

# 150 million years of sustained increase in pterosaur flight efficiency

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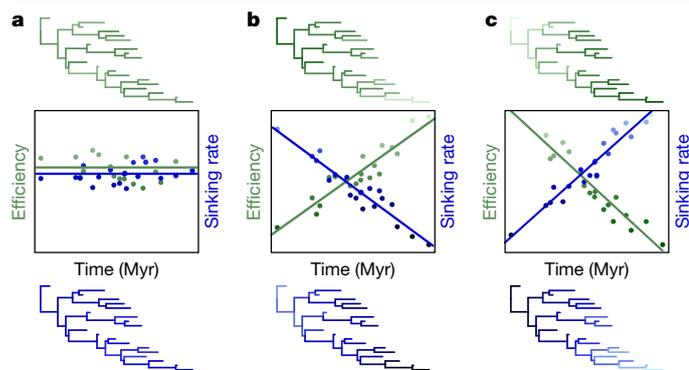
The long-term accumulation of biodiversity has been punctuated by remarkable evolutionary transitions that allowed organisms to exploit new ecological opportunities. Mesozoic flying reptiles (the pterosaurs), which dominated the skies for more than 150 million years, were the product of one such transition. The ancestors of pterosaurs were small and probably bipedal early archosaurs<sup>1</sup>, which were certainly well-adapted to terrestrial locomotion. Pterosaurs diverged from dinosaur ancestors in the Early Triassic epoch (around 245 million years ago); however, the first fossils of pterosaurs are dated to 25 million years later, in the Late Triassic epoch. Therefore, in the absence of proto-pterosaur fossils, it is difficult to study how flight first evolved in this group. Here we describe the evolutionary dynamics of the adaptation of pterosaurs to a new method of locomotion. The earliest known pterosaurs took flight and subsequently appear to have become capable and efficient flyers. However, it seems clear that transitioning between forms of locomotion<sup>2,3</sup>—from terrestrial to volant—challenged early pterosaurs by imposing a high energetic burden, thus requiring flight to provide some offsetting fitness benefits. Using phylogenetic statistical methods and biophysical models combined with information from the fossil record, we detect an evolutionary signal of natural selection that acted to increase flight efficiency over millions of years. Our results show that there was still considerable room for improvement in terms of efficiency after the appearance of flight. However, in the Azhdarchoidea<sup>4</sup>, a clade that exhibits gigantism, we test the hypothesis that there was a decreased reliance on flight<sup>5–7</sup> and find evidence for reduced selection on flight efficiency in this clade. Our approach offers a blueprint to objectively study functional and energetic changes through geological time at a more nuanced level than has previously been possible.

To determine how the propensity for flight of pterosaurs changed during their evolutionary history, we calculated two indices of flight performance using a biophysical model of powered and gliding flight<sup>8–10</sup>. First, we used an efficiency of flight index ( $\text{kg m J}^{-1}$ ), that is the inverse of the cost of transport<sup>10</sup>,  $\text{COT}^{-1}$  (see Methods and Supplementary Table 1 for the flight model parameterization). The  $\text{COT}$  ( $\text{J kg}^{-1} \text{m}^{-1}$ ) is the metabolic energy required to move a unit mass a unit distance at the least energetically expensive travel speed. Second, we calculated the sinking rate<sup>10</sup>  $V_z$  ( $\text{m s}^{-1}$ ) (Methods), which is valid for gliding. A low sinking rate enables not only longer travel distances per glide, but also allows for climbing in updrafts in which the sinking rate must be lower than the rate at which air rises from the ground. Both  $\text{COT}^{-1}$  and  $V_z$  were calculated using published estimates of mass<sup>11,12</sup>, wingspan<sup>13</sup>, wing area<sup>11,12</sup> and projected frontal area<sup>12</sup>. The dataset that we used has mass and wing area estimates for 16 species of pterosaur<sup>11</sup> (Methods and Supplementary Table 2). Although an alternative dataset of mass and wing area estimates is available for twelve species<sup>12</sup>, the two datasets cannot be combined owing to considerable differences in the approaches of each paper to body mass estimation (and the fact that the two datasets

overlap). However, our results are qualitatively the same using mass and wing area estimates from each of the two datasets in isolation; we therefore describe only the results from one dataset<sup>11</sup>.

The changes in  $\text{COT}^{-1}$  and  $V_z$  through time can provide information about how evolutionary processes such as natural selection have acted on flight performance throughout the course of pterosaur evolution. The lack of proto-pterosaurs in the fossil record means that it is currently impossible to be sure how the pterosaurs initially overcame the high energetic burden that is necessary to achieve flight. Our aim is to study the evolutionary dynamics of adaptation of pterosaurs to a new locomotory medium (that is, from terrestrial to volant). The earliest known pterosaur fossils indicate that they were able to fly<sup>14</sup>. If during the 150 million years (Myr) of the evolution of pterosaurs, flight performance and efficiency did not improve or decrease, we would expect to see no trend in  $\text{COT}^{-1}$  and  $V_z$  over time (Fig. 1a). We might, however, expect that after the start of a transition that involves a change in the defining medium of locomotion, species would be relatively energetically inefficient at moving in the new environment. Thus, over time they would become more efficient. In this case, we would expect

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**Fig. 1 | Hypothesized scenarios of the evolutionary trajectory of flight performance metrics through time.** **a**, No relationship between flight performance metrics and time would indicate no directional change in flight ability through time. **b**, An increase in efficiency through time and a reduction in sinking rate would demonstrate a general tendency for selection favouring increased flight performance as the pterosaurs radiated. **c**, A decrease in efficiency and an increase in sinking rate would imply a reduction in flight performance through time. The branches of the phylogenetic trees are coloured by hypothesized magnitudes of efficiency (green) and sinking rate (blue).

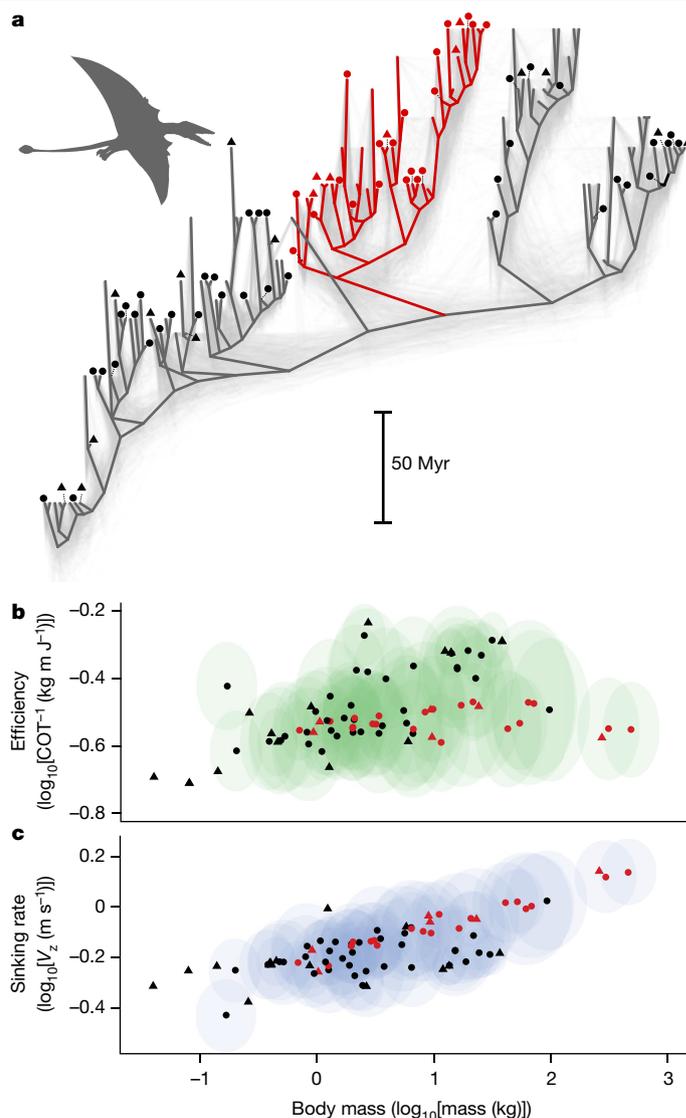
flight efficiency ( $COT^{-1}$ ) to increase through time and sinking rate ( $V_z$ ) to decrease (Fig. 1b). We would expect the opposite (a decrease in  $COT^{-1}$  and an increase in  $V_z$ ) if flight performance reduced over time (Fig. 1c).

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

Wingspan is strongly associated with pterosaur morphologies. We find that wingspan explained 97% (range of the posterior distribution, 95–98%) of the variation in mass, 97% (96–98%) of the variation in wing area and 75% (71–87%) of the variation in frontal area. Then, using a phylogenetic prediction method<sup>17</sup>, we derived a posterior distribution of imputed masses, projected frontal area and wing area for a further 59 species of pterosaurs on the basis of the results of the phylogenetic regression analyses and our phylogenetic tree (Supplementary Table 2). Our use of Bayesian phylogenetic methods means that we integrate our analyses over all phylogenetic (topology and divergence dates) and model uncertainties. Therefore, on the basis of our imputations, we calculated a posterior distribution of 1,000  $COT^{-1}$  and 1,000  $V_z$  estimates for use in our analyses of flight performance through time (Methods). These imputations are robust to jack-knife resampling (Extended Data Fig. 1). Our final set of analyses used information, including the uncertainty from imputed values, from 75 species that span the majority of the phylogenetic diversity of all known pterosaurs (Fig. 2a).

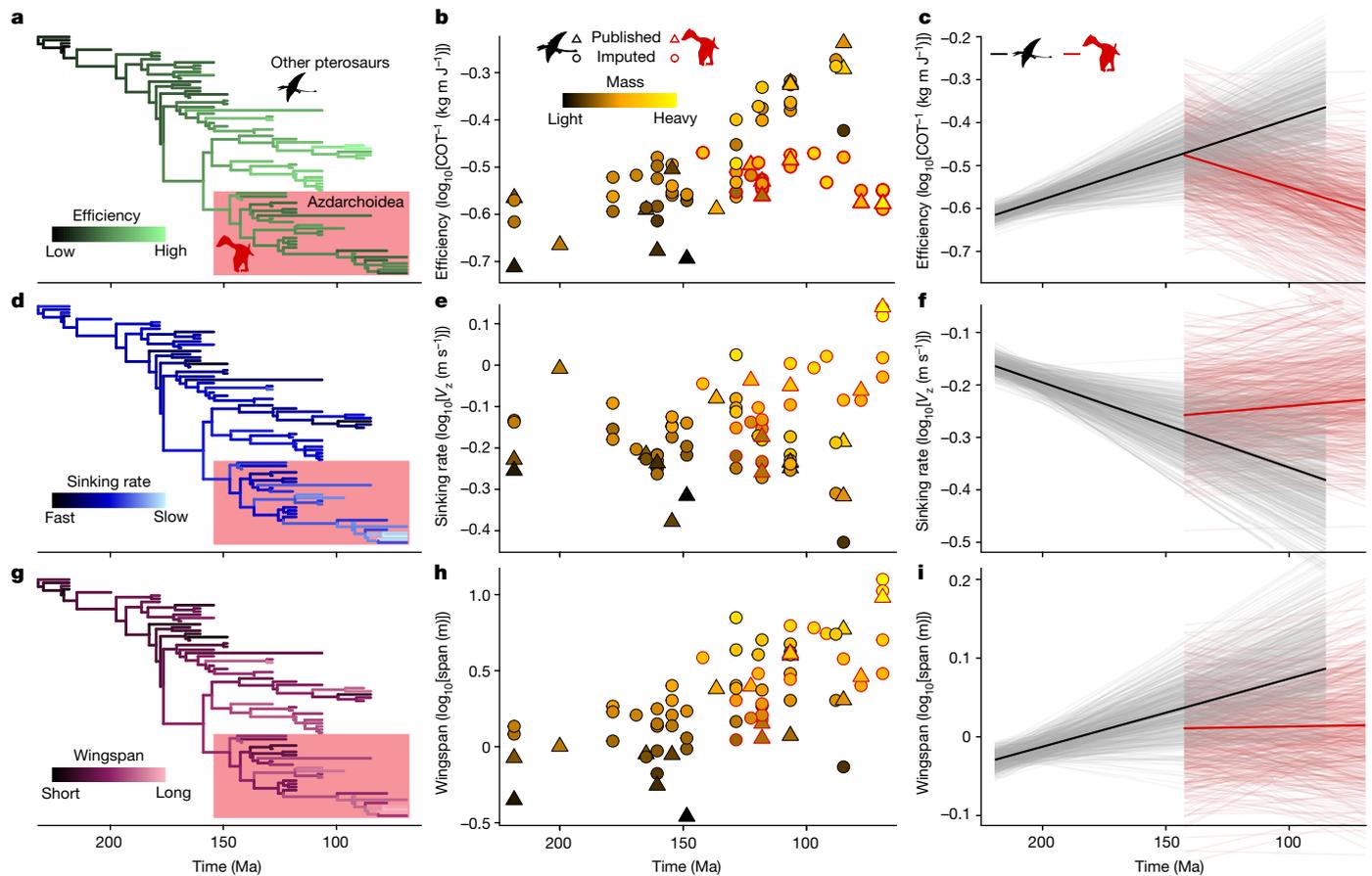
Although  $COT^{-1}$  is an efficiency index that is related to the amount of energy needed to travel a given distance, independently of how long it takes, we do expect it to correlate with mass<sup>18</sup>. It is energetically cheaper for a large animal to move a given mass over a particular distance than for a small animal to travel the same distance<sup>19</sup> (Fig. 2b). Sinking rate is similarly affected by mass (Fig. 2c) and reflects the relationships that is known for birds and bats (Extended Data Fig. 2 and Supplementary Information).

This relationship with mass means that we need to simultaneously consider mass and its evolutionary association with flight performance in our analyses of flight efficiency and sinking rate through time. With this in mind, pterosaurs have been reported to conform with Cope’s



**Fig. 2 | Pterosaur phylogeny and the relationship of flight performance metrics with mass.** **a**, Density diagram<sup>23</sup> showing the uncertainty in our phylogenetic reconstruction for pterosaurs ( $n = 128$ , see Methods for details). The maximum clade credibility tree is superimposed. Triangles indicate species for which we have published data on mass, wing area, frontal area and wingspan. Circles indicate species for which we have only wingspan data. Red, azhdarchoids. **b**, The relationship between flight efficiency and mass ( $n = 75$ ), with our mean phylogenetic imputations plotted with standard deviations shown by the green ellipses. **c**, The relationship between sinking rate and mass ( $n = 75$ ), with our mean phylogenetic imputations plotted with standard deviations shown by the blue ellipses. The silhouette of *Eudimorphodon* is from phylopic.org and is available for reuse under the Public Domain Dedication 1.0 licence (<https://creativecommons.org/publicdomain/zero/1.0/>); credit: Steven Traver.

rule<sup>13</sup>—a phenomenon in which species increase in size through geological time. The most compelling evidence for Cope’s rule in pterosaurs is derived from analyses that report an increase in wingspan from around 150 Myr ago (Ma) to the end of the Cretaceous period (around 66 Ma), which coincided with the origin of birds (Avialae)<sup>13</sup>. However, such a trend could emerge as a consequence of increased flight efficiency rather than increase in body size per se. Animals with a larger wingspan for their mass are likely to be more efficient flyers<sup>9</sup>. Using a phylogenetic regression model that accounts for the uncertainty in our inferred tree and our estimates of species masses, frontal area and wing area



**Fig. 3 | Flight performance through time.** **a–i**, Summary plots for each of our three main traits of interest (efficiency **(a–c)**, sinking rate **(d–f)** and wingspan **(g–i)**). A phylogeny of the species included in each analysis (**a, d, g**) is shown with branches shaded by reconstructed trait values ( $n = 75$ ); Azhdarchoidea ( $n = 26$ ) is highlighted in red. **b, e, h**, Trait data are shown plotted against time, in which all species with imputed values are shown as circles—except for wingspan data, which is all from published sources. Points are coloured by the body mass of each species and azhdarchoid species are outlined in red. **c, f, i**, The posterior distribution of model predictions for each trait against time shows how these traits evolved during pterosaur history. These relationships demonstrate that—after accounting for size—pterosaurs continuously increased their efficiency (**c**) ( $P_x = 0.00$ ) and wingspan

(**i**) ( $P_x = 0.03$ ) whereas there was a continuous reduction in sinking rate (**f**) ( $P_x = 0.00$ ) through time (grey lines, median is shown in black). This applies to all pterosaurs except azhdarchoids (pink lines, median in red), which show no significant trends (all  $P_x > 0.05$ )—although they do have relatively short wings for their mass (**i**). The silhouette of *Eudimorphodon* (black) is from phylopic.org and is available for reuse under the Public Domain Dedication 1.0 licence (<https://creativecommons.org/publicdomain/zero/1.0/>); credit: Steven Traver. The silhouette representing Azhdarchoidea (red) is taken from phylopic.org and is available for reuse under the Creative Commons Attribution 3.0 Unported licence (<https://creativecommons.org/publicdomain/zero/1.0/>); credit: Darren Naish (vectorized by T. Michael Keesey).

(Methods), we show that pterosaur size did increase through time. A model that allows the rate of mass increase through time to differ before and after the origin of birds fits better than a model without such an inflection. In line with previously published conclusions<sup>13</sup>, we find that there is no significant increase in size until around 150 Ma (proportion of the posterior distribution that crosses zero,  $P_x = 0.59$ ). From that point the average pterosaur grew significantly in size from 0.60 kg to 6.05 kg ( $P_x = 0.02$ ), an approximately tenfold increase in size, over 65 million years.

Turning now to flight performance, there is a growing body of evidence that indicates that the Azhdarchoidea had strong terrestrial affinities<sup>5–7,20</sup>. In this study, the Azhdarchoidea are considered to comprise the common ancestor and all descendants of *Tapejara*, *Quetzalcoatlus* and *Dsungaripterus*<sup>5</sup> (posterior nodal support = 0.83 in our phylogeny). Evidence suggests that azhdarchoid pterosaurs had relatively inflexible necks<sup>7</sup>, left tracks that indicate terrestrial proficiency<sup>5</sup> and possessed other adaptations associated with ground-dwelling generalist foraging<sup>6,7</sup> (although see ref. <sup>21</sup>). *Dsungaripterids* (the most basal azhdarchoids in our phylogeny in Fig. 2) are reported to have been wading foragers<sup>14,20</sup> that fed on hard-shelled organisms at water margins<sup>22</sup>.

Given the terrestrial tendencies in the Azhdarchoidea compared to what we know about other pterosaurs, we might expect diminished reliance on flight, leading to the expectation that they might have differed from other pterosaurs in the selection pressures for adaptations associated with flight and locomotion. Thus, in our analyses we tested whether the evolution of flight performance through time in the Azhdarchoidea is distinct from other pterosaur species.

Applying phylogenetic regression to flight efficiency through time we find that, even after accounting for mass, efficiency increased significantly ( $P_x = 0.00$ ) (Fig. 3a–c) in non-azhdarchoid pterosaurs. However, in contrast to our finding for mass, there is no significant effect associated with the arrival of birds ( $P_x = 0.47$ ). Early pterosaurs (less than 200 Ma) had an average efficiency of 0.29 kg m J<sup>-1</sup> but by 70 Ma they were more than 50% more efficient (COT<sup>-1</sup> = 0.51 kg m J<sup>-1</sup>). Consistent with this result, we find that the sinking rate (after accounting for mass) for non-azhdarchoid pterosaurs reduced 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 history ( $P_x = 0.00$ ) (Fig. 3d–f). By contrast, azhdarchoids exhibited no change in efficiency or sinking rate from their origin to extinction ( $P_x = 0.06$  and  $P_x = 0.64$ , respectively).

Our results show that, except for azhdarchoids, after their transition to volant locomotion, the pterosaurs exhibited a sustained increase in flight efficiency over 150 Myr until their extinction. To achieve this, natural selection acted to decouple the evolution of body size and wingspan (Fig. 3g–i) to sculpt these creatures from what might have been inefficient flyers that took to the air for only short spells to creatures that could fly long distances over extended periods. At their origin, around 147 Ma, 85 Myr after the origin of crown pterosaurs, azhdarchoids had a slightly lower flight efficiency and higher sinking rates compared with their contemporaries—and showed no temporal trends in either trait until their eventual extinction (Fig. 3a–f). This reduced pattern of flight efficiency is also shown in analyses of gross morphology—azhdarchoids arose with short wings for their size and maintained this condition until these species went extinct.

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

## Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41586-020-2858-8>.

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## Methods

### Phylogenetic inference

All morphological data were obtained from a published phylogenetic character matrix<sup>15</sup>. However, we retained only discrete morphological characters, excluding the continuously varying characters, and treating all ordered characters as unordered, resulting in a total of 220 discrete morphological characters coded for 128 pterosaur species. No statistical methods were used to predetermine sample size.

We constructed a posterior sample of time-calibrated phylogenetic trees for pterosaurs using the birth–death serial-sampling model<sup>24,25</sup> as implemented in BEAST v.2.4<sup>26</sup> allowing for simultaneous estimation of both the topology and divergence times. For each species, we tip-dated using the midpoint of the stratigraphic age that represents the first appearance of each species using published time intervals<sup>1,13,15</sup>. The origin of the birth–death process was estimated from a uniform prior distribution ranging from the age of the youngest species in the tree (*Eudimorphodon rosenfeldi*) up to an arbitrary upper limit of 350 Ma.

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

We modelled rate heterogeneity across lineages using an uncorrelated relaxed morphological clock<sup>27</sup>. We placed an exponential prior (mean = 1) on the mean of the log-normal distribution from which the branch-wise clock rates are drawn, and a gamma prior ( $\alpha = 0.5396$ ,  $\beta = 0.3819$ ) on the standard deviation. Characters were partitioned on the basis of the number of discrete states, and we applied Lewis’ Markov k model of morphological character evolution<sup>28</sup> across all partitions, estimating a shared gamma shape parameter ( $\Gamma_4$ )<sup>29</sup> using an exponential prior distribution with mean = 1.

The Markov chain Monte Carlo analysis was run for one billion iterations, sampling every 100,000 iterations after convergence. To produce the posterior sample of 1,000 phylogenetic trees used in the main analyses, we randomly sampled 1,000 iterations from this chain, ensuring that all parameters had an effective sample size of more than 500, calculated using Tracer v.1.7<sup>30</sup>. We ensured that all parameters that were estimated using a uniform uninformative prior (origin, effective reproductive number, become uninfected rate and the sampling rate) returned a posterior distribution of estimates that differed from the prior. The analysis was repeated multiple times to ensure convergence was reached. All chains were inspected visually using Tracer v.1.7<sup>30</sup>.

The full sample is visualized in Fig. 2a as a density tree produced in R<sup>31</sup> using functions available in the package phangorn<sup>23</sup>, and is available to download in nexus format from Supplementary Data 1.

### Imputation of pterosaur measurements

To calculate our efficiency index (see ‘Estimation of energetic efficiency’), we required mass, frontal area and wing area data for adult pterosaur species. Estimates for mass and wing area are available for  $n = 16$  species from ref.<sup>11</sup> and  $n = 12$  species from ref.<sup>12</sup> (Supplementary Table 2). Frontal area values are taken from ref.<sup>12</sup> ( $n = 12$ ; but see below). Independently for each of the two datasets, we used the phylogenetic method outlined in a previous study<sup>17</sup> to impute a posterior sample of 1,000 estimates of mass, frontal area and wing area for a total of  $n = 75$  species. We obtained wingspans for additional species from a previously published study<sup>13</sup> (a list of species used can be found in Supplementary Table 2) and used the relationship of each morphological trait with wingspan (that is, a phylogenetic regression of each trait against wingspan) to impute species-specific values. As part of this

procedure, we also imputed the frontal area for the  $n = 7$  species in the dataset from ref.<sup>11</sup> for which data were not available in the dataset from ref.<sup>12</sup> (Supplementary Table 2).

### Flight energetics model

Animal-powered flight energetics, although perhaps kinematically different for bats, birds and pterosaurs, are still ultimately constrained by physics. It has previously been demonstrated that it is possible to infer the flight performance of pterosaurs using biophysical models of flight in combination with metabolic scaling estimates from birds<sup>8</sup>. Here we used an actuator-disc-based model owing to the pedigree of this approach and because more complex wake dynamics models and computational approaches are particularly difficult to parameterize, requiring a number of kinematic parameters such as wingbeat frequency that are impossible to infer from fossil material. We used a modified version of Pennycuik’s flight model (v.1.25)<sup>9</sup> that was developed in previous work<sup>8</sup> and implemented in MATLAB v.R2018A (The Mathworks) and that includes published parasite power estimates<sup>32</sup>. Flight performance is estimated on the basis of morphological measurements such as body mass, wingspan and wing area (Supplementary Table 1) and the model produces a U-shaped power-to-airspeed relationship, from which a minimum power speed ( $V_{mp}$ ) can be calculated. This  $V_{mp}$  is the least energetically expensive flight speed and so provides a useful proxy for efficiency<sup>10</sup> when incorporated into the COT.

We used the model to estimate the metabolic and mechanical power required for powered (flapping) flight given information on a minimal set of morphological traits and estimates of physiology, as well as aerodynamic constants (Supplementary Table 1). The intersection of the power curve with the available metabolic power of an animal ( $P_{BMR}$ , calculated from the mass and estimated basal metabolic rate (BMR)) allows us to characterize flight ability<sup>9,33</sup>. Consistent with current thought<sup>34,35</sup>, and in line with previous studies<sup>8</sup>, we assume that pterosaurs had a basal metabolic rate similar to that of birds.

### Estimation of energetic efficiency

A number of energetic efficiency measures exist<sup>10</sup> but one useful proxy is the inverse of the mass-specific COT—the energy required to move a unit mass a unit distance, independent of the time taken to do so. We estimate COT as  $P_{BMR}/(V \times M)$  where  $V$  is the least energetically expensive travel speed (that is,  $V_{mp}$ ) and other parameters are as in Supplementary Table 1.

For species with available data (Supplementary Table 2), we produced a single estimate of  $COT^{-1}$  using the inverse of the above formula. For each of the species for which we imputed mass, frontal area and wing area (Supplementary Table 2 and ‘Imputation of pterosaur measurements’), we use the full sample of our imputed values to produce a posterior sample of 1,000 estimates of  $COT^{-1}$ .

As formulated, COT accounts for mass. However, as energy efficiency appears to increase with body size<sup>18,19</sup>, we included size in our regression model of  $COT^{-1}$  through time (main text and see ‘Phylogenetic regression models testing temporal trends in mass and efficiency’) to account for this.

### Estimation of sinking rate

The sinking rate while gliding ( $V_z$ ) was calculated as  $D \times V_{mp}/M \times g$  (in which  $D$  is the total aerodynamic drag that results from the addition of the induced, parasite and profile drags) and assuming a linear wingspan reduction<sup>33</sup>.

### Phylogenetic regression models testing temporal trends in mass and efficiency

To test the evolutionary trajectories of pterosaur mass and measures of flight efficiency through time, we use phylogenetic generalized least squares<sup>36,37</sup> multiple regression models in a Bayesian framework. We assessed the significance of regression parameters using the proportion

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of the posterior distribution that crosses zero,  $P_x$ , in which we consider  $P_x < 0.05$  as significant. In addition to the 16 species for which we have single estimates of body mass,  $V_2$  and  $COT^{-1}$  from ref.<sup>11</sup> (or  $n = 12$  from ref.<sup>12</sup>), in all of our models we include the full set of posterior estimates of both body mass and  $COT^{-1}$  for all species for which the data are imputed (Supplementary Table 2). These values are sampled in proportion to their probability during the running of the Markov chain Monte Carlo analysis. This enables us to incorporate information about the variance of our imputations, which avoids problems associated with summarizing the posterior distribution into a single point estimate.

## Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

## Data availability

The phylogeny that we generated in this study (Fig. 2a) is included as Supplementary Information (Supplementary Data 1) with this Article. No other data were generated or analysed during the current study. All data used are available from published sources and are cited in the text as appropriate.

## Code availability

All analyses in this study were conducted using readily available, published programs and are cited in the text. Version numbers of the programs we used are as follows: Tracer v.1.7 (2018), MATLAB v.9.2 (2017), R v.3.4.4 (2017), BEAST 2 (2014) and BayesTraits v.3 (2018).

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**Competing interests** The authors declare no competing interests.

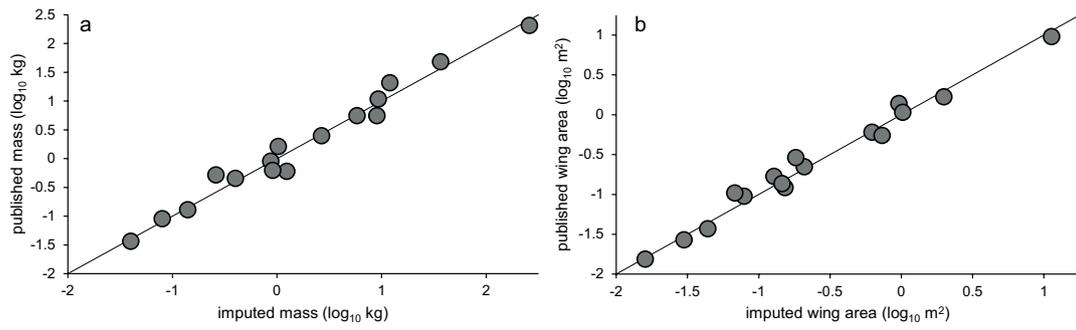
## Additional information

**Supplementary information** is available for this paper at <https://doi.org/10.1038/s41586-020-2858-8>.

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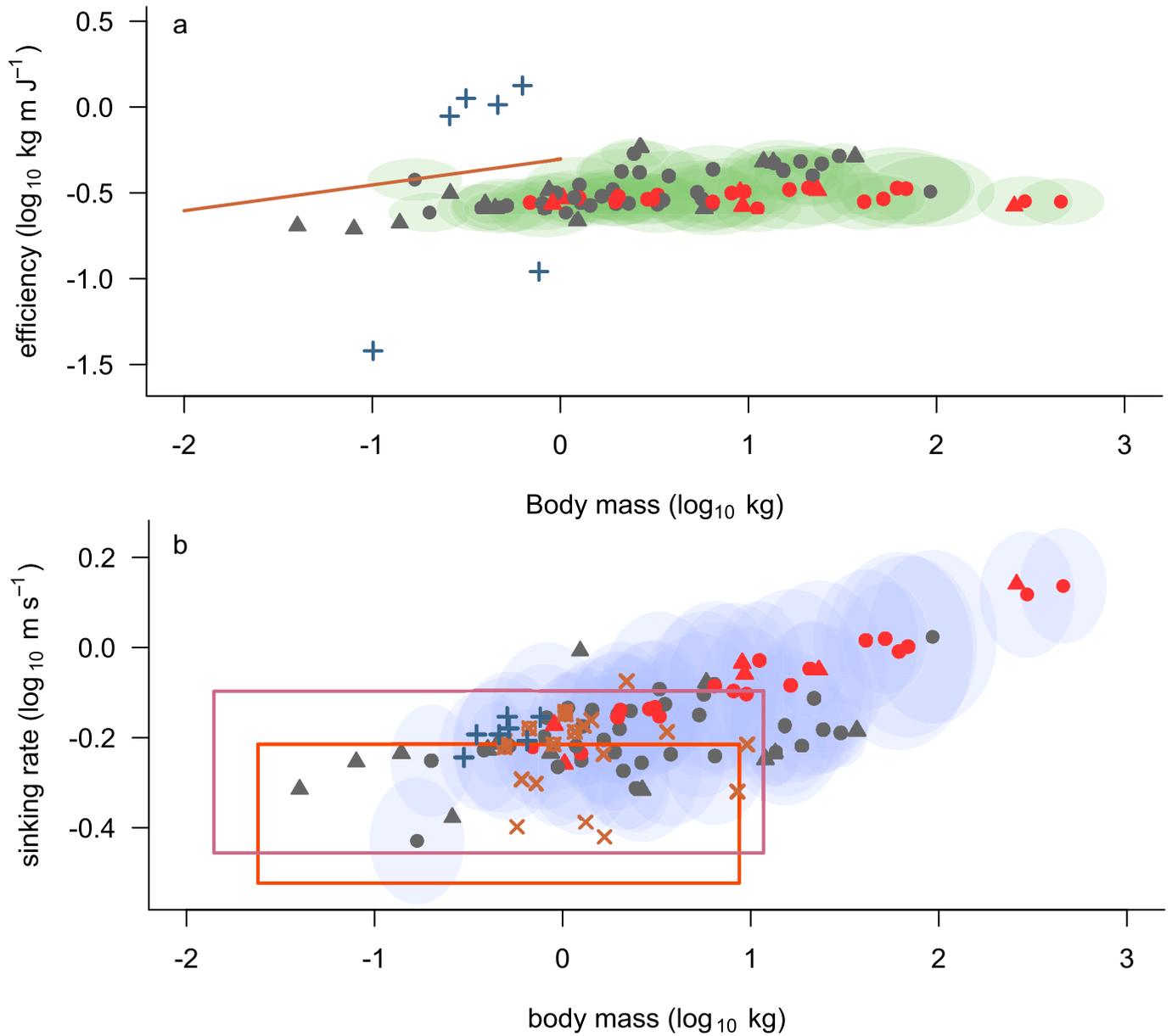
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**Extended Data Fig. 1 | Results of our  $n-1$  jack-knife procedure for the mass and wing area. a, b.** We compared the imputed values for each species from our phylogenetic imputation procedure with the published values for mass

(a) and wing area (b), for studies in which that species had been excluded from the published value. Each point represents an individual species.



**Extended Data Fig. 2 | Comparison of flight performance metrics between pterosaurs and extant bats and birds. a.** We show the relationship between flight efficiency and mass in pterosaurs (Fig. 2b), with our mean phylogenetic imputations plotted with standard deviations shown as green ellipses. We superimpose a previously reported relationship between flight efficiency and mass for extant birds (orange line), as well as data points for six bat species (blue crosses). **b.** The relationship between sinking rate and mass for pterosaurs (Fig. 2c), with our mean phylogenetic imputations plotted with

standard deviations shown by the blue ellipses. Superimposed, we show the range of the relationship between sinking rate and mass for Procariiformes (orange box) and Accipitriformes<sup>7</sup> (pink box) and individual data points for six specimens of an extinct Cretaceous bird (*Sapeornis chaoyangensis*) (orange circles with crosses), eleven extant bird species (orange crosses) and seven bat species (blue crosses). Triangles indicate pterosaur species for which we have published data on mass, wing area and wingspan. Circles indicate species for which we have only wingspan data. All azhdarchoids are coloured in red.

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Data Availability Statement

The phylogeny we generated in this study (presented in Figure 2a) is included as extended data to this article. No other data was generated or analysed during the current study. All data used are available from published sources and are cited in the main text where appropriate.

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Sampling strategy	We used all data available.
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