

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 archosaurs¹, 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^{2,3} - 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 Azdarchoidea⁴, a clade exhibiting gigantism, we test the***
35 ***hypothesis that there was a decreased reliance on flight⁵⁻⁷ 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 flight⁸⁻¹⁰. Firstly, we used an efficiency of
45 flight index (kg m J^{-1}), that is the inverse of the cost of transport¹⁰, 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 rate¹⁰, 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^{11,12}, wingspan¹³, wing area^{11,12}, and
53 projected frontal area¹². The dataset we use in this paper has mass and wing area
54 estimates for 16 species of pterosaur¹¹ (Table S2, Methods). Although an alternative
55 dataset of mass and wing area estimates is available for 12 species¹², 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 dataset¹¹. We use published frontal areas¹² and wingspans¹³ (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 fly¹⁴. 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 (CoT^{-1}) to increase through time and sinking rate (V_z) to decrease (Figure 1b). We
76 would expect the opposite (a decrease in 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 data¹⁵ (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 method¹⁸ 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 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 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 mass¹⁹. 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 distance²⁰
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 rule¹³ – 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)¹³.
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 flyers⁹. 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 conclusions¹³, 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^{5-7,21} (cf. ²²). Here the
127 Azhdarchoidea are considered to comprise the common ancestor and all
128 descendants of *Tapejara*, *Quetzlcoatlus*, and *Dsungaripterus*¹ (posterior nodal
129 support = 0.83 in our phylogeny). Evidence suggests that azhdarchoid pterosaurs
130 had relatively inflexible necks⁷, left tracks indicating terrestrial proficiency⁵, and
131 possessed other adaptations associated with ground-dwelling generalist foraging
132 (reviewed^{6,7}). *Dsungaripterids* (the most basal azhdarchoids in our phylogeny, Figure
133 2) are reported to have been wading foragers^{14,21} feeding on hard-shelled organisms
134 at water margins²³. 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⁻¹ but by 70 Ma they
145 were greater than 50% more efficient (CoT⁻¹ = 0.51 kg m J⁻¹). Congruently we find
146 that sinking rate (after accounting for mass) for non-azdarchoid pterosaurs reduced
147 from 0.80 m s⁻¹ to 0.50 m s⁻¹ 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 ¹⁷ 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

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262 **Methods**

263 *Phylogenetic Inference*

264 All morphological data were obtained from a published phylogenetic character
265 matrix¹⁵. 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^{24,25} as implemented in
271 BEAST v2.4²⁶ 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^{1,13,15}. 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 tree²⁴.

284 We modelled rate heterogeneity across lineages using an uncorrelated
285 relaxed morphological clock²⁷. 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 evolution²⁸ across all partitions,
290 estimating a shared gamma shape parameter (Γ_4)²⁹ 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 v1.6³⁰. 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 v1.6³⁰.

302 The full sample is visualized in Figure 2a as a density tree produced in R³¹
303 using functions available in the package phangorn¹⁷, 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 Witton¹¹ and N=12 species from Henderson¹² (see
309 Table S2). For frontal area values are taken from Henderson¹² (N = 12, though see
310 below). Independently for each of the two datasets, we used the phylogenetic
311 method outlined in¹⁸ 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 from¹³ (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 Witton¹¹ dataset
317 which did not have data in Henderson¹² (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 birds⁸. 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)⁹ that we
328 developed from earlier work⁸ and implemented in Matlab^{®32}, and which includes
329 published parasite power estimates³³. 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 efficiency¹⁰ 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_{BMR} ,
339 calculated from mass and estimated basal metabolic rate, BMR) allows us to
340 characterise flight ability^{9,34}. Consistent with current thought^{35,36}, and in line with
341 previous studies⁸, we assume that pterosaurs had a BMR similar to that of birds.

342 *Estimation of energetic efficiency*

343 A number of energetic efficiency measures exist¹⁰ 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_{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 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 CoT^{-1} .

353 As formulated, CoT accounts for mass. However, as energy efficiency
354 appears to increase with body size^{19,20} we included size in our regression model of
355 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 (see³⁴).

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^{37,38} 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} from¹¹ (or $N = 12$
367 from¹²), 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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416 **Author Contributions**

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).