

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

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

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## 13 **Summary**

14 ***The long-term accumulation of biodiversity has been punctuated by***  
15 ***remarkable evolutionary transitions that allowed organisms to exploit new***  
16 ***ecological opportunities. Mesozoic flying reptiles – the pterosaurs – which***  
17 ***dominated the skies for over 150 million years (myr) were the product of one***  
18 ***such transition. The ancestors of pterosaurs were small and likely bipedal***  
19 ***early archosaurs<sup>1</sup>, which were certainly well adapted to terrestrial locomotion.***  
20 ***Pterosaurs diverged from dinosaur ancestors in the Early Triassic (~245 myr***  
21 ***ago, Ma), and yet their first fossils come 25 myr later, in the Late Triassic.***  
22 ***Thus, in the absence of proto-pterosaur fossils, it is difficult to study how***  
23 ***flight first evolved in this group. Our aim here is to study the evolutionary***

24 ***dynamics of pterosaurs' adaptation to a new locomotory medium. The earliest***  
25 ***known pterosaurs took flight and subsequently appear to have become***  
26 ***capable and efficient flyers. However, it seems clear that transitioning between***  
27 ***forms of locomotion<sup>2,3</sup> - from terrestrial to volant – challenged early pterosaurs***  
28 ***by imposing a steep energetic hill to climb, thus requiring flight to provide***  
29 ***some offsetting fitness benefits. Using novel phylogenetic statistical methods***  
30 ***and biophysical models combined with information from the fossil record, we***  
31 ***detect an evolutionary signal of natural selection acting to increase flight***  
32 ***efficiency over millions of years. Our results show that there was still***  
33 ***significant room for improvement in terms of efficiency after the appearance of***  
34 ***flight. However, in the Azdarchoidea<sup>4</sup>, a clade exhibiting gigantism, we test the***  
35 ***hypothesis that there was a decreased reliance on flight<sup>5-7</sup> and find evidence***  
36 ***for reduced selection on flight efficiency in this clade. By combining***  
37 ***biophysical models and phylogenetic statistical methods with the fossil***  
38 ***record, we offer a blueprint to study functional and energetic changes through***  
39 ***geological time objectively at a far more nuanced level than has ever before***  
40 ***been possible.***

41

42 In order to determine how pterosaurs' propensity for flight changed during their  
43 evolutionary history, we calculated two indices of flight performance using a  
44 biophysical model of powered and gliding flight<sup>8-10</sup>. Firstly, we used an efficiency of  
45 flight index ( $\text{kg m J}^{-1}$ ), that is the inverse of the cost of transport<sup>10</sup>,  $\text{CoT}^{-1}$  (see  
46 Methods and Table S1 for the flight model parameterization). The CoT ( $\text{J kg}^{-1}\text{m}^{-1}$ ) is  
47 the metabolic energy required to move a unit mass a unit distance at the least  
48 energetically expensive travel speed. Secondly, we calculated a sinking rate<sup>10</sup>,  $V_z$  (m

49  $s^{-1}$ , see Methods) valid for gliding. A low sinking rate allows for longer travel  
50 distances per glide, but also for climbing in updrafts where sinking rate must be  
51 lower than the rate at which air rises from the ground. Both  $CoT^{-1}$  and  $V_z$  were  
52 calculated using published estimates of mass<sup>11,12</sup>, wingspan<sup>13</sup>, wing area<sup>11,12</sup>, and  
53 projected frontal area<sup>12</sup>. The dataset we use in this paper has mass and wing area  
54 estimates for 16 species of pterosaur<sup>11</sup> (Table S2, Methods). Although an alternative  
55 dataset of mass and wing area estimates is available for 12 species<sup>12</sup>, the two  
56 datasets cannot be combined owing to considerable differences in the approaches of  
57 each paper to body mass estimation (and the fact that the two datasets overlap).  
58 However, our results are qualitatively the same using mass and wing area estimates  
59 from each of the two datasets in isolation, and so here we only report the results  
60 from one dataset<sup>11</sup>. We use published frontal areas<sup>12</sup> and wingspans<sup>13</sup> (see Methods  
61 for details).

62         Studying the changes in  $CoT^{-1}$  and  $V_z$  through time can inform us about how  
63 evolutionary changes such as natural selection have acted on flight performance  
64 throughout the course of pterosaur evolution. The lack of proto-pterosaurs in the  
65 fossil record means that it is currently impossible to be sure how the pterosaurs  
66 initially overcame the energetic hill necessary to achieve flight. Our aim is to study  
67 the evolutionary dynamics of pterosaurs' adaptation to a new locomotory medium.  
68 The earliest known pterosaur fossils indicate they were able to fly<sup>14</sup>. If during their  
69 150 myr of evolution their flight performance and efficiency did not improve or  
70 decrease we would expect to see no trend in  $CoT^{-1}$  and  $V_z$  over time (Figure 1a). We  
71 might however expect that after the start of a transition involving a change in the  
72 defining medium of locomotion (i.e. from terrestrial to volant), species would be  
73 relatively energetically inefficient at moving in the new environment. Thus, over time

74 they would become more efficient. In this case, we would expect flight efficiency  
75 ( $\text{CoT}^{-1}$ ) to increase through time and sinking rate ( $V_z$ ) to decrease (Figure 1b). We  
76 would expect the opposite (a decrease in  $\text{CoT}^{-1}$  and an increase in  $V_z$  over time) if  
77 flight performance reduced over time (Figure 1c).

78         In order to study the evolution of flight (including calculation of the flight  
79 performance indices), it is necessary to account for shared ancestry owing to  
80 phylogeny. Several phylogenetic trees for pterosaurs exist in the literature e.g. 1,15,16,  
81 but none of these provides well-justified estimates of the uncertainty among species  
82 relationships and divergence dates. To account for phylogenetic and temporal  
83 uncertainty in our analyses we constructed a Bayesian dated posterior sample of  
84 phylogenetic trees for 128 pterosaurs using published character state data<sup>15</sup> (Figure  
85 2, Supplementary Data 1, and see Methods).

86         Wingspan is strongly associated with pterosaur morphologies. We find  
87 wingspan explained 97% (range of the posterior distribution, 95–98%) of the  
88 variation in mass, 97% (96–98%) of the variation in wing area, and 75% (71–87%) of  
89 the variation in frontal area. Then using a phylogenetic prediction method<sup>18</sup> we  
90 derived a posterior distribution of imputed masses, projected frontal area and wing  
91 area for a further 59 species of pterosaurs based on the results of the phylogenetic  
92 regression analyses and our phylogenetic tree (Table S2). Our use of Bayesian  
93 phylogenetic methods means we integrate our analyses over all phylogenetic  
94 (topology and divergence dates) and model uncertainties. Thus, based on our  
95 imputations, we calculated a posterior distribution of 1000  $\text{CoT}^{-1}$  and 1000  $V_z$   
96 estimates for use in our analyses of flight performance through time (see Methods).  
97 Our final set of analyses used information from 75 species, including the uncertainty

98 from imputed values that span the majority of the phylogenetic diversity of all known  
99 pterosaurs (Figure 2a).

100 While  $\text{CoT}^{-1}$  is an efficiency index related to the amount of energy needed to  
101 travel a given distance, independently of how long it takes, we do expect it to  
102 correlate with mass<sup>19</sup>. It is energetically cheaper for a large animal to move a given  
103 mass over a particular distance than for a small animal to travel the same distance<sup>20</sup>  
104 (Figure 2b). Sinking rate is similarly affected by mass (Figure 2c) and reflects the  
105 relationships we know for birds and bats (Supplementary Information).

106 This relationship with mass means that we need to simultaneously consider  
107 mass and its evolutionary association with flight performance in our analyses of flight  
108 efficiency and sinking rate through time. With this in mind, pterosaurs have been  
109 reported to conform with the well-known Cope's rule<sup>13</sup> – a phenomenon where  
110 species increase in size through geological time. The most compelling evidence for  
111 this is derived from analyses reporting an increase in wingspan from ~150 Ma to the  
112 end of the Cretaceous (~66 Ma) coincident with the origin of birds (Avialae)<sup>13</sup>.  
113 However, such a trend could emerge as a consequence of increased flight efficiency  
114 rather than increase in body size *per se*. Animals with a larger wingspan for their  
115 mass are likely to be more efficient flyers<sup>9</sup>. We find using a phylogenetic regression  
116 model that accounts for the uncertainty in our inferred tree and our estimates of  
117 species masses, frontal area and wing area (see Methods), that pterosaur size did  
118 increase significantly through time. In addition, a model that allows the rate of mass  
119 increase through time to differ before and after the origin of the birds fits significantly  
120 better than a model without such an inflection. In line with earlier conclusions<sup>13</sup>, we  
121 find that there is no significant increase in size until ~150 Ma ( $p_x = 0.59$ ). From that  
122 point the average pterosaur grew significantly from 0.60 kg to 6.05 kg (proportion of

123 the posterior distribution that crosses zero,  $p_x = 0.02$ ), a ~10-fold increase in size,  
124 over 65 million years.

125         Turning now to flight performance, there is a growing body of evidence  
126 indicating that the Azhdarchoidea had strong terrestrial affinities<sup>5-7,21</sup> (cf. <sup>22</sup>). Here the  
127 Azhdarchoidea are considered to comprise the common ancestor and all  
128 descendants of *Tapejara*, *Quetzlcoatlus*, and *Dsungaripterus*<sup>1</sup> (posterior nodal  
129 support = 0.83 in our phylogeny). Evidence suggests that azhdarchoid pterosaurs  
130 had relatively inflexible necks<sup>7</sup>, left tracks indicating terrestrial proficiency<sup>5</sup>, and  
131 possessed other adaptations associated with ground-dwelling generalist foraging  
132 (reviewed<sup>6,7</sup>). *Dsungaripterids* (the most basal azhdarchoids in our phylogeny, Figure  
133 2) are reported to have been wading foragers<sup>14,21</sup> feeding on hard-shelled organisms  
134 at water margins<sup>23</sup>. Given the terrestrial tendencies in the Azhdarchoidea compared  
135 to what we know about other pterosaurs, we might expect diminished reliance on  
136 flight, leading to the expectation that they might have differed from other pterosaurs  
137 in the selection pressures for adaptations associated with flight and locomotion.  
138 Thus, in our analyses we test whether the evolution of flight performance through  
139 time in the Azhdarchoidea is distinct from other pterosaur species.

140         Applying phylogenetic regression to flight efficiency through time we find that,  
141 even after accounting for mass, efficiency increased significantly ( $p_x = 0.00$ , Figure  
142 3a–c) in non-azdarchoid pterosaurs. However, in contrast to our finding for mass,  
143 there is no significant effect associated with the arrival of birds ( $p_x = 0.47$ ). Early  
144 pterosaurs (<200 Ma) had an average efficiency of 0.29 kg m J<sup>-1</sup> but by 70 Ma they  
145 were greater than 50% more efficient (CoT<sup>-1</sup> = 0.51 kg m J<sup>-1</sup>). Congruently we find  
146 that sinking rate (after accounting for mass) for non-azdarchoid pterosaurs reduced  
147 from 0.80 m s<sup>-1</sup> to 0.50 m s<sup>-1</sup> over the course of the 150 myr of their evolutionary



148 history (Figure 3d–f). In contrast, azdarchoids exhibited no change in efficiency or  
149 sinking rate from origin to extinction.

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

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

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222

223 **Figure 1: Hypothesised scenarios of the evolutionary trajectory of flight**

224 **performance metrics through time.** a) No relationship between flight performance  
225 metrics and time would indicate no directional change in flight ability through time. b)  
226 An increase in efficiency through time and a reduction in sinking rate would  
227 demonstrate a general tendency for selection favouring increased flight performance  
228 as the pterosaurs radiated. c) A decrease in efficiency and an increase in sinking  
229 rate would imply a reduction in flight performance through time. The branches of the  
230 phylogenetic trees are coloured by hypothesised magnitudes of efficiency (green)  
231 and sinking rate (blue).

232

233 **Figure 2: Pterosaur phylogeny and the relationship of flight performance**

234 **metrics with mass.** a) Density diagram <sup>17</sup> showing the uncertainty in our  
235 phylogenetic reconstruction for pterosaurs (n=128, see Methods for details).  
236 Superimposed is the maximum clade credibility tree and triangle points indicate  
237 species for which we have published data on mass, wing area, frontal area, and  
238 wingspan. Circle points indicate species for which we have wingspan only. Red  
239 denotes azhdarchoids. b) The relationship between flight efficiency and mass (n=75),

240 with our mean phylogenetic imputations plotted with standard deviations shown by  
241 the green ellipses. c) The relationship between sinking rate and mass (n=75), with  
242 our mean phylogenetic imputations plotted with standard deviations shown by the  
243 blue ellipses.

244

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

258

259

260

261

## 262 **Methods**

### 263 *Phylogenetic Inference*

264 All morphological data were obtained from a published phylogenetic character  
265 matrix<sup>15</sup>. However, we retained only discrete morphological characters, excluding the  
266 continuously varying characters, and treating all ordered characters as unordered,  
267 resulting in a total of 220 discrete morphological characters coded for 128 pterosaur  
268 species.

269 We constructed a posterior sample of time-calibrated phylogenetic trees for  
270 pterosaurs using the birth-death serial-sampling model<sup>24,25</sup> as implemented in  
271 BEAST v2.4<sup>26</sup> allowing for simultaneous estimation of both the topology and  
272 divergence times. For each species, we tip-dated using the midpoint of the  
273 stratigraphic age representing the first appearance of each species using published  
274 time intervals<sup>1,13,15</sup>. The origin of the birth-death process was estimated from a  
275 uniform prior distribution ranging from the age of the youngest species in the tree  
276 (*Eudimorphodon rosenfeldi*) up to an arbitrary upper limit of 350 Ma.

277 Owing to the lack of information about speciation and extinction rates in the  
278 pterosaur literature we took a conservative approach by placing a wide uninformative  
279 prior distribution (uniform ranging between 0 and infinity) on both the effective  
280 reproductive number (the birth-death ratio) and the “become uninfected rate” (total  
281 death rate). Similarly, we placed an uninformative uniform prior between 0 and 1 on  
282 the sampling proportion. Together, these parameters enable direct estimation of  
283 birth-death rates throughout the phylogenetic tree<sup>24</sup>.

284 We modelled rate heterogeneity across lineages using an uncorrelated  
285 relaxed morphological clock<sup>27</sup>. We placed an exponential prior (mean = 1) on the  
286 mean of the lognormal distribution from which the branch-wise clock rates are drawn,

287 and a gamma prior ( $\alpha = 0.5396$ ,  $\beta = 0.3819$ ) on the standard deviation. Characters  
288 were partitioned on the basis of the number of discrete states, and we applied Lewis'  
289 Markov k (Mk) model of morphological character evolution<sup>28</sup> across all partitions,  
290 estimating a shared gamma shape parameter ( $\Gamma_4$ )<sup>29</sup> using an exponential prior  
291 distribution with mean = 1.

292 The MCMC chain was run for one billion iterations, sampling every 100,000  
293 iterations after convergence. To produce the posterior sample of 1,000 phylogenetic  
294 trees used in the main analyses, we randomly sampled 1,000 iterations from this  
295 chain, ensuring that all parameters had an effective sample size of >500, calculated  
296 using Tracer v1.6<sup>30</sup>. We ensured that all parameters that were estimated using a  
297 uniform uninformative prior (origin, effective reproductive number, become  
298 uninfected rate, and the sampling rate) returned a posterior distribution of  
299 estimates that differed from the prior. The analysis was repeated multiple times to  
300 ensure convergence was reached. All chains were inspected visually using Tracer  
301 v1.6<sup>30</sup>.

302 The full sample is visualized in Figure 2a as a density tree produced in R<sup>31</sup>  
303 using functions available in the package phangorn<sup>17</sup>, and is available to download in  
304 nexus format as Supplementary Data 1 of this article.

### 305 *Imputation of pterosaur measurements*

306 To calculate our efficiency index (see below) we required mass, frontal area and  
307 wing area for adult pterosaur species. Estimates for mass and wing area are  
308 available for N=16 species from Witton<sup>11</sup> and N=12 species from Henderson<sup>12</sup> (see  
309 Table S2). For frontal area values are taken from Henderson<sup>12</sup> (N = 12, though see  
310 below). Independently for each of the two datasets, we used the phylogenetic  
311 method outlined in<sup>18</sup> to impute a posterior sample of 1000 estimates of mass, frontal

312 area and wing area for a total of  $N = 75$  species. We obtained wingspans for  
313 additional species from<sup>13</sup> (a list of species used is found in Table S2) and used each  
314 morphological trait's relationship with wingspan (i.e. a phylogenetic regression of  
315 each trait against wingspan) to impute species-specific values. As a part of this  
316 procedure, we also imputed frontal area for the  $N=7$  species in the Witton<sup>11</sup> dataset  
317 which did not have data in Henderson<sup>12</sup> (see Table S2).

### 318 *Flight energetics model*

319 Animal powered flight energetics, while perhaps kinematically different for bats, birds  
320 and pterosaurs, are still ultimately constrained by physics. It has previously been  
321 demonstrated that it is possible to infer flight performance of pterosaurs using  
322 biophysical models of flight in combination with metabolic scaling estimates from  
323 birds<sup>8</sup>. Here we used an actuator-disc based model owing to the pedigree of this  
324 approach and because more complex wake dynamics models and computational  
325 approaches are particularly difficult to parameterize, requiring a number of kinematic  
326 parameters such as wingbeat frequency that are impossible to infer from fossil  
327 material. We used a modified version of Pennycuick's Flight model (v1.25)<sup>9</sup> that we  
328 developed from earlier work<sup>8</sup> and implemented in Matlab<sup>®32</sup>, and which includes  
329 published parasite power estimates<sup>33</sup>. Flight performance is estimated based on  
330 morphological measurements such as body mass, wingspan and wing area (Table  
331 S1) and the model produces a U-shaped power-to-airspeed relationship, from which  
332 a minimum power speed ( $V_{mp}$ ) can be calculated. This  $V_{mp}$  is the least energetically  
333 expensive flight speed and so provides a useful proxy for efficiency<sup>10</sup> when  
334 incorporated into the CoT.

335 We used the model to estimate the metabolic and mechanical power required  
336 for powered (flapping) flight given information on a minimal set of morphological



337 traits and estimates of physiology, as well as aerodynamic constants (Table S1). The  
338 intersection of the power curve with an animal's available metabolic power ( $P_{\text{BMR}}$ ,  
339 calculated from mass and estimated basal metabolic rate, BMR) allows us to  
340 characterise flight ability<sup>9,34</sup>. Consistent with current thought<sup>35,36</sup>, and in line with  
341 previous studies<sup>8</sup>, we assume that pterosaurs had a BMR similar to that of birds.

#### 342 *Estimation of energetic efficiency*

343 A number of energetic efficiency measures exist<sup>10</sup> but one useful proxy is the inverse  
344 of the mass specific Cost of Transport (CoT, the energy required to move a unit  
345 mass a unit distance, independent of the time taken to do so). We estimate CoT as  
346  $P_{\text{BMR}}/(V \times M)$  where  $V$  is the least energetically expensive travel speed (i.e.  $V_{\text{mp}}$ ) and  
347 other parameters are as in Table S1.

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

353 As formulated, CoT accounts for mass. However, as energy efficiency  
354 appears to increase with body size<sup>19,20</sup> we included size in our regression model of  
355  $\text{CoT}^{-1}$  through time (main text and see below) to account for this.

#### 356 *Estimation of sinking rate*

357 Sinking rate while gliding ( $V_z$ ) was calculated as  $D \times V_{\text{mp}} / M \times g$  (where  $D$  is the total  
358 aerodynamic drag resulting from the addition of the induced, parasite and profile  
359 drags) and assuming a linear wingspan reduction (see<sup>34</sup>).

360 *Phylogenetic regression models testing temporal trends in mass and efficiency*  
361 To test the evolutionary trajectories of pterosaur mass and measures of flight  
362 efficiency through time we use phylogenetic generalized least squares<sup>37,38</sup> multiple  
363 regression models in a Bayesian framework. We assessed the significance of  
364 regression parameters using the proportion of the posterior distribution that crosses  
365 zero,  $p_x$ , where we consider  $p_x < 0.05$  as significant. In addition to the 16 species for  
366 which we have single estimates of body mass,  $V_z$  and  $CoT^{-1}$  from<sup>11</sup> (or  $N = 12$   
367 from<sup>12</sup>), in all our models we include the full set of posterior estimates of both body  
368 mass and  $CoT^{-1}$  for all species for which the data are imputed (Table S2). These  
369 values are sampled in proportion to their probability during the running of the MCMC  
370 chain. This allows us to incorporate information about the variance of our  
371 imputations, avoiding problems associated with summarizing the posterior  
372 distribution into a single point estimate.  
373

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417 All authors contributed to all aspects of this research.

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428 The authors declare no competing financial interests.

## 429 **Data Availability Statement**

430 The phylogeny we generated in this study (presented in Figure 2a) is included as  
431 Supplementary Information (Supplementary Data File 1) with this article. No other  
432 data was generated or analysed during the current study. All data used are available  
433 from published sources and are cited in the main text where appropriate.

**434 Software and Code**

435 All analyses in this research were conducted using readily available, published  
436 programs and are cited in the text. Version numbers of the programs we used are as  
437 follows: Tracer v1.6. (2015), MATLAB v9.2 (2017), R v3.4.4 (2017), BEAST 2 (2014),  
438 BayesTraits v3 (2018).