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Exploring the limits of wing design in pterosaurs‡

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Article

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Abstract

Wing shape is integrally related to flight performance and function in extant animals. Analyzing this relationship in pterosaurs is complicated by the fragmentary nature of the fossil record and because the flight dimensions of wing membranes do not preserve. In the absence of fully extended pterosaur wing fossils, scientific reconstruction of the pterosaur Bauplan presents the clearest alternative for analysis. However, these wing shapes are subject to multiple conflicting scientific opinions and the artistic styles of the researchers and illustrators reconstructing them. Here we test the functional ramifications of different wing-shape reconstructions. We use theoretical morphospace analysis to establish whether modern reconstructions of pterosaur wings exhibit the diversification and functional performance expected of living animals. Pterosaur wing reconstructions show little by way of taxonomic separation either in shapespace or functional performance, with all pterosaur groups overlapping independent of time, size or proposed niche. This suggests that published pterosaur reconstructions underestimate the diversity of wing shapes expected of such a diverse group and are not reflective of flying animals. Stylistic approaches have little effect on the occupation and diversity of pterosaur reconstructions, suggesting that the underpinning issues lie in the lack of scientific consensus on the shape and structure of the wings, rather than how they are reconstructed.

Non-technical Summary

Pterosaurs are significant because they independently evolved flight and, through the course of their evolutionary history, established new extremes in the maximum size for flying vertebrates. Nevertheless, the precise shape of pterosaur wings remains poorly understood. The link between form and function makes wing shape a valuable tool for beginning to answer questions about how well they flew. The published literature on pterosaur flight abounds, with a variety of life reconstructions. We compare theoretical pterosaur wings with published reconstructions over a series of shape and function tests to understand whether the current scientific understanding of pterosaur wing shape is likely to accurately represent the diversity of pterosaur wing shapes and whether issues in depicting pterosaurs stem from the style or substance of life reconstructions. Our results reveal that reconstructions do not perform as expected and thus do not accurately represent the flight abilities of pterosaurs. This inadequacy stems from disagreement between researchers surrounding the placement of key wing attachment points more so than any particular stylistic element. This demonstrates just how much remains unknown about pterosaurs and highlights the challenges of using soft tissues, like wings, to look at the performance of extinct animals.

Introduction

As the first group of volant vertebrates to evolve, pterosaurs have a fossil record that provides valuable insight into how animals tackle the challenges of becoming and staying airborne (Padian 1985). Pterosaurs diversified to occupy a variety of flight niches throughout the Mesozoic, ranging from small anurognathids to the largest animals to ever fly (Wellnhofer 1991; Witton 2013). For this reason, pterosaur wings present an ideal opportunity to examine the adaptation and optimization of wings for flight at the extreme of what is biologically possible for large flying animals. There have been numerous attempts to deduce the flight ability of pterosaurs, utilizing proxies such as bone strength, endocranial morphology, musculoskeletal reconstruction, and performance optimization, although a common method involves placing pterosaurs within a morphospace of flying animals (Brower and Veinus 1981; Hazlehurst and Rayner 1992; Chatterjee and Templin 2004; Wilkinson 2008; Witton 2008; Witton and Habib 2010; Palmer 2011; Naish et al. 2021; Pittman et al. 2021; Goto et al. 2022; Bronzati et al. 2025). Most ecomorphospace studies have focused on linear measurements of bones, rather than the role played by flight membranes themselves in pterosaur wing shape. Despite their value for flight research, the fossil record of pterosaur wings is poor. While preserved flight membranes exist for several pterosaur taxa, often in sufficient detail to observe the structure of the membrane itself (Martill and Unwin 1989; Martill et al. 1990; Frey et al. 2003; Witton 2013), all known examples of preserved wing

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membranes exhibit partial wing closure or taphonomic distortion, obscuring their full extent (Elgin et al. 2011).

In the absence of undistorted fossil wing specimens, shape-based analysis of pterosaur flight necessarily requires a proxy for the wing planform. One potentially promising source of pterosaur wing shapes is the scientific record of reconstructions, which often accompany discussions of pterosaur fossils and flight ability. These academic reconstructions are produced for multiple purposes, including both simple schematic representations of animals and more complex models used in aerodynamic calculations and mass-estimation analyses (Wilkinson et al. 2006; Henderson 2010). All these reconstructions reflect features that characterize the academic understanding of pterosaur shape, such as the position of key membrane attachment sites and the extent of the wing. Even pterosaur silhouettes, such as those in Witton (2013), serve to illustrate the diversity of the pterosaur Bauplan, and therefore present an academic understanding of the pterosaur wing. In this capacity, reconstructions have largely gone untested. We consider reconstructions from the published academic literature as indicative of the authors' understanding of the pterosaur wing and treat them as hypotheses of shape for the purposes of functional analysis. We differentiate this from paleoart, which while often produced by the same individuals and endeavoring to create accurate life reconstructions of animals, does not strictly imply scientific hypotheses of form. We make no attempt to comment on the viability of paleoart, focusing instead on academic renderings of the pterosaur Bauplan.

There have been numerous attempts to reconstruct the pterosaur wing, taking into account a myriad of potential shape-influencing factors, with particular debate over two regions (Fig. 1A): the propatagium, anchored by the pteroid bone, and the distal extent of the brachiopatagium (Unwin 1999; Palmer and Dyke 2010; Elgin et al. 2011). Consensus suggests a medially directed pteroid and a single concave distal brachiopatagium attaching at the ankle for all pterosaurs (Elgin et al. 2011; Witton 2013), although papers both before and after the early 2010s continue to reproduce a variety of forms. Other factors, such as variation in the degree of anterior sweep of the wing and the position of the leg in flight, continue to be reflected in planform reconstructions, resulting in a wide array of plausible wing shapes for the same animal (Palmer and Dyke 2010; Manafzadeh and Padian 2018; Fig. 1B–D). As these features appear in the literature, the effects of variation in these traits on the dataset is encapsulated by these analyses. Both anterior sweep and flexion of the leg serve to thin the wing chord, which will affect the position of reconstructions with these features in the performed tests.

We perform a five-part test using theoretical morphospace analysis to determine whether reconstructed pterosaur planforms are viable wing-shape proxies:

1. Intrageneric homogeneity: examples of the same pterosaur taxa should group together in shape space. Strong heterogeneity within planforms of the same genus would indicate that there is strong disagreement in planform shape.

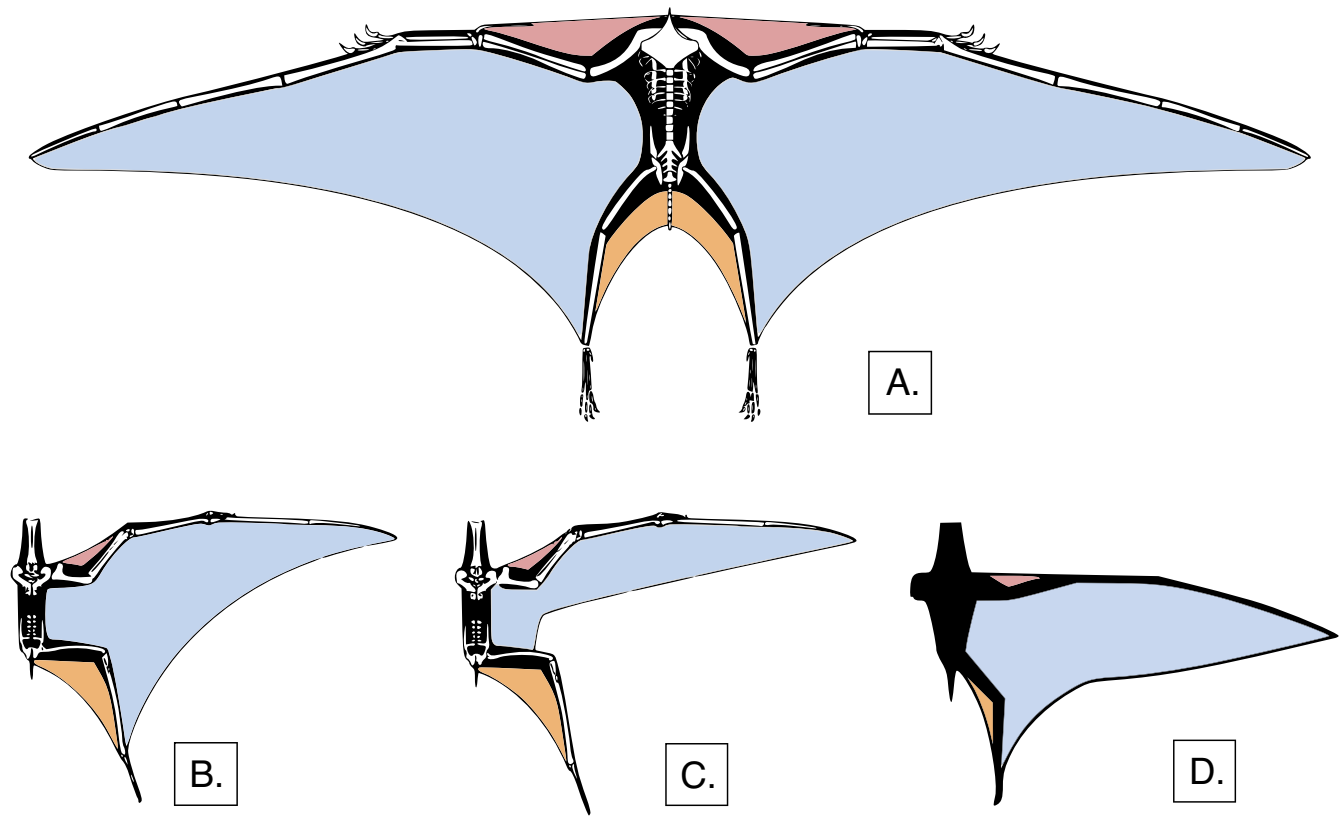


Figure 1. Examples of the pterosaur Bauplan. Individual wing membranes colored for differentiation, propatagium in red between wrist and shoulder, brachiopatagium in blue stretching from the end of the wing digit, and uropatagium in orange between the legs. **A,** The best consensus pterosaur wing structure, redrawn from Eglin et al. (2011), followed by disparate reconstructions of the wing of *Quetzalcoatlus*, redrawn from Padian et al. (2021); **B,** with a single curved trailing edge and ankle attachment; **C,** with an angular trailing edge and attachment point higher on the leg above the knee; and **D,** reconstruction of the wing of *Quetzalcoatlus* with a distinct individual style of reconstruction, composing the trailing edge from two intersecting curves, redrawn from Witton (2013).

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2. Stylistic heterogeneity: reconstructions should not cluster based on the individual who produced them (style should not be a prevalent influence on morphology).
3. Temporal heterogeneity: reconstructions of the pterosaur wing produced before the consensus established by Elgin et al. (2011) and after should differ in the distribution and amount of morphospace occupied. This would suggest that more recent planforms represent the modern consensus of pterosaur wing shape.
4. Morphological diversity: when compared with the ecomorphospace established for pterosaurs based on bone measurements, pterosaur reconstructions should occupy a similar extent of shape space and niche occupation.
5. Functional diversity: when subjected to functional testing, variation in performance between pterosaur taxa with differing proposed niches should be expected. If pterosaur reconstructions as a whole pass these tests, they can be considered as viable representations of pterosaur wings.

Theoretical morphospace is an ideal tool for performing these tests, as it combines tests of space occupation through standard principal components analysis (PCA) with functional performance relative to a global optimum. This is accomplished through the creation of a separate dataset of theoretical shapes that can be extended beyond the range of variation seen in pterosaur reconstructions to create a global shape environment (McGhee 2006). Testing performance for each theoretical shape produces a performance surface, the highest-performing value in which is the global optimum for that trait. Projecting planforms onto the performance surface makes it possible to compare the relative performance of each reconstruction without assuming optimality for any single shape (Deakin et al. 2022; Rawson et al. 2024; Liu et al. 2024; Berks et al. 2025; Fadel et al. 2025; Griffin et al. 2026; Walters et al. 2026). This makes theoretical morphospace useful for testing the subjectivity of pterosaur wing shapes and exploring whether planforms vary in a way expected of a group with significant size variation and a diversity of inferred niches.

We captured the planform element of 79 reconstructions of pterosaur wings belonging to eight frequently depicted genera and two families of pterosaurs from scientific papers. These taxa encompassed pterosaur size diversity from ~40 cm to 10.5 m wingspans (Bakhurina and Unwin 1995; Bennett 2003, 2007; Witton 2013; Bestwick et al. 2018) and phylogenetic affinity from the earliest emerging to the most derived pterosaurs, thus covering a variety of presumed niche occupations and performances. We then performed five tests of clustering and performance analyses to determine whether pterosaur reconstructions demonstrate the variability expected. Our results demonstrate that pterosaur reconstructions undersample the variation in form expected of pterosaurs and that they are a poor proxy for wing shape.

Methods

Data Collection

Eight representative pterosaur genera were selected, chosen to cover the range of pterosaur diversity in size, age, and proposed niche. Additionally, two broader families of rhamphorhynchids and ornithocheirids were selected, as many reconstructions of these animals exist but either were not attributed to a distinct genus or represent a closely related genus such as *Sordes*, a potential relative of *Rhamphorhynchus* (Unwin 2003; Elgin et al. 2011). Only genera with more than three depictions were chosen, as multiple representations are necessary to form clusters. *Nyctosaurus*, with only two reconstructions, was included, as it represents an extreme of known pterosaur wing anatomy.

For these taxa and groups, a total of 79 images of pterosaur planforms were sourced from the published scientific literature. Wing planforms constitute adult individuals and include all three main wing elements—propatagium, brachiopatagium, and uropatagium (Fig.1A)—to ensure that differences in shape resulting from differences in pteroid and leg position in flight were included. As this analysis considers wing planform shape alone rather than the aerodynamics of the whole animal, the relative position of the wing relative to the body was not directly recorded. However, as the position of the wing has an effect on the breadth of the wing chord, particularly if anteriorly flexed, differences in the position of the wing between authors is captured as part of the outline shape.

Reconstructions published after 1990 were selected to capture a spread of time both before and after broad consensus on the nature of the pterosaur wing was established by Elgin et al. (2011) and to encompass an up-to-date understanding of pterosaur biology. Furthermore, only reconstructions with the wing fully spread in planform were analyzed. Where multiple pterosaur taxa were depicted by a single author or individual, authorship was recorded to test whether individual styles of reconstruction bias flight performance of reconstructions. A complete image list and all sampled planform outlines used in the analysis are available in Supplementary Data 1, along with all of the planform outlines used in our analyses (Supplementary Data 3).

Planform Shape

Outline shape of pterosaur planforms was characterized using elliptical Fourier analysis following the method outlined in Deakin et al. (2022) and Walters et al. (2026) (Fig. 2A). Reconstructions were first converted to single-pixel outlines using Fiji v. 1.54 (Schindelin et al. 2012), with all successive analysis performed in MATLAB v. R2022b (MathWorks 2022). For each outline, 1200 landmarks and 15 shape harmonics were chosen, the maximum number of points possible given the resolution of the outline. All planform shapes were automatically scaled to remove the size component of variation and uniformly oriented relative to the base of the wing. This ensures that elements of variation between planforms such as the anterior flexion of the wing relative to the body wall are preserved.

For tests 1–3 (intrageneric homogeneity, stylistic and temporal heterogeneity), the resulting elliptical harmonics for each reconstruction were analyzed by clustering in PCA. For test 1, reconstructions were grouped according to the taxa or group to which they belong. For tests 2 and 3, the same data were grouped according to first the identity of the researcher who published them and then the date of publication, whether before or after the Elgin et al. (2011) consensus paper. For test 4 (morphological diversity), pterosaur reconstructions were divided by taxa and superimposed on the wing-shape morphospace produced in Walters et al. (2026). This permitted direct comparison between shape-based ecomorphospace and distributions of bird and pterosaurs based on length measurements, such as that of Witton and Habib (2010). Code used for extraction processing of reconstruction shapes is supplied in Supplementary Code 1.

Theoretical Morphospace

For a group as diverse in size as pterosaurs, it is expected that different taxa specialized for different niches, as is seen in extant

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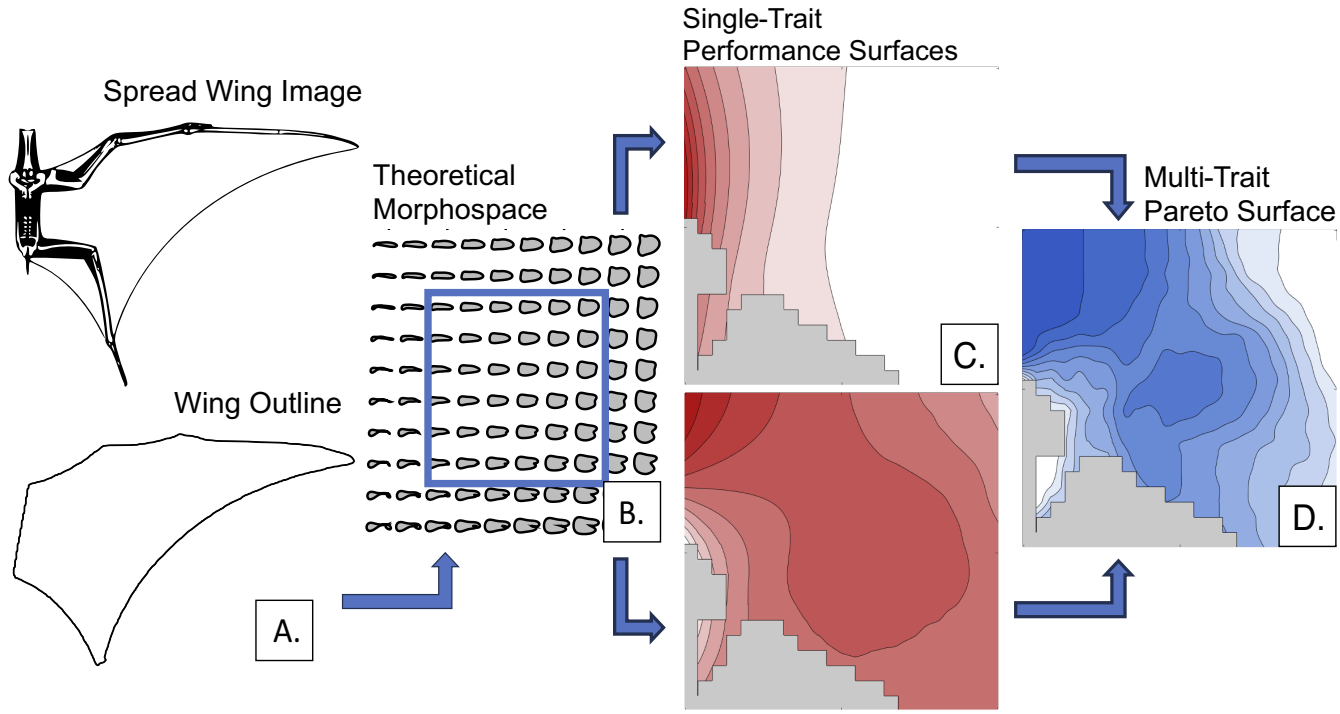


Figure 2. Theoretical morphospace workflow. **A,** Reduction of planform to single-pixel outline and characterisation of shape using elliptical Fourier analysis. **B,** Theoretical shape generation. Blue box indicates extent of realised empirical morphospace. **C,** Generation of performance surface topology by plotting the relative performance values for each theoretical shape. **D,** Combination of single-metric performance surfaces using Pareto ranking to produce multicomponent optimality surfaces.

birds. Multiple possible pterosaur niches have been proposed, including oceangoing dynamic soaring for taxa such as *Pteranodon* and *Nyctosaurus* and aerial hawking for *Anurognathus*. In extant birds, there is a clear (though variable) influence of functional constraints on wing shape, with energetically demanding flight styles driving the evolution of better-performing wings (Walters et al. 2026). It is therefore assumed for test 5 (functional analysis) that pterosaur taxa should exhibit variable optimization, based on their niches, resulting in the evolution of different wing shapes in different taxa. If reconstructions represent viable pterosaur planforms, then there should be variable optimization in wing shape between the sampled taxa. Analyzing performance in empirical shapes, whether they be extant wings or reconstructions of extinct animals, however, is a difficult process leading to circular logic, as there is no way of determining whether a given wing is optimal (Deakin et al. 2022; Walters et al. 2026). This issue is further compounded by potential variation in how the wing is constructed, as the wing of an animal with an extended leg will perform differently than one with a flexed leg posture. One solution to this is theoretical morphospace.

Theoretical morphospace permits identification of shapes that are optimal for a given functional trait. These shapes take the place of real planforms in functional analyses and, being theoretical, do not possess and are not bounded by the anatomical considerations of animals. Instead, theoretical shapes exist to create an even sampling of possible wing planforms, entirely independent of empirical taxa. As a result, theoretical shape space can be expanded beyond the bounds of what is realized either in nature or in reconstructions and is considered to represent a "global" shape landscape, which encompasses all possible variation in form (McGhee 2006). Testing performance in such a global landscape highlights the best-performing shape possible, regardless of whether it exists in nature. These optimal shapes are then compared with the empirical data to determine how closely specific taxa match optimal flight forms, thus sidestepping the limitations of traditional functional analyses that assume functional optimality.

For test 5 (functional diversity), pterosaur planform reconstructions constitute the empirical dataset and a second, separate, theoretical shape dataset was created, which could then be tested for traits relating to flight style. Theoretical shape construction followed the approach of Raup (1962), previously outlined in Walters et al. (2026) and others (Polly et al. 2016; Dickson and Pierce 2019; Stayton 2019a,b; Dickson et al. 2021; Jones et al. 2021; Deakin et al. 2022; Liu et al. 2024; Rawson et al. 2024; Berks et al. 2025; Fadel et al. 2025; Griffin et al. 2026). This method, by means of a constructor variable, remains the prevailing method of producing theoretical morphospaces.

Theoretical shapes (Fig. 2B) are produced by taking the elliptical formula captured from the empirical dataset and modifying it to iteratively produce new shapes. Using the elliptical formula serves as a guide to restrict shape generation to an amount of shape space that it is possible analyze and that is relevant to questions of wing shape, but the resultant theoretical shapes themselves are treated separate from actual pterosaur morphology (Deakin et al. 2022; Liu et al. 2024; Rawson et al. 2024; Berks et al. 2025; Fadel et al. 2025; Griffin et al. 2026; Walters et al. 2026). Iterative changes to the elliptical formula were used to plot a 26 × 19 grid of 494 theoretical shapes, expanding beyond the range of variation found in PCA analyses by 20%. Encompassing a region of shape space greater than that realized by pterosaur reconstructions makes it possible to identify planforms that, while possible and potentially higher performing, have not been considered as viable options for the shape of pterosaur wings. Shape generation at the edges of possible space can result in self-intersecting forms, which represent impossible wing

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planforms. As a result, self-intersecting theoretical shapes were excluded from functional analysis (represented as a gray box in performance and optimality surfaces). All theoretical shapes were scaled to isolate the shape element of variation.

Functional Testing

Tests of functional performance were performed on the theoretical shape dataset following the method and metrics outlined in Walters et al. (2026). Four flight-related metrics were tested: aspect ratio, second moment of area, pitch agility, and tip angle, each of which has a demonstrated relationship to flight performance and flight style niche (Liu et al. 2024; Fadel et al. 2025; Walters et al. 2026).

Thinner, higher-aspect planforms are closely linked with reduced cost of transport (Rayner 1990; Taylor and Thomas 2014) in living animals. Thus, high aspect ratio is considered an optimal trait for long-distance flying or dynamic soaring behaviors where conserving energy is important. It is therefore hypothesized that pterosaurs with this expected niche, such as *Nyctosaurus* and *Pteranodon*, should plot closer to the optimal peak for this metric than more primitive pterosaurs such as *Dimorphodon*.

Second moment of area describes the distribution of the surface of the wing relative to the base chord, a factor that relates to the generation of rotational moment. This has been suggested to correlate with more maneuverable wing planforms (Saville 1957; Norberg and Rayner 1987; Rayner 1988; Walters et al. 2026). High second moment of area is therefore considered optimal for flight modes requiring rapid response to the environment, such as dynamic soaring and hunting on the wing. It is therefore hypothesized that *Anurognathus* reconstructions should plot closer to the optimal peak for this metric than pterosaurs that have not been suggested as aerial predators.

Pitch agility records the ease with which a platform can be made unstable at higher angles of attack (Harvey et al. 2022). The ease of initiating aerodynamic instability relates to the ability of an animal to rapidly change direction in flight around the y-axis, and instigate complex maneuvers (Hazlehurst and Rayner 1992; Harvey et al. 2022). This is particularly useful for chasing prey, and thus high pitch agility is considered optimal for flight niches like aerial predation. Performance for this metric should favor pterosaurs with proposed aerial predator niches over larger-winged taxa such as *Quetzalcoatlus*.

Tip angle relates directly to planform lift generation, with broader, more obtuse tip angles producing greater lift at the cost of increasing aerodynamic drag (Norberg 1986; Rayner 1990; Swaddle and Lockwood 2003; Pennycuick 2008). For this reason, broad tip angles are considered optimal for short bursts of flight and in taxa with proportionally higher body mass where more lift is required to stay airborne. It is hypothesized that more primitive pterosaurs like *Dimorphodon* should plot closer to the optima for this trait. More pointed planform tips are considered optimal for aerodynamic-focused flight modes like dynamic soaring.

For each of the four functional metrics, a value was calculated for each theoretical shape. Theoretical shapes form an even grid of shape space, this results in a grid of performance values that can be viewed as a landscape (Fig. 2C). These are treated as relative rather than absolute indictors of performance, with the highest-performing theoretical shape interpreted as the optimal peak. Because theoretical morphospace extends beyond the limits of empirical space, the highest performance value in each surface was considered the global performance optimum.

To examine performance for specific flight styles, functional proxies were then combined to produce niche-specific metrics following methods used to analyze flight style in birds (Walters et al. 2026; Fig. 2D). Three flight styles were examined: dynamic soaring (the combination of performance for second moment of area and tip angle), long-distance sustained flight like migration (a combination of aspect ratio and tip angle), and aerial predation (a combination of second moment of area, pitch agility, and tip angle) (Walters et al. 2026). Multimetric performance surfaces were created using the Pareto ranking method developed by Deakin et al. (2022). This identifies optimal subsets of data with uneven variables, allowing comparison between datasets where taxa exhibit different, even diametric, functional performance (Deakin et al. 2022). The code and all running files needed to reproduce this analysis are provided in Supplementary Code 1 and Supplementary Data 2.

Results

Theoretical Space

The first two principal components (PC) of reconstructed planform variation (Fig. 3) account for about 80% of total variation, with the majority expressed on PC 1 (62.51%). This component describes the breadth of the wing chord, particularly at the root, with low PC 1 values characterized by thin, rod-like theoretical planforms and higher values represented by broader-based subtriangular forms. PC 2 (17.39% of total variance) characterizes planform curvature, with higher values representing anteriorly flexed theoretical shapes and low values posteriorly curved. PC 3 (Supplementary Fig. 1) represents only 7% of variance and characterizes the breadth of the theoretical planform chord at the tip relative to the base. Low PC 3 planforms exhibit a broad base chord and reduced tip chord, whereas high PC 3 planforms exhibit a reduced base chord with a broader chord at the planform tip. Posterior curving of the final wing phalange may result in rounding of the planform tip in some pterosaur taxa (Hone et al. 2015), which would have the effect of increasing the tip chord. No known pterosaur soft tissue, however, supports the possibility that the wingtip could be expanded posteriorly to produce tip chords wider than the base of the wing. Furthermore, the aerodynamic requirement to keep the wing in tension to prevent fluttering and lack of a tendon along the trailing edge of the wing necessitate that the trailing edge curve from tip to base (Elgin et al. 2011). This results in a morphology in which the base chord will always be larger than the tip chord. For this reason, this component of variation is largely unhelpful for discussing pterosaurs.

For aspect ratio (Fig. 4A), there is a single performance peak, located at the extreme left of the graph with a PC 2 value around 0. Performance decreases steadily from this peak, with all high values of PC 1 presenting as least optimal. The second moment of area surface (Fig. 4B) also presents a single optimal peak, situated in the extreme bottom left of possible space, but unlike for aspect ratio, performance for this trait is unevenly distributed with a large plateau of mid-high performance occupying the center of the graph. Areas of lower performance exist only for the highest PC 2 values with low PC 1 scores, an area of shape space characterized by the thinnest, anteriorly flexed theoretical shapes. The single peak for pitch agility (Fig. 4C) resides in the top left corner of the graph with a small area of highest performance. Performance decreases to all sides of this peak, dipping more sharply along PC 2 than PC 1, thus elongating the higher-performance region along PC 1. The most

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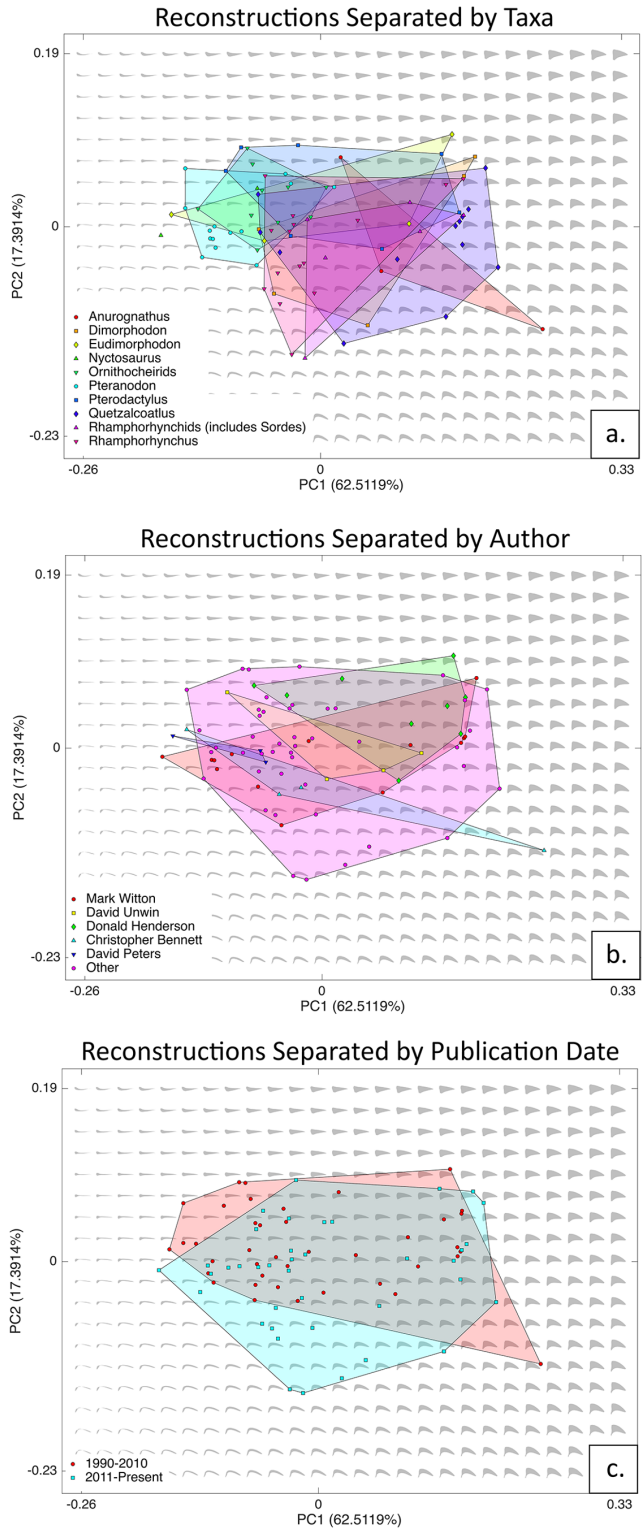


Figure 3. Theoretical morphospaces of reconstructed pterosaur wings. **A,** Wing reconstructions colored by taxa group, gray wing shapes represent generated theoretical planforms. **B,** Wing reconstructions colored by researcher. **C,** Wing reconstructions colored by date of publication.

optimal theoretical shapes for this metric are uncurved and needle-like (Fig. 3). The tip angle performance surface (Fig. 4D) presents a graph with values roughly inverse to those of aspect ratio, with an area of high performance in the top right of the graph, decreasing as a slope for lower values of PC 1. Three isolated islands of high performance also exist in the upper left corner of the graph, each centered around a single theoretical form and surrounded by low-performance space. These islands are likely anomalous, resulting from the extrapolation of theoretical shapes at the edge of shape space.

Combining performance surfaces through Pareto optimization allows for the derivation of three optimality surfaces tied to specific styles of flight (Walters et al. 2026). The combination optimal for dynamic soarers (Fig. 5A) presents two adjacent areas of optimal shape space, one in the upper left, characterized by thin anteriorly flexed theoretical shapes, and a larger region, covering most of the extreme left of the graph. This larger peak is adjacent to impossible space and is characterized by thin, posteriorly flexed forms. The optimal combination for long-distance flight (Fig. 5B) is broadly similar, although the optimal region is expanded to encompass the entirety of the extent of PC 2 for the lowest values of PC 1. In both spaces, optimality decreases for higher PC 1 values, although this decrease is irregular for dynamic soaring. The optimal region for the aerial predation metric combination (Fig. 5C) extends to cover the majority of possible space. This encompasses a large variety of theoretical shapes, ranging from thin, posteriorly curved to stout, subtriangular forms. Lowest-optimality theoretical shapes exist only at the extreme upper left of the plot, with a second, less pronounced decrease in optimality in the lower right.

Intrageneric Homogeneity

The pterosaur genera exhibit considerable overlap in morphospace, with most groups characterised by broad convex hulls (Fig. 3A). The most constrained hulls (tightest grouping of sampled reconstructions) are those of medium-sized oceangoing pterosaurs, such as *Pteranodon*, but even these cover a broad area of morphospace and overlap with the hulls for multiple other less-derived pterosaurs, including *Eudimorphodon*. There is no separation in morphospace between the smallest and largest pterosaur groups, as both *Anurognathus* and *Quetzalcoatlus* occupy an overlapping central morphological position.

Stylistic Heterogeneity

Using the same morphospace but with convex-hull groupings defined by the individuals responsible for the reconstructions rather than taxon presents similar results, with considerable overlap between different pterosaur illustrators (Fig. 3B). These convex hulls occupy a large area of available morphospace, with one exception. Reconstructions produced by David Peters in peer-reviewed publications occupy a small convex hull with low PC 1 and mid PC 2 scores. This hull is smaller than that of any taxa, suggesting that these reconstructions, which include individuals of multiple genera, are more self-same than reconstructions of any single group of pterosaurs.

Temporal Heterogeneity

Planforms produced before and after the establishment of the modern consensus of the pterosaur wing exhibit large overlap, although there is some dissimilarity, primarily along PC 2 (Fig. 3C). Reconstructions from before Elgin et al. (2011), tend to be straighter, with a less pronounced curvature, whereas more modern planforms expand into lower PC 2 areas of shape space with a highly curved trailing edge. The broadest chord planform in the dataset belongs to the earlier group of reconstructions.

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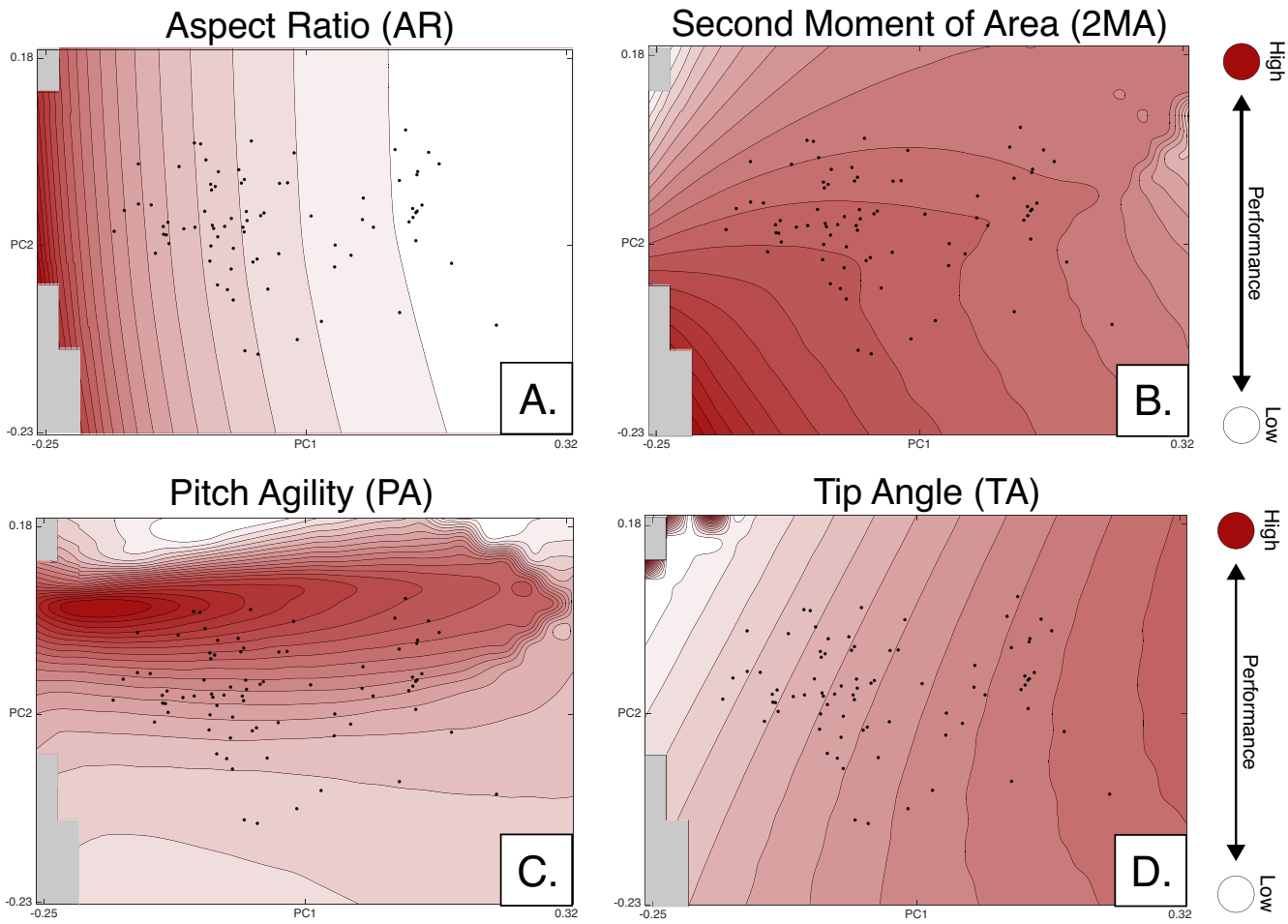


Figure 4. Performance surfaces calculated from theoretical shapes for each examined functional trait. In all plots darker colors indicate higher functional performance. **A,** Aspect ratio (AR); **B,** second moment of area (2MA); **C,** pitch agility (PA); and **D,** tip angle (TA).

Morphological Diversity

Multiple studies of the pterosaur wing from measurements of bone lengths have established an ecomorphospace of pterosaurs, comparing pterosaur wing dimensions with those of birds, principally using the aspect/loading space created by Rayner (1988). In these analyses, pterosaurs occupy a region of space that overlaps with birds of multiple different flight styles, as well as extending into unoccupied areas (Witton 2008; Witton and Habib 2010; Fig. 6A). As this is derived directly from fossils, it provides a helpful rendering of the likely extent of pterosaur shape space. For a direct comparison with previous linear measurement analyses, reconstructed pterosaur wings were projected into the bird planform shape morphospace created by Walters et al. (2026). This shape-based bird wing space (Fig. 6B) closely mirrors the aspect/loading morphospace of birds created by Rayner (1988), allowing direct comparison of space occupation between reconstructed wing shapes and the understood shape space occupation of pterosaurs. When projected into bird morphospace (yellow highlighted region in Fig. 6A), reconstructed shapes cluster tightly into the upper left quadrant, an area characterized by dynamic soaring and waterbird planforms. The only extension beyond bird-occupied morphospace is toward thinner needle-like planforms, with the exceptionally high-aspect *Nyctosaurus* occupying space separate from the rest on the extreme left of PC 1.

Functional Diversity

No pterosaur reconstruction is optimal for any individual performance metric. For aspect ratio (Fig. 4A), the most optimal planform, that of *Nyctosaurus*, occupies a region only about halfway up the optimal peak. All other taxa occupy lower-performing positions, with examples of *Dimorphodon*, *Eudimorphodon*, *Quetzalcoatlus*, and *Anurognathus* in the lowest possible performance space. Planforms occupy more optimal space for second moment of area (Fig. 4B), with most occupying a high, though suboptimal, area of morphospace with relatively flat performance contours. No pterosaur reconstructions occupy the lowest-optimality space for this metric. Planforms occupy a spread of performance for pitch agility, with the majority plotting around halfway up the optimal peak. The most optimal planforms for this metric are *Pterodactylus* and ornithocheirid reconstructions, with the thinnest wing chord and the least posterior curve. The lowest-performing planforms are reconstructions of rhamphorhynchids and *Quetzalcoatlus*, which portray highly curved trailing edge margins. For tip angle, pterosaur reconstructions cover a spread of low to middling optimality space, with the best performing, though suboptimal, planforms being the broader-winged examples of *Anurognathus* and *Quetzalcoatlus*.

Of the flight style combinations tested (Fig. 5A–C), examples of multiple pterosaur taxa occupy regions of high or highest optimality for all metrics. This is especially true for the combination of traits

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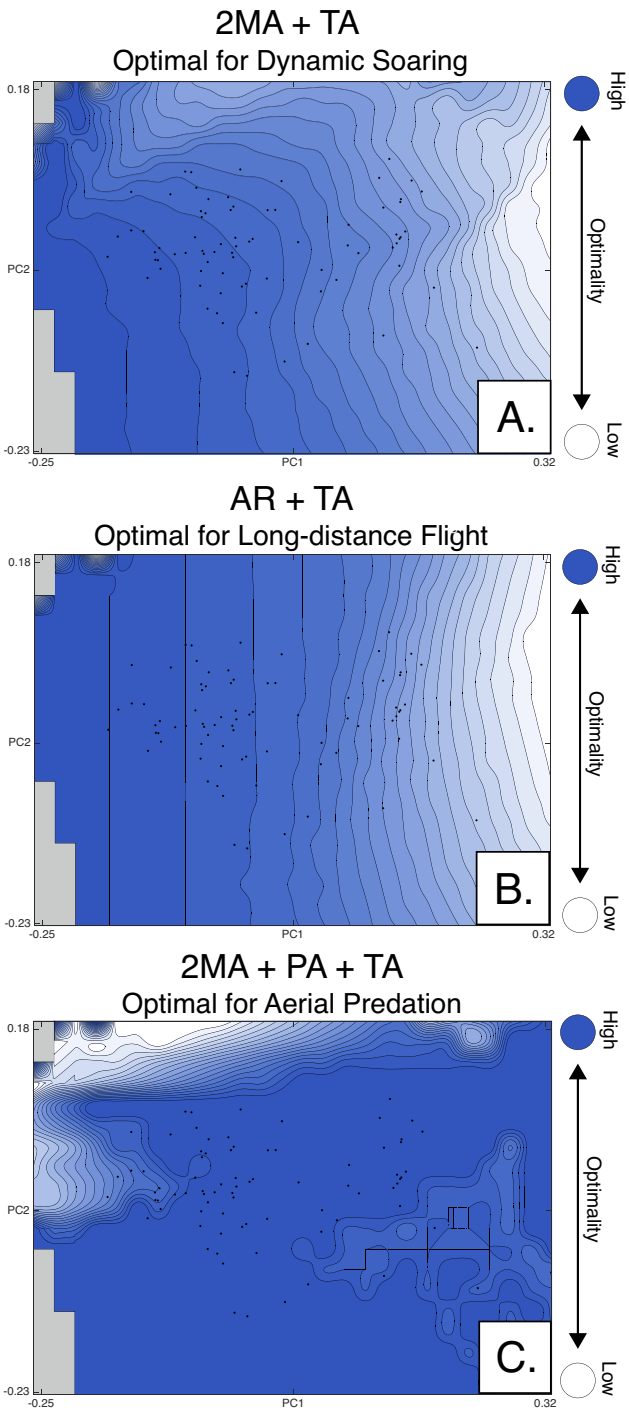


Figure 5. Optimality surfaces for the examined metric combinations relating to flight style. In all plots, darker colors indicate greater optimality. **A,** Second moment of area (2MA) and tip angle (TA) combination; **B,** aspect ratio (AR) and tip angle (TA) combination; **C,** combination of second moment of area (2MA), pitch agility (PA), and tip angle (TA).

proposed as optimal for aerial predation (Fig. 5C), where almost every pterosaur reconstruction plots within the highest-optimality region. The lowest-performing planforms for this metric are the thinnest winged example of *Nyctosaurus*, the *Eudimorphodon* by Peters, and the broadest-winged example of *Anurognathus*. For both dynamic soaring and long-distance flight combinations (Fig. 5A,B), *Nyctosaurus* is the most optimal, although the upper two levels of optimality are occupied by examples from four pterosaur groups.

Discussion

While there is some variation in the space occupation of pterosaur reconstructions, the lack of discrete clustering makes it difficult to identify pterosaurs by genus. This would be expected for closely related taxa or those with convergent flight niches, but the effect is observed across the broadest extents of the taxa sampled. Part of this homogenization may result from authors treating pterosaur reconstructions as simple diagrammatic interpretations of a pterosaur wing, rather than hypotheses of shape; however, this is unlikely to completely explain the result for two reasons. First, there is diversity in the dataset in the usage of the reconstructions analyzed, covering both simple diagrams and models that were used in aerodynamic and mass calculations (Wilkinson et al. 2006; Henderson 2010). Second, all the reconstructions used in this analysis are attributed to a family or genus, implying a degree of specificity in their construction that may be absent from generic pterosaur schematics.

In avians, there is a well-defined link between wing shape and the flight styles and niches of particular taxa (Saville 1957; Pennycuick 1975,1989; Rayner 1988, 1989; Norberg 2002; Taylor and Thomas 2014; Walters et al. 2026). The differences in wing construction between birds and pterosaurs make direct comparison of ecomorphospace between these two groups difficult, particularly due to the connection between the wing and leg in pterosaurs. It is highly likely that the construction of the pterosaur wing with a single digit at the leading edge constrains pterosaur shape to a greater degree than the wing of birds, and this is borne out in previous analyses (Witton 2008; Witton and Habib 2010; Fig. 6A). Nonetheless these established morphospaces based on bone measurements show a greater spread of space occupation for pterosaurs than does reconstructed planform shape. Birds are also useful as a point of comparison due to their broad range of ecologies and flight niches, encompassing dynamic soaring oceangoing niches that are hypothesized for pterosaurs and are not represented in bats. Extant bats, like pterosaurs, occupy a constrained ecomorphospace, although they do not achieve the diversity in size and proposed niches of pterosaurs. The previous use of birds as a source of comparison and shaped niches like dynamic soaring leave bird wings as the best, if imperfect, comparison. It is highly unlikely that animals adapted for environments and niches as varied as open oceans and tiered forests would possess similarly shaped wings, yet this is the pattern observed in this pterosaur dataset.

The overlap between the largest and smallest pterosaurs in morphospace also presents an issue for pterosaur reconstructions, as the aerodynamic profiles of large soaring wings should differ from those of smaller fliers due to the increased lift demand incurred by larger body size. This feature is observed in bird wings, with a division between larger soaring birds and smaller passerines (Walters et al. 2026). Although shape in this analysis was considered independent of mass, differences in the body-mass scaling relationship of birds and pterosaurs may have some effect on wing shape. Pterosaurs are often interpreted as lighter than birds for their given wingspans (Henderson 2010; Witton and Habib 2010), which may reduce the demand for increased lift and allow for the development of more generalized wings at a range of sizes. However, this feature would only be present in reconstructions that attempt to accurately depict pterosaur wings, rather than in simple schematics.

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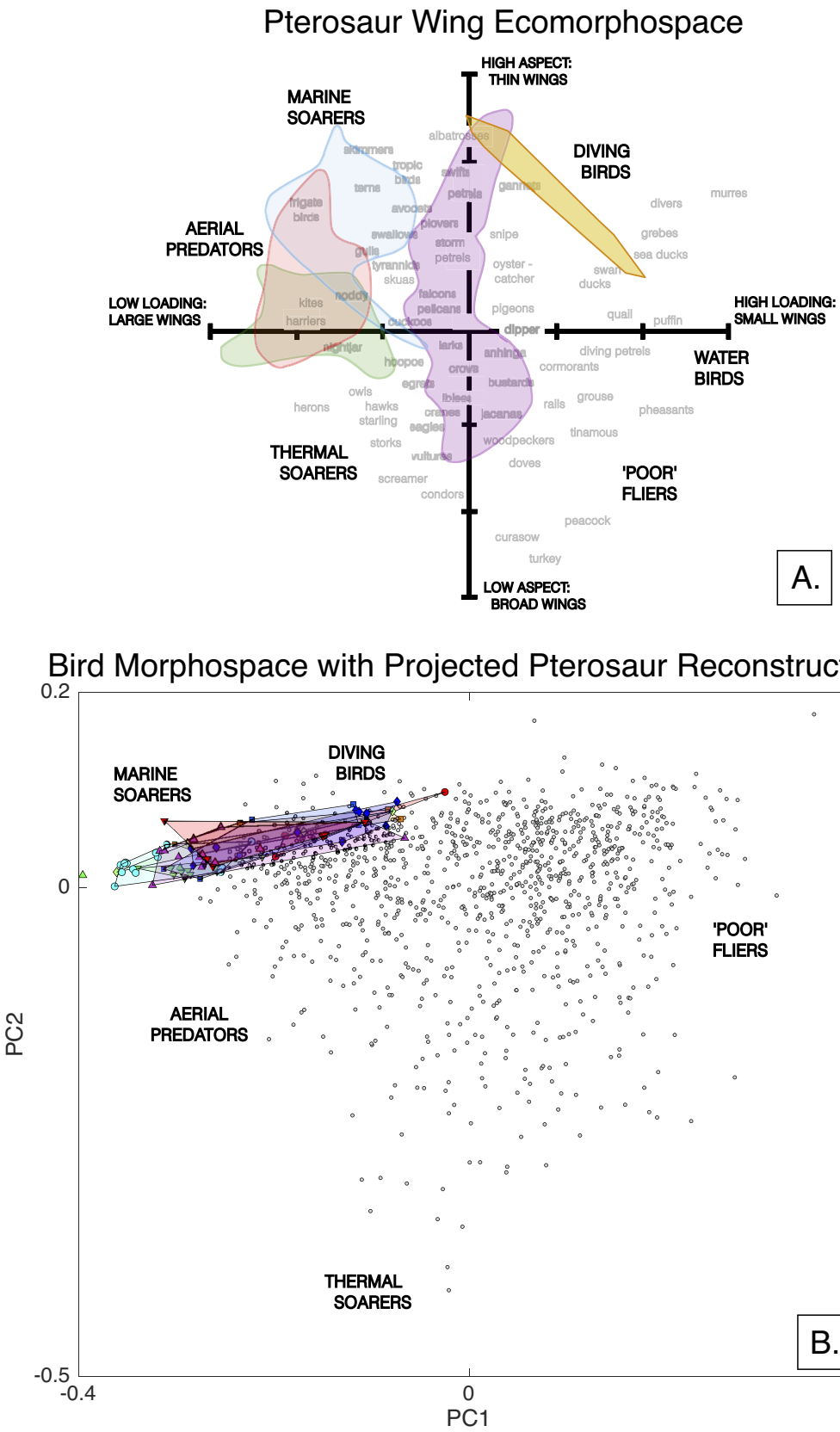


Figure 6. Comparison of bird and pterosaur wing-shape space. **A,** Ecomorphospace of pterosaur and bird wings based on bone length measurements. Bird morphospace redrawn from Rayner (1988). Colored hulls represent prior placement of pterosaurs from Witton and Habib (2010): blue, Brower and Veinus (1981); green, Hazlehurst and Rayner (1992); red, Chatterjee and Templin (2004); purple, Witton and Habib (2010). Approximate position of pterosaur planform reconstructions from this study in yellow. **B,** Morphospace of bird wing planforms (Walters et al. 2026) with pterosaur reconstructions projected over to show relative position. Colored hulls represent pterosaur groups.

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Of the sampled genera, examples of *Pteranodon* cluster loosely while also including the greatest number of representations ($n = 14$), suggesting homogeneity. Better representation of this taxon than other pterosaurs may be down to multiple factors. The relative popularity of *Pteranodon* in popular culture as the default "pterodactyl" may have broad influence over reconstructions, resulting in a degree of consensus between reconstructors, where this may be less true for more obscure pterosaurs like *Eudimorphodon*. This effect is likely minimized in the dataset, as only academic reconstructions were included, although pterosaur research does not operate in a vacuum and prior exposure likely plays a role in the way that prehistoric animals are reconstructed in manners that are difficult to quantify. In this regard it could be said that *Pteranodon* reconstructions are produced with greater consensus, although this does not speak to the utility of these reconstructions as proxies for shape. Alternatively, the very long high-aspect wing of oceangoing pterosaurs may be more predisposed to clustering in morphospace than broader-winged forms due to the nature of PC 1 describing the thickness of the wing chord. The overall shape of thinner, higher-aspect planforms is proportionally less affected by differences in brachiopatagium attachment sites than lower-aspect planforms. As a result, higher-aspect reconstructions are more likely to cluster in this region regardless of the reconstruction of the attachment, leading to the illusion of consensus. This may also explain why ornithocheirid examples with both knee and ankle reconstructions occupy this same region of morphospace. Differences in the body size of these taxa may result in flight performance variation, as mass and size scale differentially, but this would not be testable using unscaled reconstructions or with the shape-based metrics of this analysis.

From these results, pterosaur reconstructions lack sufficient homogeneity for planforms to be useful as models for a particular genus, as too much variation remains to distinguish a definitive wing shape. Even broader distinction between pterodactyloid and non-pterodactyloid pterosaurs is absent from reconstructed planforms.

Style in reconstruction, with one exception, has little influence over placement within the morphospace, suggesting that the lack of genera-specific homogeneity cannot be attributed to the idiosyncrasies of individual researchers. Even where an individual's particular style applies uniformly to all examples, best exemplified by the characteristic distal brachiopatagium of pterosaur Bauplans by Mark Witton, reconstructions occupy varied shape space. The one area where this does not hold true is with published works by David Peters, which exhibit tight clustering irrespective of pterosaur genus. This reflects Peters's approach of reconstructing pterosaur wings with narrower chords than is representative in the fossil record more than it does the functional abilities of pterosaur wings (Naish 2020).

Lack of clustering is instead likely due to differences in key aspects of wing morphology between reconstructions, particularly the distal propatagium attachment and the degree of curvature of the distal propatagium. Dividing the dataset by time (Fig. 3C) shows that there has been little difference made to planform shapes post broad consensus in the attachment points of the wing. Even if the ankle attachment is considered universal in more recent reconstructions, some reconstructions, such as those of *Quetzalcoatlus* from Padian et al. (2021), possess a higher attachment point, which will introduce variation on PC 1, as reconstructions favoring a hip or knee attachment will have thinner wing chords. Examples with a less strongly curved trailing edge could in turn plot more positively on PC 1. The link between the two main axes of morphospace variation and two of the largest debates surrounding pterosaur wing shape highlights the degree to which lack of consensus affects understanding of pterosaur flight performance. This is likely to change with further pterosaur research, but currently, consensus on wing properties does not appear to effect reconstruction shape.

The lack of clear taxon-specific clusters in pterosaur-specific morphospace (Fig. 3A), in contrast with the tight clustering observed when compared with birds, again highlights potential problems with pterosaur reconstructions. Previous analyses of pterosaur wings present varied morphospace occupation, corresponding to a number of different niches supported by dietary analyses (Bestwick et al. 2018; Pêgas et al. 2025). This is a result expected for pterosaurs preserved in different depositional environments and varying drastically in wingspan. While it is possible that some taxa, such as *Pteranodon*, overlap with modern marine soarers, the positioning of almost all sampled taxa with this niche does not fit with prior research and presents unreasonable assumptions about pterosaur flight ability. From their robust skeletal anatomy, early pterosaurs such as *Dimorphodon* were denser animals and likely relatively poor fliers, preferring to spend time on the ground (Witton 2008, 2013; Witton and Habib 2010).

The association of *Dimorphodon* with albatross and waterbirds instead of extant poor-flying taxa suggests either that pterosaur wing shape is only loosely linked with flight ability or that current reconstructions of these taxa do a poor job of reflecting the living animal. In extant birds, several proposed factors may contribute to flight performance, with shape acting as a driving force across multiple clades (Wang and Clarke 2015; Baliga et al. 2019; Rader and Hedrick 2023; Walters et al. 2026). The niche of specific pterosaur genera is poorly constrained, complicating ecological comparison with birds, but the fundamental pressures associated with developing powered flight are shared by these groups, and constrict wing shape (Rayner 1988). It is therefore likely that the reconstructions of these earlier-diverging taxa, and broader-winged taxa more generally, are represented as thinner than they would likely be in life. Again, this discrepancy is likely due to the lack of adherence to consensus surrounding the attachment of the trailing edge of the brachiopatagium to the body or leg, as attachments higher up the body truncate the wing chord, producing disproportionally thinner wings more greatly resembling those of oceangoing taxa.

Functional analysis exhibits the same clustering issue observed in the comparison with bird morphospace. It is highly unlikely that animals as taxonomically and temporally disparate as the sampled pterosaurs would all be optimal for a single functional peak (Fig. 5C). This is especially true for pterosaurs with different inferred ecological niches. While optimization for agile flight fits with the understanding of small forest-dwelling taxa such as *Anurognathus*, interpreted as an insect hawker similar to a bat or nightjar (Wellnhofer 1991; Bakhurina and Unwin 1995; Unwin et al. 2000; Bennett 2001, 2003, 2007; Bestwick et al. 2018), it does not fit with the inferred niche of *Pteranodon* and *Nyctosaurus* as oceangoing dynamic soarers, analogous to the modern albatross (Marsh 1876; Wellnhofer 1991; Bennett 1993, 1994; Unwin 2006; Witton 2013; Bestwick et al. 2018). The most extreme example, *Nyctosaurus*, is the closest taxon to the optimal functional combination for marine soaring, suggesting the possibility of some functional specialization, although functional variability remains broadly limited.

Interestingly, some taxa classically interpreted as oceangoing soarers appear close to optimal for the functional combination associated with long-distance flight (Fig. 5B), likely on account of the more acute wingtip produced by a more slender planform. Conspicuously absent from this optimal region is *Quetzalcoatlus*, which, with its wingspan of 10 or more meters, is often considered to have traveled long distances, potentially across continents, in a

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mode analogous to modern terrestrial soarers (Chatterjee and Templin 2004; Witton 2008, 2013; Witton and Naish 2008; Witton and Habib 2010; Padian et al. 2021). Placement of *Quetzalcoatlus* nowhere near the optimal peak, however, likely speaks more to the lack of consensus in reconstructions than the actual flight ability of these animals.

It is tempting to use these results as an analytical tool to make suggestions as to what wing shapes should look like in more lifelike pterosaur reconstructions, although this approach is not without hazard. Making suggestions based on optimal forms for performance in a certain flight style runs the risk of assuming that pterosaur wings were optimally shaped for flight, which is an unfounded expectation (Liu et al. 2024; Fadel et al. 2025; Walters et al. 2026). Furthermore, because the reconstructions input in these analyses perform poorly as a proxy for real pterosaur planforms, there is no guarantee that any extrapolated "consensus" shape for a specific taxon would necessarily be more accurate. Using theoretical morphospace to make predictions about the shapes of taxa to improve reconstructions is a potentially useful tool, but would require better understood inputs, extant taxa and well-resolved phylogenetic trees that unfortunately do not currently exist for pterosaurs.

Conclusion

Of the five tests of pterosaur wing planform viability, pterosaur reconstructions only pass one element, reconstructor heterogeneity. Examples of the same taxa do not cluster together, demonstrating a lack of consensus among researchers concerning the shape of the wing. Furthermore, reconstructions fail to capture the level of form and function variation expected from a group as large as Pterosauria, as has been demonstrated by linear measurement analyses. This result is insufficient for reconstructions to pass the bar and be treated as functional reconstructions of living animals, and they are thus not useful for morphological analysis of pterosaur flight. This result likely stems from a lack of consensus over fundamental elements of the pterosaur wing, particularly the nature of the distal brachiopatagium. To produce functionally viable pterosaur reconstructions, a consensus on the pterosaur wing, such as that of Elgin et al. (2011), needs to be adhered to, even if this one-size-fits-all approach likely represents a simplification of variation of pterosaur wing properties. Otherwise, pterosaur reconstructions will remain a visual shorthand, but one that poorly reflects the living animal and is unfit to fly.

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Competing Interests. The authors declare no competing interests.

Data Availability Statement. All datasets produced and analyzed for the study are contained within this article and its Supplementary Material and are available for download without restriction. The taxon dataset, wing reconstruction outlines, and all code needed to run the analysis are accessible for download from https://doi.org/10.6084/m9.figshare.31444192. The base code for MATLAB is available for download from GitHub: https://github.com/Bristol-Palaeobiology/theofun). Supplementary Figure 1: Distribution of first and third principal components. Pterosaur wing reconstructions colored according to genera with theoretical wing shapes in gray. Supplementary Data 1: Full list of reconstructions used in analysis and their provenance, related to Figures 2–5 and data collection. Supplementary Data 2: All files required to run the analyses described and for the production of Figures 2–5. Supplementary Data 3: Platform outline files for elliptical Fourier analysis. Supplementary Code 1: MATLAB code used in analysis.

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