

The Earliest Pterodactyloid and the Origin of the Group

Brian Andres,^{1,*} James Clark,² and Xing Xu³

¹School of Geosciences, University of South Florida, Tampa, FL 33620, USA

²Department of Biological Sciences, George Washington University, Washington, DC 10024, USA

³Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China

Summary

The pterosaurs were a diverse group of Mesozoic flying reptiles that underwent a body plan reorganization, adaptive radiation, and replacement of earlier forms midway through their long history, resulting in the origin of the Pterodactyloidea, a highly specialized clade containing the largest flying organisms. The sudden appearance and large suite of morphological features of this group were suggested to be the result of it originating in terrestrial environments, where the pterosaur fossil record has traditionally been poor [1, 2], and its many features suggested to be adaptations to those environments [1, 2]. However, little evidence has been available to test this hypothesis, and it has not been supported by previous phylogenies or early pterodactyloid discoveries. We report here the earliest pterosaur with the diagnostic elongate metacarpus of the Pterodactyloidea, *Kryptodrakon progenitor*, gen. et sp. nov., from the terrestrial Middle-Upper Jurassic boundary of Northwest China. Phylogenetic analysis confirms this species as the basal-most pterodactyloid and reconstructs a terrestrial origin and a predominantly terrestrial history for the Pterodactyloidea. Phylogenetic comparative methods support this reconstruction by means of a significant correlation between wing shape and environment also found in modern flying vertebrates, indicating that pterosaurs lived in or were at least adapted to the environments in which they were preserved.

Results and Discussion

The Pterodactyloidea are a clade of elongate-metacarpus, short-tailed pterosaurs [3] that appeared in the middle Late Jurassic (Kimmeridgian) and quickly became the most diverse pterosaur group, replacing all others [1]. The reorganization of their body plan was so extensive that a consensus has not been reached on its basal relationships, or how to define its name based on its relationships [4, 5]. An apomorphy-based definition was therefore proposed based on the elongation of the metacarpus that is found only in the pterodactyloid pterosaurs [6] and is the only original character [3] still diagnostic for the clade. A new pterosaur species, *Kryptodrakon progenitor*, gen. et sp. nov., from Northwest China is the earliest and most basal pterosaur to bear this diagnostic apomorphy, extending the fossil record of the Pterodactyloidea by at least 5 megannum (Ma) to the Middle-Upper Jurassic boundary.

In previous phylogenetic analyses, the Pterodactyloidea have traditionally had the longest branch in terms of apomorphy number [5] and temporal duration of gaps without fossils implied by phylogeny [4]. This long branch was hypothesized to be the result of the pterodactyloids originating in terrestrial environments [1, 2], where the pterosaur fossil record has historically been undersampled [1]. Due in part to the fragile construction of their skeletons, pterosaurs have been predominantly preserved in quiet marine environments [7], to such an extent that they were hypothesized to have been an almost exclusively marine group [8, 9]. A number of terrestrial deposits from China have yielded new pterosaurs in recent years [10, 11], but when preservation in terrestrial or marine environments is reconstructed for previous pterosaur phylogenies, they still support a predominantly marine history for the pterosaurs and a marine origin of the Pterodactyloidea (see Table S1 available online). Here we show that comprehensive phylogenetic and comparative analysis of the Pterosauria and *Kryptodrakon* supports a terrestrial origin and a predominantly terrestrial history for the Pterodactyloidea. In support of this reconstruction, we provide a novel test of the quality of the fossil record and demonstrate that pterosaurs were adapted to the environments in which they were preserved to a significant degree.

The material described here is assigned to Pterosauria Owen 1842, Pterodactyloidea Plieninger 1901 sensu Padian 2004, *Kryptodrakon progenitor*, gen. et sp. nov.

Etymology

Kryptodrakon progenitor, from the Greek “krypto” (hidden) and “drakon” (serpent), referring to the movie *Crouching Tiger, Hidden Dragon*, filmed near where the species was discovered, and the Latin “progenitor” (ancestral or firstborn), referring to its status as the earliest pterodactyloid.

Material

A single specimen (holotype) consisting of an incomplete postcranium: IVPP V18184 (Figures 1, 2B, and S1), collected from a 30 cm² area separated from all other fossils by at least 10 m distance. The specimen is housed at the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

Locality and Stratigraphy

The fossil was collected from a mudstone in the alluvial facies of the lower part of the Shishugou Formation at Wucaiwan, Junggar Basin, Xinjiang, China. The specimen is from 35 m below the T-1 marker tuff [13], which had been dated as 161.2 ± 0.2 Ma [14]. Recalibration of the age of the Fish Canyon sanidine monitor mineral [15] suggests that the age of the T-1 marker tuff should be adjusted 0.6% older. Thus, we regard its age as 162.2 ± 0.2 Ma. In the context of an average sediment accumulation rate of 7.2 cm per 1,000 years for this part of the basin [16], the fossil specimen would have an age of approximately 162.7 Ma. Following the Geologic Time Scale adjustments of Gradstein et al. (2012) [17], this age is the very earliest Oxfordian of the Upper Jurassic but within the error margin of the end of the Middle Jurassic [17],

*Correspondence: brianandres@usf.edu



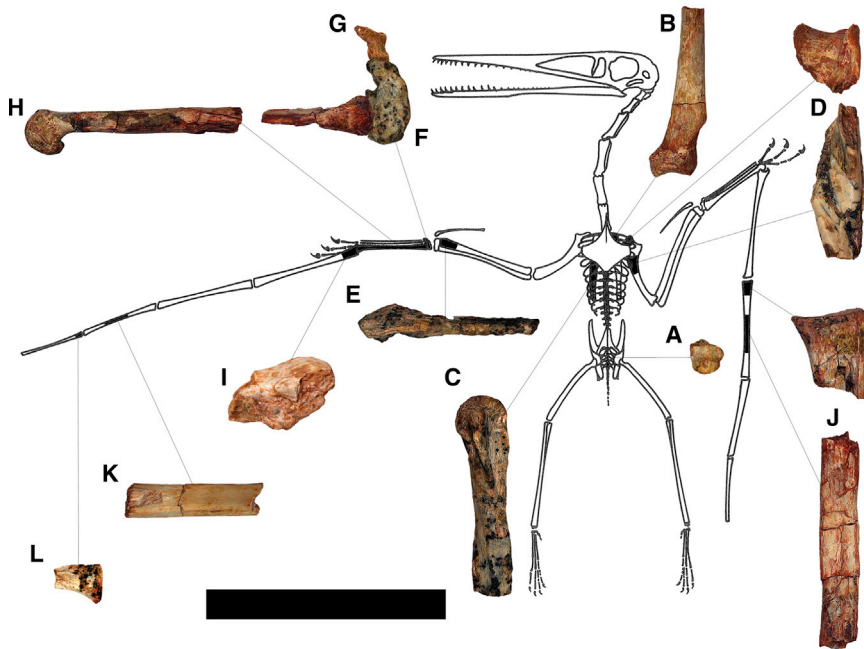


Figure 1. Preserved Remains of *Kryptodrakon progenitor*, gen. et sp. nov., IVPP V18184

- (A) Partial sacrum.
 - (B) Ventral ramus of left coracoid.
 - (C) Anterior end of right scapulocoracoid.
 - (D) Proximal end and shaft of left humerus.
 - (E) Distal end of right radius.
 - (F) Right distal syncarpal.
 - (G) Right preaxial carpal.
 - (H) Right metacarpal.
 - (I) Proximal end of right first wing phalanx.
 - (J) Proximal end and shaft of left second wing phalanx.
 - (K) Shaft of right third wing phalanx.
 - (L) Proximal end of right fourth wing phalanx.
- The skeleton is *Pterodactylus antiquus* reprinted with permission from Wellnhofer (1991) [12], with preserved elements of *Kryptodrakon progenitor* infilled in black. Scale bar represents 50 mm. See also Figure S1.

and so it may be conservatively considered as dating to the Middle-Upper Jurassic boundary. This timescale contains significant age adjustments from previous scales, which had dated this and other Wucuiwan specimens to the Middle Jurassic.

Diagnosis

Small pterodactyloid pterosaur differentiated from all other pterosaurs in having autapomorphic distal radius with distinct ventral flange and dorsally positioned anterior tubercle, autapomorphic preaxial carpal wider than long due to two expanded proximal flanges, and unique combination of elongate wing metacarpal with length more than eight times dorsoventral width at midpoint and anteroposteriorly compressed proximal end with large ventral expansion.

Description

The preserved remains of *Kryptodrakon progenitor* include a partial sacrum, ventral ramus of the left coracoid, anterior end of the right scapula, proximal end and shaft of the left humerus, distal end of the right radius, right distal syncarpal, right preaxial carpal, right wing metacarpal, proximal end of the right first wing phalanx, proximal end and shaft of the left second wing phalanx, shaft of the right third wing phalanx, proximal end of the right fourth wing phalanx, and a number of indeterminate fragments (Figures 1 and S1). This individual is considered an osteological adult based upon the fusion of the sacrum, scapulocoracoid, and distal syncarpal [18]. It is a small pterodactyloid with an estimated wingspan of 1.4 m (Supplemental Experimental Procedures).

The characters that determine the phylogenetic relationships of *Kryptodrakon* are predominantly found in the most complete element, the wing metacarpal (Figures 1H, 2B, and S1). The metacarpus of pterosaurs consists of the robust wing metacarpal (metacarpal IV) and the slender metacarpals I–III that lie along the anterior surface of the wing metacarpal to articulate with the claw-bearing digits. The right wing metacarpal is missing a small segment of the shaft, but the attenuation of its cross-section and the continuation of a posterior

fossa onto the distal end indicate that only about 1 cm of length is absent. The combined minimum length of the preserved fragments is at least 84% of the humerus length estimate. This is more than the 80% necessary for referral to the Pterodactyloidea [4, 6].

The wing metacarpal in this species exhibits a predominantly nonpterodactyloid proximal end and a pterodactyloid distal end. Like the nonpterodactyloids, the proximal end of the wing metacarpal has an anteroposteriorly compressed cross-section, a proximal fossa on the posterior surface, a low proximal tuberculum, and a large ventral expansion (Figures 2A and 2B). By contrast, the proximal ends of the other pterodactyloid wing metacarpals are anteroposteriorly broadened into a rectangular cross-section, have a much thicker anteriorly curving flange that is the broadest part of the proximal end, have a taller proximal tuberculum, and have a much smaller ventral expansion (Figure 2C). Like other pterodactyloids, the distal end of the wing metacarpal in *Kryptodrakon* has an oval cross-section and an elongate shaft, bringing the total length to over nine times the mid-width (Figures 2B and 2C). By contrast, the distal end of nonpterodactyloid wing metacarpals have an anteroposteriorly compressed cross-section, a dorsal ridge on the posterior surface of the shaft, and a short shaft, bringing the total length to less than seven times the mid-width (Figure 2A). Two pterodactyloid features are present on the proximal surface of the wing metacarpal of *Kryptodrakon*, a dorsoventrally oriented ventral articular surface and a proximal tuberculum surrounded by a crescentic sulcus (Figures 2B and 2C), allowing greater rotation to absorb shocks and stresses during active flight [19].

Comprehensive phylogenetic analysis of *Kryptodrakon* and the relationships of the Pterosauria confirm this species as the basalmost member of the Pterodactyloidea (tree length = 874.692, consistency index = 0.357, retention index = 0.800) (Figures 3 and S2). This is the largest phylogenetic analysis of pterosaurs and is significantly larger than earlier versions of the analysis [11, 20, 21]. It incorporates the valid species (Table S2; Supplemental Experimental Procedures) and characters used in the previous 145 years of pterosaur phylogenetic study (112 species, 224 characters). Because many of the characters that determine the relationships of pterosaurs in general and *Kryptodrakon* specifically are continuous and



Figure 2. Comparison of Three-Dimensionally Preserved Pterosaur Wing Metacarpals Illustrating the Character States of Nonpterodactyloid and Pterodactyloid Pterosaurs in Anterior and Proximal Views

(A) Nonpterodactyloid *Comodactylus ostromi* Galton 1981 (YPM 9150), courtesy of the Yale Peabody Museum of Natural History.

(B) Basal pterodactyloid *Kryptodrakon progenitor* (IVPP V18184).

(C) Derived pterodactyloid cf. *Santanadactylus pricei* Wellnhofer 1985 (AMNH 22552), courtesy of the American Museum of Natural History.

Abbreviations: da, dorsal articular surface; dc, distal condyles; cs, crescentic sulcus that encircles proximal tuberculum; McI-III, metacarpals I-III; pt, proximal tuberculum; va, ventral articular surface; ve, ventral expansion. Scale bar represents 50 mm.

have been subjectively coded differently in previous analyses, the continuous coding option of TNT [22] was implemented. The phylogenetic position of *Kryptodrakon* is supported by changes in two continuous and two discrete characters of the wing metacarpal, further reducing the long branch of the Pterodactyloidea (Table S3).

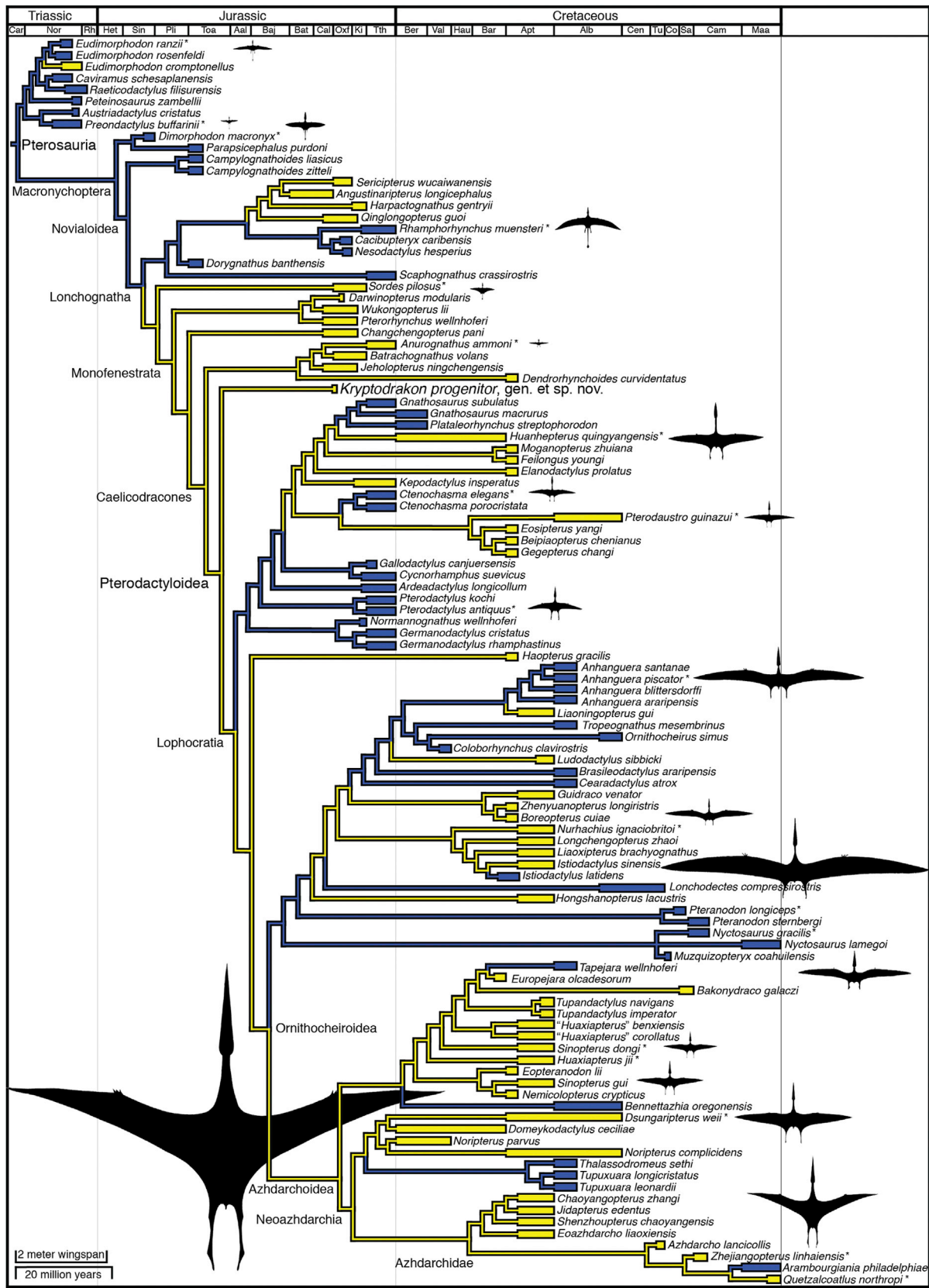
The Pterodactyloidea are most parsimoniously reconstructed as originating in terrestrial environments as part of an extensive lineage that had been living there for at least 5 Ma (Figure 3). Whereas previous analyses and previously known pterodactyloid discoveries support a predominantly marine history for pterosaurs with repeated invasions of terrestrial environments (Table S1), our analysis implies a change in their ecology near the origin of the Pterodactyloidea wherein pterosaurs became predominantly terrestrial and repeatedly invaded marine environments (Figure 3). When subjected to a phylogenetic signal test [23], occurrence in terrestrial or marine preservational environments is very highly correlated with phylogeny in the comprehensive analysis, suggesting that segments of pterosaur evolution occurred in specific environments (one-tailed $p = 0.00000001$, $n = 10,000,000$).

The pterosaur fossil record has been considered to be highly incomplete and biased, with the greatest bias being toward specimens found in marine environments [9, 12, 24], and so the preservational environments of pterosaurs may reflect more their contact with environments of exceptional preservation than their preferred environments. However, there is a substantial literature identifying the ecology of extinct organisms using modern species as models. When this had been previously applied to pterosaurs as a whole, size-independent measures of their wing shapes (wing aspect) were compared to those of modern birds and used to suggest a marine ecology for almost all pterosaurs (e.g., [25, 26]) [27]. Modern

vertebrates flying in terrestrial environments typically have broader (low-aspect) wings than the narrower (high-aspect) wings of their marine counterparts [28, 29]. This correlation is attributed to more maneuverable flight utilized by terrestrial fliers for cluttered habitats [28], escape [29], greater landing frequencies [25], and higher takeoff angles [30]. However, pterosaurs as a whole have narrow wings in comparison with other flying vertebrates by virtue of their flight membranes being attached to an extremely elongate wing finger and a much shorter hindlimb.

To test whether the same morphological difference between the wings of terrestrial and marine species exists in pterosaurs, the wing aspects of 19 pterosaur species from the literature [27] were correlated with terrestrial or marine occurrence using phylogenetic independent contrasts [31] to remove the effect of phylogeny ($r = 0.563$, two-tailed $p = 0.012$, $n = 19$) (Figure S3). Preservational environment is significantly correlated with wing shape in pterosaurs, such that terrestrial pterosaurs have lower wing aspects than their marine relatives and marine pterosaurs have higher wing aspects than their terrestrial relatives (sign test, two-tailed $p = 0.008$, $n = 19$), as in modern flyers. Pterosaurs have the appropriate wing shapes for the environments in which they were preserved.

The physical demands of flight are extreme and vary with environment [29]. At the origin of the Pterodactyloidea, the greatest change in the flight apparatus was the change in the metacarpus, which transitions from being the shortest and least variable in length of the major wing elements in nonpterodactyloid pterosaurs to being the longest and most variable in length within the pterodactyloid pterosaurs. This increased variation in metacarpal length begins right at the transition of pterosaurs to terrestrial environments (Figure 3), with *Sordes* and the Anurognathidae having the relatively shortest



(legend on next page)

metacarpals of all pterosaurs. The subsequent elongation of the metacarpus is the diagnostic apomorphy of the Pterodactyloidea, but the increased variation in length producing this elongation is likely a key innovation [32] allowing new and more varied wing shapes for the pterosaurs to radiate into new and more varied environments.

The sudden appearance and many diagnostic features of the pterodactyloid pterosaurs have been suggested to be the result of the group originating in terrestrial environments where the pterosaur fossil record has traditionally been poor, but this hypothesis was largely based on lack of evidence. Here we report the earliest and basalmost pterodactyloid and verify that it was found in a terrestrial environment. Phylogenetic comparative methods reconstruct both a terrestrial origin of the Pterodactyloidea and a predominantly terrestrial history for the group. This ecological history is supported by a significant correlation recovered between wing shape and environment that is also reported in modern flying vertebrates. This novel test of the fossil record demonstrates that pterosaurs lived in or were at least adapted to the environments in which they were preserved, and that ecology can be objectively and quantitatively reconstructed in extinct organisms.

Experimental Procedures

Comprehensive phylogenetic analysis was conducted with TNT v1.1 [22] using continuous and discrete partitions. Continuous characters were scaled so that their values ranged from 0 to 1. Ordered and unordered characters were used, and all were equally weighted. Inapplicable features were reductively coded, and polymorphic coding was used to denote variation within species. Four outgroups were used with *Euparkeria capensis* (Broom 1913) as the first outgroup. A basic tree-searching analysis with ratchet was implemented in TNT using 2,000 random addition sequence replicates. The ratchet proved to not be necessary. Ambiguous branch support was not used, zero-length branches were automatically collapsed, and resultant trees were filtered for best score. The analysis resulted in a single most parsimonious tree (Figures 3 and S1).

Phylogenetic comparative analyses were conducted using Mesquite v2.75 [33]. These analyses consist of an ancestral state reconstruction, a phylogenetic signal test [23], and phylogenetic independent contrast tests [31]. Ancestral state reconstruction was conducted with maximum parsimony, resulting in eight equally parsimonious optimizations for 18 preservational environment changes, differing only within the Ctenochasmatidae and Pteranodontia. The ACCTRAN character optimization of preservational environment is illustrated in Figure 3. The phylogenetic signal test was conducted by randomly reshuffling the terminal taxa and optimizing the preservational environment character 10 million times to create a null distribution of the number character changes. Only one random optimization equaled the 18 preservational environment changes from the ancestral state reconstruction. The phylogenetic independent contrast tests were conducted using PDAP:PDTREE module v1.15 [34] on a pruned subset of the comprehensive phylogenetic analysis containing the 19 pterosaur species that have calculated wing aspects (Figure S3). Wing aspect and preservational environment contrasts were successfully standardized using the subset phylogenetic analysis. When subjected to Pearson product-moment correlation, wing aspect as Y contrast was positively significantly correlated with preservational environment as X contrast. A more conservative sign test confirmed that the actual predicted direction of changes in wing aspect and paleoenvironment are significantly correlated.

Accession Numbers

Color illustrations of individual elements and additional analysis figures are available at <http://morphobank.org/> under project number 860.

Supplemental Information

Supplemental Information includes three figures, three tables, Supplemental Experimental Procedures, and two Supplemental Data Sets and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.03.030>.

Acknowledgments

Chris Sloan collected the fossil. Hai-Jun Wang assisted with fieldwork and prepared the specimen. The fieldwork was supported by the National Natural Science Foundation of China, the National Science Foundation Division of Earth Sciences, the Chinese Academy of Sciences, the National Geographic Society, the Jurassic Foundation, the Hilmar Sallee bequest, and George Washington University. Study of the specimen was supported by the Chinese Academy of Sciences, the National Science Foundation Division of Earth Sciences, and the National Natural Science Foundation of China.

Received: October 20, 2013

Revised: January 17, 2014

Accepted: March 11, 2014

Published: April 24, 2014

References

1. Unwin, D.M. (2006). Pterosaurs from Deep Time (New York: Pi Press).
2. Lü, J., Unwin, D.M., Jin, X., Liu, Y., and Ji, Q. (2010). Evidence for modular evolution in a long-tailed pterosaur with a pterodactyloid skull. *Proc. Biol. Sci.* 277, 383–389.
3. Plieninger, F. (1901). Beiträge zur Kenntnis der Flugsaurier. *Palaeontographica* 48, 65–90.
4. Unwin, D.M. (2003). On the phylogeny and evolutionary history of pterosaurs. In *Evolution and Palaeobiology of Pterosaurs, Volume 217*, Buffetaut, E., and Mazin, J.-M., eds. (London: Geological Society), pp. 139–190.
5. Kellner, A.W.A. (2003). Pterosaur phylogeny and comments on the evolutionary history of the group. In *Evolution and Palaeobiology of Pterosaurs, Volume 217*, Buffetaut, E., and Mazin, J.-M., eds. (London: Geological Society), pp. 105–137.
6. Padian, K. (2004). The nomenclature of Pterosauria (Reptilia, Archosauria). In *First International Phylogenetic Nomenclature Meeting*, M. Laurin, ed. (Paris: Muséum National d'Histoire Naturelle), p. 27.
7. Padian, K., and Rayner, J.M.V. (1993). The wings of pterosaurs. *Am. J. Sci.* 293, 91–166.
8. Wellnhofer, P. (1978). Pterosauria (Stuttgart: Gustav Fischer Verlag).
9. McGowan, C. (1991). Dinosaurs, Spitfires, and Sea Dragons (Cambridge: Harvard University Press).
10. Wang, X., Kellner, A.W.A., Zhou, Z., and Campos, Dde.A. (2005). Pterosaur diversity and faunal turnover in Cretaceous terrestrial ecosystems in China. *Nature* 437, 875–879.
11. Andres, B., Clark, J., and Xu, X. (2010). A new rhamphorhynchid pterosaur from the Upper Jurassic of Xinjiang, China, and the phylogenetic relationships of basal pterosaurs. *J. Vertebr. Paleontol.* 30, 163–187.
12. Wellnhofer, P. (1991). *The Illustrated Encyclopedia of Prehistoric Flying Reptiles* (London: Salamander Books).
13. Eberth, D.A., Xu, X., and Clark, J.M. (2010). Dinosaur death pits from the Jurassic of China. *Palaeos* 25, 112–125.
14. Clark, J.M., Xu, X., Eberth, D.A., Forster, C.A., Malkus, M., Hemming, S., and Hernandez, R. (2006). The Middle- to Late Jurassic terrestrial

Figure 3. Single Most Parsimonious Tree from the Comprehensive Phylogenetic Analysis of *Kryptodrakon progenitor*, gen. et sp. nov., and the Relationships of the Pterosauria

Ranges for species denote the greatest temporal resolution of stratigraphic dating. Parsimony reconstruction using ACCTRAN optimization for the occurrence of pterosaur taxa preserved in terrestrial or marine environments is shown via yellow or blue lineages, respectively. Species used in the phylogenetic comparative analysis of paleoenvironment occurrence and wing aspect are denoted by asterisks and depicted as silhouettes reprinted with permission from Wellnhofer (1991) [12], drawn to scale. Outgroup relationships are not shown. Branch lengths and support measures are listed in Table S3. See also Figures S2 and S3 and Tables S1, S2, and S3.

- transition: New discoveries from the Shishugou Formation, Xinjiang, China. In Ninth International Symposium on Mesozoic Terrestrial Ecosystems and Biota, P.M. Barrett and S.E. Evans, eds. (Manchester: Cambridge Publications), pp. 123–126.
15. Kuiper, K.F., Deino, A., Hilgen, F.J., Krijgsman, W., Renne, P.R., and Wijbrans, J.R. (2008). Synchronizing rock clocks of Earth history. *Science* *320*, 500–504.
 16. Eberth, D.A., Brinkman, D.B., Chen, P.J., Yuan, F.T., Wu, S.Z., Li, G., and Cheng, X.S. (2001). Sequence stratigraphy, paleoclimate patterns, and vertebrate fossil preservation in Jurassic Cretaceous strata of the Junggar Basin, Xinjiang Autonomous Region, People's Republic of China. *Can. J. Earth Sci.* *38*, 1627–1644.
 17. Gradstein, F., Ogg, J., Schmitz, M., and Ogg, G. (2012). *The Geologic Time Scale 2012* (Burlington: Elsevier).
 18. Bennett, S.C. (1993). The ontogeny of *Pteranodon* and other pterosaurs. *Paleobiology* *19*, 92–106.
 19. Padian, K. (1984). A large pterodactyloid pterosaur from the Two Medicine Formation (Campanian) of Montana. *J. Vertebr. Paleontol.* *4*, 516–524.
 20. Andres, B., and Ji, Q. (2008). A new pterosaur from the Liaoning Province of China, the phylogeny of the Pterodactyloidea, and convergence in their cervical vertebrae. *Palaeontology* *51*, 453–470.
 21. Andres, B., and Myers, T.S. (2013). Lone Star Pterosaurs. *Earth Environ. Sci. Trans. R. Soc. Edinb.* *103*, 383–398.
 22. Goloboff, P.A., Farris, J.S., and Nixon, K.C. (2008). TNT, a free program for phylogenetic analysis. *Cladistics* *24*, 774–786.
 23. Maddison, W.P., and Slatkin, M. (1991). Null Models for the Number of Evolutionary Steps in a Character on a Phylogenetic Tree. *Evolution* *45*, 1184–1197.
 24. Kellner, A.W.A. (1994). Remarks on pterosaur taphonomy and paleoecology. *Acta Geol. Leopoldensia* *39*, 175–189.
 25. Hazlehurst, G.A., and Rayner, J.M.V. (1992). Flight characteristics of Triassic and Jurassic Pterosauria: An appraisal based on wing shape. *Paleobiology* *18*, 447–463.
 26. Rayner, J.M.V. (1989). Mechanics and physiology of flight in fossil vertebrates. *Trans. R. Soc. Edinb. Earth Sci.* *80*, 311–320.
 27. Witton, M.P. (2008). A new approach to determining pterosaur body mass and its implications for pterosaur flight. *Zitteliana B* *28*, 143–158.
 28. Norberg, U.M., and Rayner, J.M.V. (1987). Ecological morphology and flight in bats (Mammalia; Chiroptera): Wing adaptations, flight performance, foraging strategy and echolocation. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* *316*, 335–427.
 29. Rayner, J.M.V. (1988). Form and function in avian flight. *Curr. Ornithol.* *5*, 1–66.
 30. Pennycuik, C.J. (1983). Thermal soaring compared in three dissimilar tropical bird species, *Fregata magnificens*, *Pelecanus occidentalis*, and *Cragyps atratus*. *J. Exp. Biol.* *102*, 307–325.
 31. Felsenstein, J. (1985). Phylogenies and the comparative method. *Am. Nat.* *125*, 1–15.
 32. Simpson, G.G. (1953). *The Major Features of Evolution* (New York: Columbia University Press).
 33. Maddison, W.P., and Maddison, D.R. (2008). Mesquite: A modular system for evolutionary analysis, v2.75. <http://mesquiteproject.org/mesquite/mesquite.html>.
 34. Midford, P.E., Garland, T., and Maddison, W.P. (2005). PDAP package of Mesquite documentation, v1.15. http://mesquiteproject.org/pdap_mesquite/index.html.