there was still significant room for improvement in terms of efficiency after the***
30 ***appearance of flight. However, in the Azdarchoidea⁴, a clade exhibiting gigantism, we***
31 ***test the hypothesis that there was a decreased reliance on flight⁵⁻⁷ and find evidence***
32 ***for reduced selection on flight efficiency in this clade. By combining biophysical***
33 ***models and phylogenetic statistical methods with the fossil record we offer a***
34 ***blueprint to study functional and energetic changes through geological time***
35 ***objectively at a far more nuanced level than has ever before been possible.***

36

37 In order to determine how pterosaurs' propensity for flight changed during their evolutionary
38 history, we calculated two indices of flight performance using a biophysical model of
39 powered and gliding flight⁸⁻¹⁰. Firstly, we used an efficiency of flight index (kg m J^{-1}), that is
40 the inverse of the cost of transport¹⁰, CoT^{-1} (see Methods and Table S1 for the flight model
41 parameterization). The CoT ($\text{J kg}^{-1}\text{m}^{-1}$) is the metabolic energy required to move a unit mass
42 a unit distance at the least energetically expensive travel speed. Secondly, we calculated a
43 sinking rate¹⁰, V_z (m s^{-1} , see Methods) valid for gliding. A low sinking rate allows for longer
44 travel distances per glide, but also for climbing in updrafts where sinking rate must be lower
45 than the rate at which air rises from the ground. Both CoT^{-1} and V_z were calculated using
46 published estimates of mass, wingspan, wing area, and projected frontal area. We use a
47 dataset of mass and wing area estimates for 16 species of pterosaur¹¹ (Table S2, Methods).
48 Although an alternative dataset of mass and wing area estimates is available for 12
49 species¹², the two datasets cannot be combined owing to considerable differences in the
50 approaches of each paper to body mass estimation (and the fact that the two datasets
51 overlap). However, our results are qualitatively the same using mass and wing area
52 estimates from each of the two datasets in isolation, and so here we only report the results

53 from one dataset¹¹. We use published frontal areas¹² and wingspans¹³ (see Methods for
54 details).

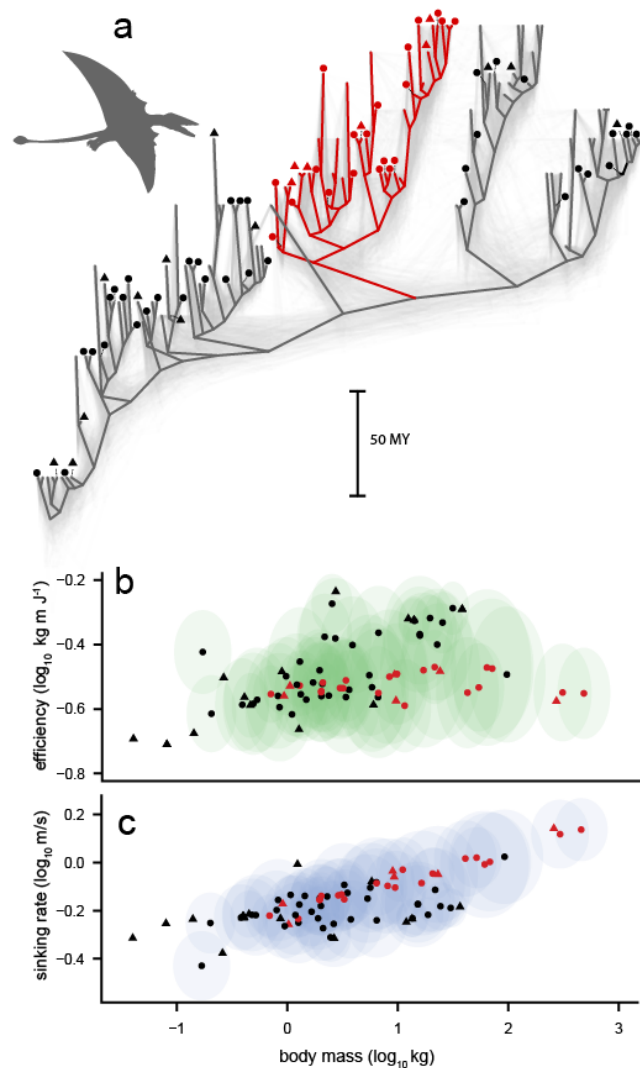
55 Studying the changes in CoT^{-1} and V_z through time can inform us about how natural
56 selection has acted on flight performance throughout the course of pterosaur evolution. The
57 lack of proto-pterosaurs in the fossil record means that it is currently impossible to be sure
58 how the pterosaurs initially overcame the energetic hill necessary to achieve flight. Our aim
59 is to study the evolutionary dynamics of pterosaurs' adaptation to a new locomotory medium.
60 The earliest known pterosaur fossils indicate they were able to fly¹⁴. If during their 150 Myr of
61 evolution their flight performance and efficiency did not improve or decrease we would
62 expect to see no trend in CoT^{-1} and V_z over time (Figure 1a). We might however expect that
63 after the start of a transition involving a change in the defining medium of locomotion (i.e.
64 from terrestrial to volant), species would be relatively energetically inefficient at moving in the
65 new environment. Thus, over time they would become more efficient. In this case, we would
66 expect flight efficiency (CoT^{-1}) to increase through time and sinking rate (V_z) to decrease
67 (Figure 1b). We would expect the opposite (a decrease in CoT^{-1} and an increase in V_z over
68 time) if flight performance reduced over time (Figure 1c).



70 **Figure 1: Hypothesised scenarios of the evolutionary trajectory of flight performance**
71 **metrics through time.** a) No relationship between flight performance metrics and time
72 would indicate no directional change in flight ability through time. b) An increase in efficiency
73 through time and a reduction in sinking rate would demonstrate a general tendency for

74 selection favouring increased flight performance as the pterosaurs radiated. c) A decrease in
 75 efficiency and an increase in sinking rate would imply a reduction in flight performance
 76 through time. The branches of the phylogenetic trees are coloured by hypothesised
 77 magnitudes of efficiency (green) and sinking rate (blue).

78 In order to study the evolution of flight (including calculation of the flight performance
 79 indices), it is necessary to account for shared ancestry owing to phylogeny. Several
 80 phylogenetic trees for pterosaurs exist in the literature e.g. 1,15,16, but none of these provides
 81 well-justified estimates of the uncertainty among species relationships and divergence dates.
 82 To account for phylogenetic and temporal uncertainty in our analyses we constructed a
 83 Bayesian dated posterior sample of phylogenetic trees for 128 pterosaurs using published
 84 character state data¹⁵ (Figure 2 and see Methods).



86 **Figure 2: Pterosaur phylogeny and the relationship of flight performance metrics with**
87 **mass.** a) Density diagram ¹⁷ showing the uncertainty in our phylogenetic reconstruction for
88 pterosaurs (see Methods for details). Superimposed is the maximum clade credibility tree,
89 and triangle points indicate species for which we have published data on mass, wing area,
90 frontal area, and wingspan. Circle points indicate species for which we have wingspan only.
91 Red denotes azdarchoids. b) The relationship between flight efficiency and mass, with our
92 mean phylogenetic imputations plotted with standard deviations shown by the green ellipses.
93 c) The relationship between sinking rate and mass, with our mean phylogenetic imputations
94 plotted with standard deviations shown by the blue ellipses.

95 Wingspan is strongly associated with pterosaur morphologies. We find wingspan
96 explained 97% (range of the posterior distribution, 95–98%) of the variation in mass, 97%
97 (96–98%) of the variation in wing area, and 75% (71–87%) of the variation in frontal area.
98 Then using a phylogenetic prediction method¹⁸ we derived a posterior distribution of imputed
99 masses, projected frontal area and wing area for a further 59 species of pterosaurs based on
100 the results of the phylogenetic regression analyses and our phylogenetic tree (Table S2).
101 Our use of Bayesian phylogenetic methods means we integrate our analyses over all
102 phylogenetic (topology and divergence dates) and model uncertainties. Thus, based on our
103 imputations, we calculated a posterior distribution of 1000 CoT^{-1} and 1000 V_z estimates for
104 use in our analyses of flight performance through time (see Methods). Our final set of
105 analyses used information from 75 species, including the uncertainty from imputed values
106 that span the majority of the phylogenetic diversity of all known pterosaurs (Figure 2a).

107 While CoT^{-1} is an efficiency index related to the amount of energy needed to travel a
108 given distance, independently of how long it takes, we do expect it to correlate with mass¹⁹.
109 It is energetically cheaper for a large animal to move a given mass over a particular distance
110 than for a small animal to travel the same distance²⁰ (Figure 2b). Sinking rate is similarly
111 affected by mass (Figure 2c) and reflects the relationships we know for birds and bats
112 (Supplementary Information).

113 This relationship with mass means that should simultaneously consider mass and its
114 evolutionary association with flight performance in our analyses of flight efficiency and
115 sinking rate through time. With this in mind, pterosaurs have been reported to conform with
116 the well-known Cope's rule¹³ – a phenomenon where species increase in size through
117 geological time. The most compelling evidence for this is derived from analyses reporting an
118 increase in wingspan from ~150 Myr ago to the end of the Cretaceous (~66 Myr ago)
119 coincident with the origin of birds (Avialae)¹³. However, such a trend could emerge as a
120 consequence of increased flight efficiency rather than increase in body size *per se*. Animals
121 with a larger wingspan for their mass are likely to be more efficient flyers⁹. We find using a
122 phylogenetic regression model that accounts for the uncertainty in our inferred tree and our
123 estimates of species masses, frontal area and wing area (see Methods), that pterosaur size
124 did increase significantly through time. In addition, a model that allows the rate of mass
125 increase through time to differ before and after the origin of the birds fits significantly better
126 than a model without such an inflection. In line with earlier conclusions¹³, we find that there is
127 no significant increase in size until ~150 Ma ($p_x = 0.59$). From that point the average
128 pterosaur grew significantly from 0.60 kg to 6.05 kg (proportion of the posterior distribution
129 that crosses zero, $p_x = 0.02$), a ~10-fold increase in size, over 65 million years.

130 Turning now to flight performance, there is a growing body of evidence indicating that
131 the Azhdarchoidea had strong terrestrial adaptations^{5-7,20} (cf. ²²). Here the Azhdarchoidea
132 are considered to comprise the common ancestor and all descendants of *Tapejara*,
133 *Quetzlcoatlus*, and *Dsungaripterus*¹ (posterior nodal support = 0.83 in our phylogeny).
134 Evidence suggests that azhdarchoid pterosaurs had relatively inflexible necks⁷, left tracks
135 indicating terrestrial proficiency⁵, and possessed other adaptations associated with ground-
136 dwelling generalist foraging (reviewed^{6,7}). *Dsungaripterus* (the most basal azhdarchoids in
137 our phylogeny, Figure 2) are reported to have been wading foragers^{14,21} feeding on hard-
138 shelled organisms at water margins²³. Given the terrestrial tendencies in the Azhdarchoidea
139 compared to what we know about other pterosaurs, we might expect diminished reliance on
140 flight, leading to the expectation that they might have differed from other pterosaurs in the

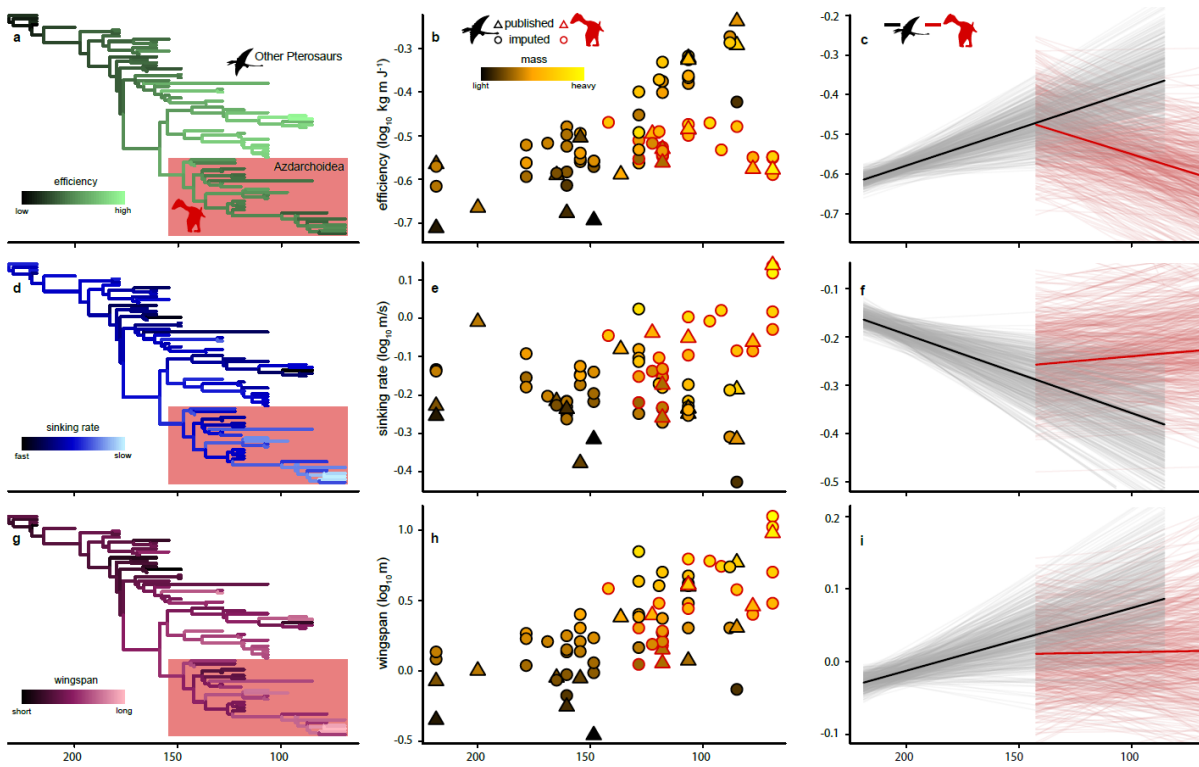
141 selection pressures for adaptations associated with flight and locomotion. Thus, in our
142 analyses we test whether the evolution of flight performance through time in the
143 Azhdarchoidea is distinct from other pterosaur species.

144 Applying phylogenetic regression to flight efficiency through time we find that, even
145 after accounting for mass, efficiency increased significantly ($p_x = 0.00$, Figure 3a–c) in non-
146 azdarchoid pterosaurs. However, in contrast to our finding for mass, there is no significant
147 effect associated with the arrival of birds ($p_x = 0.47$). Early pterosaurs (<200 Ma) had an
148 average efficiency of 0.29 kg m J^{-1} but by 70 Ma they were greater than 50% more efficient
149 ($\text{CoT}^{-1} = 0.51 \text{ kg m J}^{-1}$). Congruently we find that sinking rate (after accounting for mass) for
150 non-azdarchoid pterosaurs reduced from 0.80 m s^{-1} to 0.50 m s^{-1} over the course of the 150
151 myr of their evolutionary history (Figure 3d–f). In contrast, azdarchoids exhibited no change
152 in efficiency or sinking rate from origin to extinction.

153 Our results show that, save for azdarchoids, following their transition to volant
154 locomotion, the pterosaurs exhibited a sustained increase in flight efficiency over 150 myr
155 until their extinction. To achieve this, natural selection acted to decouple the evolution of
156 body size and wingspan (Figure 3g–i) to sculpt these enigmatic creatures from what might
157 have been inefficient flyers that took to the air for only short spells, to creatures that could fly
158 long distances over extended periods. At their origin, some ~147 Ma, 85 myr after the origin
159 of crown pterosaurs, azdarchoids had a slightly lower flight efficiency and higher sinking
160 rates compared with their contemporaries – and showed no temporal trends in either trait
161 until their eventual extinction (Figure 3a–f). This reduced pattern of flight efficiency is also

162 borne out in analyses of gross morphology - azdarchoids arose with short wings for their
 163 size, and maintained this condition until their final demise.

164



165 **Figure 3: Flight performance through time.** Summary plots for each of our three main
 166 traits of interest (efficiency, a–c; sinking rate, d–f; wingspan, g–i). A phylogeny of the species
 167 included in each analysis (a, d, g) is shown with branches shaded by reconstructed trait
 168 values; Azdarchoidea is highlighted in red. Trait data are shown plotted against time (b, e, h)
 169 where all species with imputed values are represented by circles – excepting wingspan data
 170 which is all from published sources. Points are coloured by species' body mass and
 171 azdarchoid species are outlined in red. The posterior distribution of model predictions for
 172 each trait against time (c, f, i) shows how these traits evolved during pterosaur history.
 173 These relationships demonstrate that – after accounting for size – pterosaurs continually
 174 increased their efficiency (c) and wingspan (i) whilst there was a continual reduction in
 175 sinking rate (f) through time (grey lines, median in black). This applies to all pterosaurs
 176 except azhdarchoids (pink lines, median in red) which show no significant trends – although
 177 they do have relatively short wings for their mass (i).

178 Our approach demonstrates the power of combining biophysical models and
 179 phylogenetic statistical methods with the fossil record to understand the evolution of flight in
 180 pterosaurs. In doing so we offer a blueprint to study functional and energetic changes
 181 objectively through geological time at a far more nuanced level than has ever before been
 182 possible.

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- 270

271 **Methods**

272 *Phylogenetic Inference*

273 All morphological data were obtained from a published phylogenetic character matrix¹⁵.
274 However, we retained only discrete morphological characters, excluding the continuously
275 varying characters, and treating all ordered characters as unordered, resulting in a total of
276 220 discrete morphological characters coded for 128 pterosaur species.

277 We constructed a posterior sample of time-calibrated phylogenetic trees for
278 pterosaurs using the birth-death serial-sampling model^{24,25} as implemented in BEAST v2.4²⁶
279 allowing for simultaneous estimation of both the topology and divergence times. For each
280 species, we tip-dated using the midpoint of the stratigraphic age representing the first
281 appearance of each species using published time intervals^{1,12,15}. The origin of the birth-death
282 process was estimated from a uniform prior distribution ranging from the age of the youngest
283 species in the tree (*Eudimorphodon rosenfeldi*) up to an arbitrary upper limit of 350 Ma.

284 Owing to the lack of information about speciation and extinction rates in the pterosaur
285 literature we took a conservative approach by placing a wide uninformative prior distribution
286 (uniform ranging between 0 and infinity) on both the effective reproductive number (the birth-
287 death ratio) and the “become uninfected rate” (total death rate). Similarly, we placed an
288 uninformative uniform prior between 0 and 1 on the sampling proportion. Together, these
289 parameters enable direct estimation of birth-death rates throughout the phylogenetic tree²⁴.

290 We modelled rate heterogeneity across lineages using an uncorrelated relaxed
291 morphological clock²⁷. We placed an exponential prior (mean = 1) on the mean of the
292 lognormal distribution from which the branch-wise clock rates are drawn, and a gamma prior
293 ($\alpha = 0.5396$, $\beta = 0.3819$) on the standard deviation. Characters were partitioned on the basis
294 of the number of discrete states, and we applied Lewis' Markov k (Mk) model of
295 morphological character evolution²⁸ across all partitions, estimating a shared gamma shape
296 parameter (Γ_4)²⁹ using an exponential prior distribution with mean = 1.

297 The MCMC chain was run for one billion iterations, sampling every 100,000 iterations
298 after convergence. To produce the posterior sample of 1,000 phylogenetic trees used in the
299 main analyses, we randomly sampled 1,000 iterations from this chain, ensuring that all
300 parameters had an effective sample size of >500, calculated using Tracer v1.6³⁰. We
301 ensured that all parameters that were estimated using a uniform uninformative prior (origin,
302 effective reproductive number, become uninfected rate, and the sampling rate) returned a
303 posterior distribution of estimates that differed from the prior. The analysis was repeated
304 multiple times to ensure convergence was reached. All chains were inspected visually using
305 Tracer v1.6³⁰.

306 The full sample is visualized in Figure 2a as a density tree produced in R³¹ using
307 functions available in the package phangorn¹⁷, and is available to download in nexus format
308 as Supplementary Data 1 of this article.

309 *Imputation of pterosaur measurements*

310 To calculate our efficiency index (see below) we required mass, frontal area and wing area
311 for adult pterosaur species. Estimates for mass and wing area are available for N=16
312 species from Witton¹¹ and N=12 species from Henderson¹² (see Table S2). For frontal area
313 values are taken from Henderson¹² (N = 12, though see below). Independently for each of
314 the two datasets, we used the phylogenetic method outlined in¹⁸ to impute a posterior
315 sample of 1000 estimates of mass, frontal area and wing area for a total of N = 75 species.
316 We obtained wingspans for additional species from¹³ (a list of species used is found in Table
317 S2) and used each morphological trait's relationship with wingspan (i.e. a phylogenetic
318 regression of each trait against wingspan) to impute species-specific values. As a part of this
319 procedure, we also imputed frontal area for the N=7 species in the Witton¹¹ dataset which
320 did not have data in Henderson¹² (see Table S2).

321 *Flight energetics model*

322 Animal powered flight energetics, while perhaps kinematically different for bats, birds and
323 pterosaurs, are still ultimately constrained by physics. It has previously been demonstrated
324 that it is possible to infer flight performance of pterosaurs using biophysical models of flight
325 in combination with metabolic scaling estimates from birds⁸. Here we used an actuator-disc
326 based model owing to the pedigree of this approach and because more complex wake
327 dynamics models and computational approaches are particularly difficult to parameterize,
328 requiring a number of kinematic parameters such as wingbeat frequency that are impossible
329 to infer from fossil material. We used a modified version of Pennycuick's Flight model
330 (v1.25)⁹ that we developed from earlier work⁸ and implemented in Matlab^{®32}, and which
331 includes published parasite power estimates³³. Flight performance is estimated based on
332 morphological measurements such as body mass, wingspan and wing area (Table S1) and
333 the model produces a U-shaped power-to-airspeed relationship, from which a minimum
334 power speed (V_{mp}) can be calculated. This V_{mp} is the least energetically expensive flight
335 speed and so provides a useful proxy for efficiency¹⁰ when incorporated into the CoT.

336

337 We used the model to estimate the metabolic and mechanical power required for
338 powered (flapping) flight given information on a minimal set of morphological traits and
339 estimates of physiology, as well as aerodynamic constants (Table S1). The intersection of
340 the power curve with an animal's available metabolic power (P_{BMR} , calculated from mass and
341 estimated basal metabolic rate, BMR) allows us to characterise flight ability^{9,33}. Consistent
342 with current thought^{34,35}, and in line with previous studies⁸, we assume that pterosaurs had a
343 BMR similar to that of birds.

344 *Estimation of energetic efficiency*

345 A number of energetic efficiency measures exist¹⁰ but one useful proxy is the inverse of the
346 mass specific Cost of Transport (CoT, the energy required to move a unit mass a unit
347 distance, independent of the time taken to do so). We estimate CoT as $P_{BMR}/(V \times M)$ where

348 V is the least energetically expensive travel speed (i.e. V_{mp}) and other parameters are as in
349 Table S1.

350 For species with available data (Table S2) we produced a single estimate of CoT^{-1}
351 using the inverse of the above formula. For each of the species for which we imputed mass,
352 frontal area and wing area (Table S2 and above), we use the full sample of our imputed
353 values to produce a posterior sample of 1000 estimates of CoT^{-1} .

354 As formulated, CoT accounts for mass. However, as energy efficiency appears to
355 increase with body size^{19,36} we included size in our regression model of CoT^{-1} through time
356 (main text and see below) to account for this.

357 *Estimation of sinking rate*

358 Sinking rate while gliding (V_z) was calculated as $D \times V_{mp} / M \times g$ (where D is the total
359 aerodynamic drag resulting from the addition of the induced, parasite and profile drags) and
360 assuming a linear wingspan reduction (see³⁴).

361 *Phylogenetic regression models testing temporal trends in mass and efficiency*

362 To test the evolutionary trajectories of pterosaur mass and measures of flight efficiency
363 through time we use phylogenetic generalized least squares^{37,38} multiple regression models
364 in a Bayesian framework. We assessed the significance of regression parameters using the
365 proportion of the posterior distribution that crosses zero, p_x , where we consider $p_x < 0.05$ as
366 significant. In addition to the 16 species for which we have single estimates of body mass,
367 V_z and CoT^{-1} from 11 (or $N = 12$ from¹²), in all our models we include the full set of posterior
368 estimates of both body mass and CoT^{-1} for all species for which the data are imputed (Table
369 S2). These values are sampled in proportion to their probability during the running of the
370 MCMC chain. This allows us to incorporate information about the variance of our
371 imputations, avoiding problems associated with summarizing the posterior distribution into a
372 single point estimate.

373

374 **Methods References**

375 **Data and Code Availability Statement**

376 All analyses in this research were conducted using freely available, published programs and
377 are cited where appropriate in the text. The phylogeny we generated in this study is included
378 as a supplemental data file to this article. No other data was generated or analysed during
379 the current study.

380 **Acknowledgements**

381 We thank Ciara O'Donovan, Mark Pagel, Graeme Ruxton, and Manabu Sakamoto for helpful
382 discussions during the course of this research. JB is funded by the Leverhulme Trust (ECF-
383 017-22). CV was funded by a Leverhulme Trust Research Project Grant (RPG-2017-071).
384

385 **Author Contributions**

386 All authors contributed to all aspects of this research.