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DAVID W. E. HONE & ERIC BUFFETAUT (Guest Editors)

Flugsaurier: pterosaur papers in honour of
Peter Wellnhofer

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Umschlagbild: Reconstitution of a *Rhamphorhynchus* from the Upper Jurassic of Eichstätt, Bavaria. Concept: P. Wellnhofer; design: R. Liebreich; photograph and collage: M. Schellenberger, L. Geißler, BSPG Munich.

Comparative evidence for quadrupedal launch in pterosaurs

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Abstract

Pterosaurs faced unique challenges while launching into flight, especially from the ground. The largest pterosaurs far exceeded the size of the largest known flying birds (both living and fossil). This implies that pterosaurs were able to launch and fly at very high body masses. Large-bodied flyers face special difficulties in launching, because flying species with high body mass tend to also have high wing loadings, and thus their minimum flight speeds are generally high. I suggest that pterosaurs may have utilized a quadrupedal, leaping launch sequence to enter flight, especially when launching from the ground. A quadrupedal launch would bring the flight muscles to bear while leaping, produce relatively high launch velocities (compared to a bipedal launch), and be advantageous to large-bodied pterosaurs. Under a quadrupedal launch model, the takeoff leap is dominated by power from the forelimb and pectoral musculature. As a result, one prediction of the quadrupedal launch hypothesis is that pterosaurs, especially large-bodied species, should have very high ratios of humeral to femoral bending strength. This is unlike the situation seen in birds, which initiate launch bipedally, and in which larger species tend to have relatively strong femora compared to their humeri. In this study, I test this prediction of the quadrupedal launch hypothesis by comparing estimates of pterosaur long bone structural strength (in both the hindlimb and forelimb) to measured values for the same elements in birds, and demonstrate that the structural ratios in pterosaurs fall well outside the range of values seen in birds. While this comparative approach does not provide information on the specific kinematics of pterosaur launch, it does provide one line of evidence for a quadrupedal, forelimb-dominated launch dynamic in pterosaurs that future research can build upon using specific, mechanical models. Given our current knowledge of pterosaur anatomy, terrestrial gait, and the bone strength relationships investigated here, I conclude that a quadrupedal launch model for pterosaurs is no less parsimonious than a bipedal launch model, and thus a quadrupedal take-off mechanic should be seriously considered in future research.

Key words: Pterosauria, flight, biomechanics, Aves, morphology

Zusammenfassung

Die Pterosauria sahen sich bei Abheben zum Flug, insbesondere vom Boden aus, mit einzigartigen Herausforderungen konfrontiert. Die größten Flugsaurier überschritten bei weitem die Größe aller bekannten fossilen oder heute lebenden Vögel. Dies setzte voraus, dass die Pterosauria in der Lage waren, bei relativ hoher Körpermasse abzuheben und zu fliegen. Großwüchsige Flieger haben spezielle Probleme beim Abheben, da flugfähige Arten mit hohem Körpergewicht auch zu einer hohen Flächenbelastung auf den Flügeln neigen und daher ihre Mindestfluggeschwindigkeit normalerweise hoch ist. Ich vermute, dass die Pterosauria aus dem vierbeinigen Stand heraus hochsprangen um abzuheben, insbesondere dann, wenn sie sich auf dem Boden befanden. Ein solcher Sprung aus dem vierbeinigen Stand heraus hätte während des Springens die Flugmuskeln aktiviert und eine verhältnismäßig hohe Abhebe-Geschwindigkeit im Vergleich zum zweibeinigen Anlauf ermöglicht. Bei diesem Modell würde der Absprung durch die Kraft der Vordergliedmaßen und der Brustmuskulatur unterstützt werden. Davon ausgehend wäre eine Prognose für die Hypothese des Abhebens aus dem vierbeinigen Stand, dass die Pterosauria, insbesondere die großwüchsigen Arten, eine sehr hohe Ratio der Biegefesteitkkeit der Humeri im Vergleich zu den Femora besaßen. Das unterscheidet sich von der Situation bei den Vögeln, die das Abheben zweibeinig einleiten, und bei denen die größeren Arten verhältnismäßig kräftige Femora im Vergleich zu den Humeri besitzen. In dieser Arbeit teste ich diese Prognose bei Annahme des Abspringens aus dem vierbeinigen Stand, indem ich Schätzungen der konstruktionsbedingten Stabilität von Langknochen (sowohl der vorderen als auch der hinteren Extremitäten) mit gemessenen Werten für die gleichen Knochelemente bei Vögeln vergleiche und aufzeige, dass die Konstruktionsverhältnisse bei den Pterosauria deutlich außerhalb der bei Vögeln festzustellenden Werte sich bewegen. Zwar gewährleistet diese vergleichende Annäherung keine Informationen zur spezifischen Kinetik beim Abheben der Pterosauria, sie ergibt jedoch eine Reihe von Hinweisen auf eine vierbeinige, durch die Vorderextremitäten unterstützte Absprungsdyamik. Weitere Forschungen an Hand spezifischer mechanischer Modelle können darauf aufbauen.

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Aufgrund unseres gegenwärtigen Wissens zur Anatomie der Pterosauria und ihrer Fortbewegung auf dem Boden sowie der Verhältnisse der Knochenbeschaffenheit, die hier untersucht werden, gehe ich davon aus, dass für die Pterosauria das Modell eines durch einen Sprung eingeleiteten Abhebens aus dem vierbeinigen Stand nicht weniger wahrscheinlich als ein Modell eines Abhebens aus dem zweibeinigen Stand ist. Ersteres sollte daher bei künftigen Forschungsarbeiten ernsthaft in Betracht gezogen werden.

Schlüsselwörter: Pterosauria, Flug, Biomechanik, Vögel, Morphologie

1. Introduction

Launch is one of the most strenuous aspects of animal flight (RAYNER 1988; PENNYCUICK 1989; ALEXANDER 2002). The need to take off from a substrate and enter flight places special constraints on volant organisms, and it can be especially limiting in terms of maximum body size. Launching places constraints on other aspects of morphology, as well. For example, the wingspan of a flying species may be limited by the need for the distal wing to clear a substrate while taking off. Burst launching specialists have expanded masses of high-power, anaerobic muscle (ASKEW & MARSH 2002), presumably because steep, rapid launches have high power requirements. In general, an animal that launches from the ground must quickly gain altitude at low speeds, and low-speed flight is physiologically and mechanically rigorous (RAYNER 1988; 1991, 2001; PENNYCUICK 1989; ALEXANDER 2002).

Pterosaurs faced unique challenges while launching into flight, especially from the ground. The pterosaur wing was unique among vertebrates, with the forelimb forming a single primary spar along the leading wing edge, and this placed special constraints on launch. Striking the distal tip of the wing against the substrate would likely be damaging for most pterosaur species. Even if small impacts at the wingtip were acceptable, the wing would still need to clear the substrate to complete a flight stroke, and the total span of large pterosaurs was quite expansive. An animal such as *Quetzalcoatlus northropi*, which had a span exceeding ten meters (LAWSON 1975; LANGSTON 1981; UNWIN 2006), would need a substantial amount of room for a complete flight stroke. In terms of overall body size, the largest pterosaurs far exceeded the size of the largest known flying birds (both living and fossil) (PAUL 2003), and this implies that pterosaurs were able to launch and fly at very high body masses compared to living birds and bats. Large-bodied flyers face special difficulties in launching, because their minimum flight speeds are generally high (PENNYCUICK 1989; NORBERG 1990; ALEXANDER 2002). Wing loading, which is the total weight of an animal divided over its total wing area, shows positive allometry with body mass (GREENEWALT 1962; PENNYCUICK 1989). As a result, species with a high body mass will, on average, have greater wing loadings than small-bodied taxa. Wing loading affects the minimum flight speed, and thus impacts launch requirements. All else being equal, an animal with higher wing loading must fly at a higher speed to maintain flight, and thus must reach greater velocities while launching. (Taking standard aerodynamic

equations and setting the total lift force to body weight gives the result that stall speed is equal to $(2(WL)(1/(pC_L)))^{1/2}$, where WL is wing loading, p is air density, and C_L is the coefficient of lift). Overall, large pterosaurs would have required a launch mechanism that resulted in high takeoff velocities and sufficient elevation from the substrate for a down stroke. These two factors are interrelated, because high-speed flight gaits utilize lower-amplitude flight strokes than slow-speed flight gaits (RAYNER 2001). Fast flying, large-bodied species of birds tend to use a continuous vortex gait while cruising, and this gait requires lower wing amplitudes than a slower speed gait with an aerodynamically inactive upstroke (RAYNER 1988, 1991, 2001). While the precise cruising speeds of large pterosaurs are still a matter of debate, the positive allometric relationship between mass and wing loading (which is quite ubiquitous among living flyers (GREENEWALT 1962; PENNYCUICK 1989)), indicates that large pterodactyloids must have needed substantial speed to launch. It is also of note that span is quite predictive of total body mass among living flying animals (GREENEWALT 1962), such that the largest pterosaurs were almost certainly much heavier than any living flying taxa.

I suggest that pterosaurs may have utilized a quadrupedal, leaping launch sequence to enter flight, especially when launching from the ground. Quadrupedal, leaping launch differs fundamentally from the launch kinematics used by birds (which are obligate bipeds), and also differs from the takeoff dynamics of most bats. However, vampire bats use a quadrupedal launch that accelerates them to flight speed quickly, even after a heavy meal (SCHUTT et al. 1997). In the leaping launch utilized by vampires, the forelimbs and pectoral musculature provide the primary force, allowing vampires to apply their most powerful muscle groups directly to the launch sequence. While the proposed pterosaur launch mechanic would differ significantly from those of vampire bats (especially with regards to launch angle, due to differences in mass and mobility), the use of quadrupedal launch by large pterosaurs appears to be consistent with the comparative structural evidence. A quadrupedal launch would bring the flight muscles to bear while leaping. As a result, it would produce relatively high launch velocities and thus be especially advantageous to large-bodied pterosaurs. The idea that pterosaurs may have launched quadrupedally has been proposed previously; J. CUNNINGHAM discussed the possibility as early as 1999 (CUNNINGHAM, pers. comm.). However, the concept has not been previously brought to bear in the literature, nor has the comparative evidence for such a launch dynamic been formally described.

In this study, I approach the problem of pterosaur launch reconstruction by comparing estimates of pterosaur long bone structural strength ratios to the ratio values measured in birds. Structural strength ratios have been demonstrated to strongly correlate with locomotor behavior in birds (HABIB & RUFF, in press). One prediction of the quadrupedal launch hypothesis is that pterosaurs, especially large-bodied species, should have very high ratios of humeral to femoral bending strength. Under a quadrupedal launch model, the takeoff leap is dominated by power from the forelimb and pectoral musculature. As a result, one prediction of the quadrupedal launch hypothesis is that pterosaurs, especially large-bodied species, should have very high ratios of humeral to femoral bending strength. In birds, which initiate launch bipedally, larger species tend to

have relatively stronger femora than humeri (even though the humeri are usually absolutely larger). The pterosaur species investigated all have very robust humeri compared with their femora, with the relative strength ratio between the two elements greatly exceeding the structural strength ratios for any of the examined species of birds, which matches the expectations of the quadrupedal launch hypothesis.

2. Methods and materials

The avian comparative dataset comprises a total of 155 individuals representing 20 species. All specimens were received on loan from the Bird Division at the Smithsonian Museum of Natural History in Washington, DC. I obtained complete specimens from between four and ten individuals per species, depending on availability. The humerus and femur were taken from one side of each specimen (left and right sides were chosen randomly). Specimens were chosen based on completeness (presence of proper elements) and condition of long bone elements. Both females and males were used for each species, though the specimens were chosen at random with respect to sex.

For the avian sample, I utilized peripheral quantitative computed tomography (pQCT) scans at the midshaft of each humerus and femur to obtain cross-sectional images and geometric data for the cross sections. An XCT Research SA machine (Norland Medical Systems, White Plains, New York) was used for the pQCT scanning, and software distributed with the machine was used to calculate bone densities and cross-sectional properties. Bone structural parameters derived using pQCT are highly correlated with actual bone rigidity and strength measured directly (FERRETTI et al. 1996; MARTIN et al. 2004). A scan resolution (pixel edge length) of 0.1 mm to 0.2 mm was employed, except for rheas, where a resolution of 0.4 mm was used. (Scan width is a constant 1 mm by machine default.) This was sufficient to resolve all long bone cortices of the specimens included in this study.

Bending and torsional loads predominate in vertebrate limb bones (CARTER 1978; RUBIN & LANYON 1982; SWARTZ et al. 1992; BIEWENER & DIAL 1995; BLOB & BIEWENER 1999; CARRANO & BIEWENER 1999). Thus, I evaluated structural characteristics related to bending and torsional strength in my comparative analysis. Bone strength is inversely related to maximum stress under loading. Using a beam model of the femoral and humeral diaphyses, maximum stress in bending is given by $M\gamma/I$ (where M is the bending moment, I is the second moment of area about the neutral axis, and γ is the maximum distance from the neutral axis to the edge of the section); maximum stress in torsion is given by $T\gamma/J$ (where T is the torsional moment, J is the polar second moment of area about the centroid, and r is the maximum radial distance from the centroid to the edge of the section) (GERE & TIMOSHENKO 1990). The section modulus, Z , in bending is defined as I/γ , and in torsion as J/r . M and T can be reasonably considered to be proportional to the product of body mass (B) and bone length (L) (femoral or humeral) (SELKER & CARTER 1989; POLK et al. 2000; RUFF 2000). Thus, bone structural strength $\propto Z/(B^*L)$. Because body mass is a constant within individuals, relative femoral to humeral structural strength can be assessed as $(Z_{\text{fem}}/L_{\text{fem}})/(Z_{\text{hum}}/L_{\text{hum}})$.

The polar section modulus (Z_p) is related to both torsional and (twice) average bending strength in any two perpendicular planes (RUFF 2002), and is the measure used for estimating strength in this study. A more complete examination of these methods and their results, for living avian taxa, can be found in HABIB & RUFF (in press).

In addition to comparing the structural strength of the humerus to the femur, the scaling of the structural strength of both the humerus and the femur was regressed against body mass for those avian taxa with available body mass data. As in the internal ratio comparison, the structural strength of each element was represented by the section modulus divided by element length (Z_p/L). The resulting trends were used to determine the body mass at which, on average, the structural strength of the femur can be expected to exceed that of the humerus in avian taxa.

Exact sections, as derived from CT imaging, were not available for the pterosaur species examined in this study. However, external measurements of pterosaur long bones from the Smithsonian's National Museum of Natural History (NMNH) in Washington, DC and the Bavarian State Collection for Palaeontology and Geology (BSPG) in Munich, Germany indicate that the midshaft of the humerus and femur of most pterosaurs closely approach a true ellipse. Modeling the midshaft as a true ellipse yields a simple formula for the calculation of Z_p :

$$Z_p = 0.25\pi(b^2a/b+a^2b/a)$$

Where 'a' and 'b' are the radii of the ellipse in any two perpendicular planes. For this study, 'a' and 'b' were taken as the dorsoventral and anteroposterior directions, respectively. The above formula, as written, gives the section modulus for a solid section. To calculate the value of Z_p for a hollow section, the same formula is applied using the inner breadth of the cortical bone for 'a' and 'b', and the total is then subtracted from the solid beam value. Thus, $Z_p(\text{actual})=Z_p(\text{outer}) - Z_p(\text{inner})$ where 'outer' and 'inner' designate total breadths and internal breadths, respectively.

Three pterosaur species were utilized as exemplars of the forelimb to hindlimb structural strength ratios in pterosaur taxa. These taxa were: *Anhanguera piscator* (NSM-PV 19892), *Zhejiangopterus linhaiensis* (ZMNH M1323), and *Dorygnathus banthensis* (PSB 759). These taxa were chosen because measurements of uncrushed humeri and femora were available from literature sources for each species, and because they represent three distinct, major clades of pterodactyloid pterosaurs. *Dorygnathus banthensis* was a modest sized pterosaur well within the size range of living birds, but *Anhanguera piscator* and *Zhejiangopterus linhaiensis* were quite large compared to most soaring birds. The total span of *Zhejiangopterus* was approximately 3 meters (near the maximum span seen in living birds), while that of *Anhanguera* reached 5 meters. Neither species is a giant by pterosaur standards, but both are relatively large-bodied vertebrate flyers. The external measurements for *Anhanguera* were taken from KELLNER & TOMIDA (2000). The external measurements for *Zhejiangopterus* were taken from CAI & WEI (1994). Cortical breadths for *Anhanguera* were estimated based on direct measures of broken bones of the closely related *Santanadactylus araripensis*, taken from specimens in the BSPG collections. Cortical breadths for *Zhei-*

Table 1: Literature values for allometric exponents associated with avian and pterosaur long bone dimensions. The original sources for the exponents are listed the table. The listed exponents for birds can also be found listed in the tables of Garcia & Silva (2006).

Group	element	exponent: length	diameter	Original Source
All birds	femur	0.35	0.42	PRANGE et al. (1979)
All birds	femur	0.342	0.383	OLMOS et al. (1996)
Volant birds	femur	0.37	0.42	ALEXANDER (1983)
All birds	humerus	0.46	0.39	PRANGE et al. (1979)
All birds	humerus	0.430	0.368	OLMOS et al. (1996)
Pterosaurs	femur	0.385	0.439	BROWER & VEINUS (1981)
Pterosaurs	humerus	0.353	0.404	BROWER & VEINUS (1981)

Table 2: Literature values for allometric exponents associated with avian long bone strength and bone element mass. The original sources for the exponents are listed the table. The listed exponents for I and J can also be found listed in the tables of Garcia & Silva (2006).

Group	element	mass	exponent:		Original Source
			I	J	
All birds	femur	n/a	1.662	1.647	CUBO & CASINOS (1998)
All birds	humerus	n/a	1.405	1.409	CUBO & CASINOS (1998)
All birds	femur	1.151	n/a	n/a	CUBO & CASINOS (1994)
All birds	humerus	1.007	n/a	n/a	CUBO & CASINOS (1994)

jiangopterus were estimated by scaling (against humeral length) those breadths reported in the literature for *Montanazhdarcho* (McGOWEN et al. 2002) and measured by CT imaging of the humerus of *Bennettazhia oregonensis* in the NMNH collections. Cortical breadths of the bones of *Dorygnathus banthensis* are indicated in the plates of PADIAN & WILD (1992), along with the external dimensions of the specimens. The structural strength estimates of the pterosaur long bones, as presented in this study, are only estimates. However, these estimates should closely approach the true values of structural strength for each of the long bone elements, since the cross sections of pterosaur long bones closely approximate true ellipses.

Differences between structural ratios in the avian and pterosaur species were tested using ANOVA with post-hoc Tukey-Kramer tests, making all pairwise comparisons. SPSS 12 was utilized for statistical analysis. The three species of pterosaurs were grouped together for the ANOVA tests, comparing them as a group to each other bird species, since only a single specimen for each species was utilized in the dataset. The three species of pterosaurs included in this analysis are shown separately within the figures, for qualitative comparison, but no statistical significance can be placed on the difference between the pterosaur taxa.

3. Results and discussion

Prior work has demonstrated that the diameter of the femur scales with a greater exponent than the diameter in the humerus for a wide range of avian taxa (Tab. 1). Scaling trends in length follow the opposite pattern: the humerus increases in length more rapidly than the femur across birds. These two factors, taken together, indicate that the humerus beco-

mes proportionately longer and more gracile in large-bodied birds, while the femur becomes proportionately shorter and more robust by comparison. By contrast, the humerus and femur of pterosaurs scale at approximately the same rate, in both diameter and length (Tab. 1), while the intercept for the diameter trend in the humerus is much greater than that for the femur (BROWER & VEINUS 1981). As a result, the humerus of pterosaurs is consistently more robust than the femur at all body sizes. Furthermore, in pterosaurs, elements such as the ulna and fourth metacarpal also scale rapidly in diameter, according to body size. BROWER & VEINUS (1981: 11) comment “the diameter of the bones is augmented more rapidly in the wing than in the leg of larger pterosaurs”. Interestingly, taking the scaling exponents from BROWER & VEINUS (1981) for length and breadth in the humerus, the expected scaling exponent for structural strength against body mass (assuming a linear trend in cortical breadth) is approximately 0.80; essentially identical to that found for avian femora.

Following the patterns seen in external dimensions, true structural strengths in bending and torsion scale differently in the humerus versus the femur in birds. The second moment of inertia (I) and polar moment of inertia (J) both scale with greater positive allometry in the femur than in the humerus across birds (Tab. 2). Furthermore, the mass (relative to total body mass) of the femur increases more quickly than the mass of the humerus, as body size increases, for avian taxa. The total mass of the humerus is, in most birds, greater than the mass of the femur even at large body sizes, but the expected difference is small in large species. At 100 g, the expected humeral mass for a bird is 0.351 g, while the femur would be expected to have a mass of about 0.160 g. For a 10 kg bird, on the other hand, the humerus is expected to have a mass of 36.264 g, and the femur would have an expected mass of 32.143 g (CUBO &

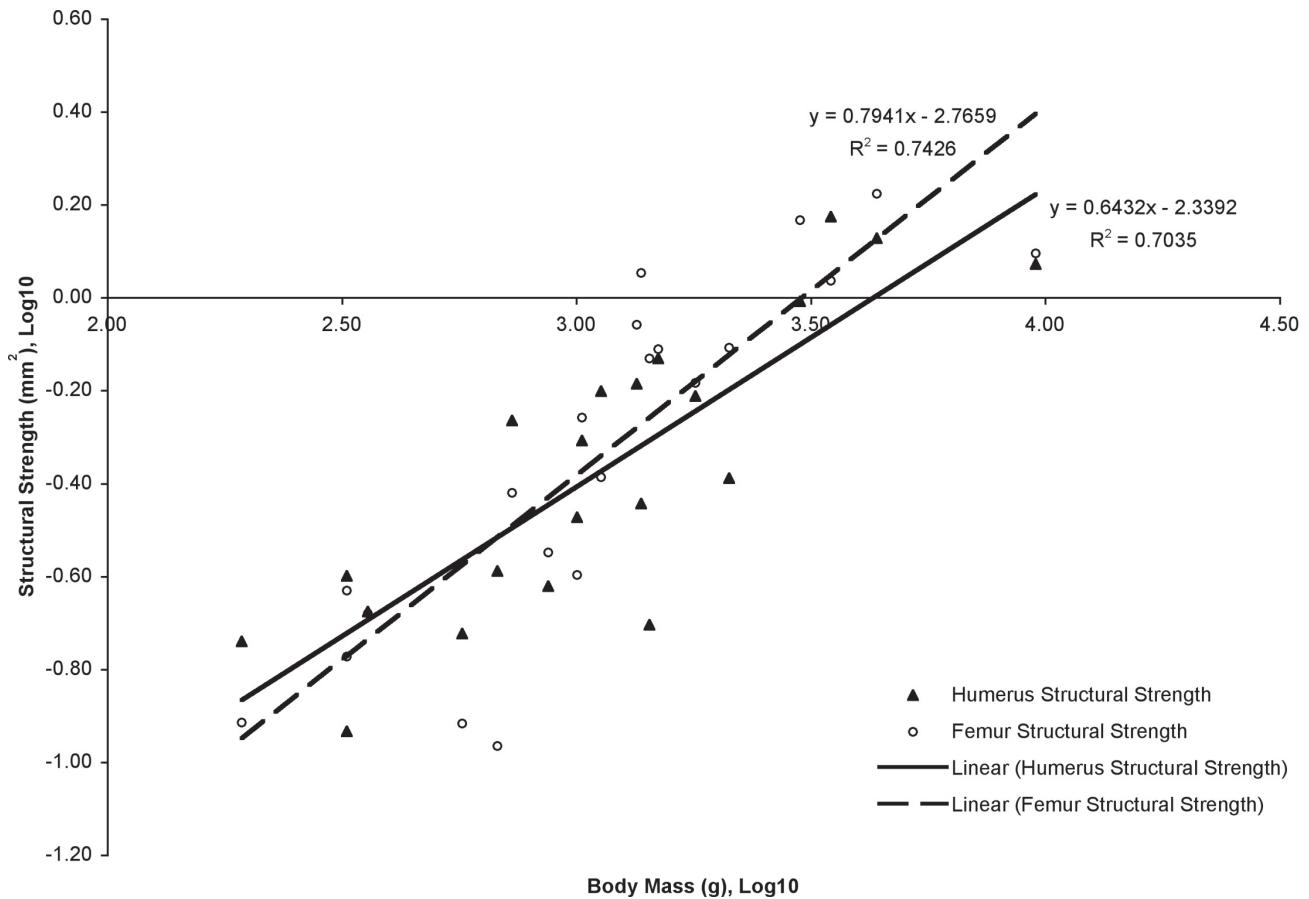


Figure 1: Scaling of bone structural strength in birds. At body masses exceeding 500 grams, the strength of the femur in birds exceeds the strength of the humerus.

CASINOS 1994). The two elements should have nearly the same mass in a large bird, and the femur would be expected to have greater strength in bending at that size.

The reported trends in avian long bone allometry are confirmed using data collected by CT imaging of specimens from the Division of Birds at the Smithsonian's NMNH. On average, at body masses exceeding 500 grams, the strength of the femur in birds exceeds the strength of the humerus (Fig. 1). The species set used to generate the bone strength regressions includes arboreal, semi-terrestrial, semi-aquatic, and fully aquatic forms. The dataset also incorporates both soaring specialists and taxa that utilize continuous flapping. The structural differences between species are most apparent when observing the *relative* long bone strengths (that is, the ratio of humeral strength to femoral strength) (Fig. 2). Interestingly, marine soaring specialists with high aspect ratios, such as the albatross, *Diomedea exulans*, or the Northern Gannet, *Morus bassanus*, have fairly weak, gracile humeri in comparison to their femora (even though the femora are quite small in absolute dimensions). This is relevant to reconstructions of marine pterosaurs, such as *Anhanguera*, which were likely to have been pelagic taxa adapted for long bouts of soaring.

Overall, allometric relationships of bird long bone dimensions and structural strength indicate that, on average, larger-bodied birds have relatively gracile humeri and robust femora. The loads on the humeri of birds are expected to be dominated by flight forces (except in flightless taxa and those

that utilize the wings for swimming), since the forelimbs are not utilized in terrestrial locomotion. Because flight kinematics vary with size and speed, it is likely that humeral loads are gait-mediated in birds. Femoral loads, by contrast, are not expected to be gait-mediated (except, perhaps, with regards to scaling in highly cursorial taxa). Essentially, at large sizes, the forelimbs may require proportionately less power to generate fluid forces capable of weight support, because of the lower flapping frequencies and reduced flapping amplitudes used at the higher airspeeds utilized by large-bodied flyers. On the other hand, femoral strength is probably not mediated by similar changes in gait. Regardless, while it is not known why avian femora become stouter at larger body sizes (compared with the humeri), launch loads are likely to have a substantial influence. In general, if pterosaurs were mechanically similar to birds (including the use of bipedal launching by leaping or running) then pterosaur femora should be short and robust at large body sizes. Even if the 500 gram threshold for femoral to humeral strength ratios seen in birds (Fig. 1) is avian-specific, it would seem that animals as large as *Anhanguera* or *Zhejiangopterus* should have relatively robust femora if they were mechanically and dynamically similar to birds.

Instead, all three representative pterosaur species have estimated structural strength ratios well above those seen in any of the sampled birds. Sampled across a wide range of functional groups, birds show a great deal of variability in relative forelimb to hindlimb strength. The greatest ratio of

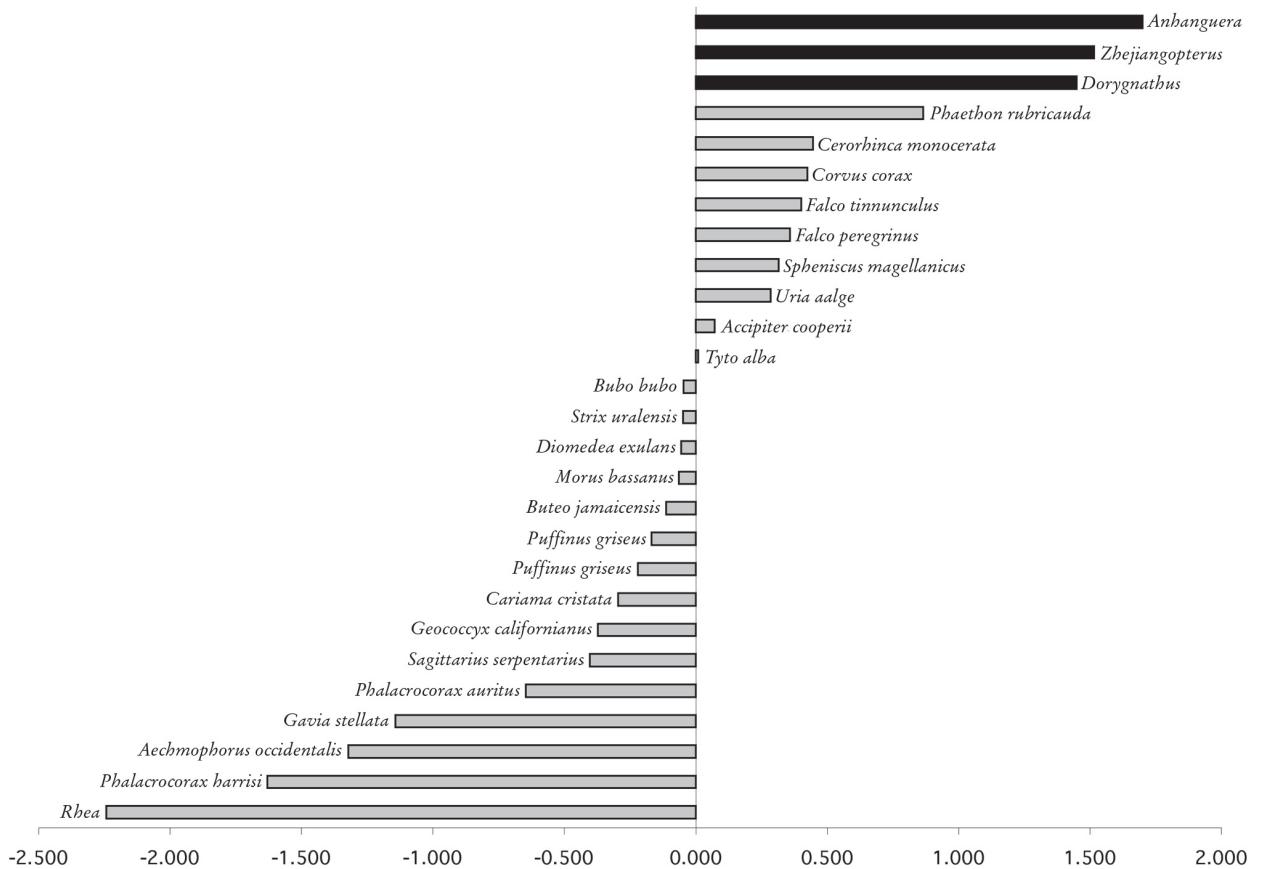


Figure 2: Structural strength ratios in a sample of birds and pterosaurs. Ratios are given as the length-corrected section modulus of the humerus, divided by the same value for the femur, and then natural logarithm transformed. Birds show a great deal of variability in relative forelimb to hindlimb strength. The greatest ratio of humeral to femoral bending strength, among birds, occurs in species with greatly reduced femora (such as *Phaethon rubricauda*). The same ratios in large pterosaurs are extreme, suggesting that pterosaurs used a different launch mode than birds.

humeral to femoral bending strength, among the sampled birds, occurs in species *Phaethon rubricauda*, which is a species with greatly reduced femora (Fig. 2). The strength ratio measured for *Phaethon* comes closest to matching those in pterosaurs, though the ratios in *Phaethon* and the three pterosaurs (taken together) differ significantly ($p < 0.001$). *Phaethon* cannot run to launch, and must take off almost entirely through use of rapid flapping with limited hindlimb assistance (BREWER & HERTEL 2007). Frigatebirds, which also have reduced femora and are somewhat larger than *Phaethon*, cannot launch from the water at all (UNWIN 2006). They are usually reliant on elevated structures for take off (PENNYCUICK 1983). Neither of these modes of launch would be reasonable for large pterosaurs, for both biomechanical and behavioral reasons. In terms of mechanics, the body mass and total span of the larger pterosaurs would preclude them from a *Phaethon* or *Fregata*-style launch. Behaviorally, it is known that large pterosaurs were not reliant on elevated perches, because trackways indicate quadrupedal, terrestrial locomotion (BENNETT 1997; PADIAN 2003). Furthermore, large pterodactyloids were simply too enormous to rely on trees or ledges for landing and launching.

The polarity of the structural strength ratios in pterosaurs also appears to differ from that of *Phaethon*. While the hindlimbs of pterosaurs appear to be quite small, PADIAN (1983) observed that pterosaur hindlimbs only appear reduced in compari-

son to the hypertrophied forelimbs. BENNETT (1995) reiterates this point, and suggests that the hindlimbs of pterosaurs were well adapted for powerful leaping. Thus, rather than having reduced hindlimbs (as in *Phaethon* or *Fregata*) pterosaurs seem to have had massively reinforced forelimbs (at least proximally). While the muscle mass of pterosaurs probably far exceeded what is often reconstructed (there is no reason to think that they were any less heavily muscled than living birds), expected flapping forces alone seem insufficient, at present, to explain the structural strength ratios of pterosaurs; it is simply implausible that pterosaurian lift coefficients would be several times higher than in birds (though they were likely to have been somewhat greater). Future work may indicate causes other than launch mechanism for the observed bone strength and shape trends in pterosaur limbs, but it is clear that long bone scaling trends differ between birds and pterosaurs, as do the trends in relative load-bearing potential between the forelimbs and hindlimbs. As a result, bipedal launch models for pterosaurs (which are essentially inspired by the known mechanisms of birds) are no more parsimonious than quadrupedal launch models. Even if the hindlimbs were well adapted for leaping, this does not exclude the forelimbs from also being used in powerful leaps (the quadrupedal launch hypothesis predicts that both the forelimbs and hindlimbs would be utilized when jumping to take off). Given that bipedal launching in pterosaurs requires a significant

shift in stance from that used while walking, a quadrupedal takeoff model is actually the simpler model in some respects (e.g. it does not require a shift to bipedal gait prior to launch). Modern quadrupedal launching is limited to bats, and only a few species seem capable of particularly powerful terrestrial, leaping launches. Vampire bats are among the most notable, and literature information indicates that they have proportionally robust forelimbs compared to other bats. The humeri of vampire bats are stronger in bending, relative to body weight, than other species (CANALS et al. 2005), while their femora are no stronger than average for a bat of their mass (RISKIN et al. 2005). At larger body masses, the gap in relative bone strength should be even greater, which explains the extreme structural strength ratios in the sampled pterosaurs.

If pterosaurs did indeed utilize a quadrupedal launch, it would also help to explain their ability to achieve large sizes. *Quetzalcoatlus northropi*, which remains one of the largest known pterosaur species, had a total span of roughly 10.4 meters (LAWSON 1975; LANGSTON 1981; UNWIN 2006). The body mass of *Quetzalcoatlus northropi* has been a matter of considerable disagreement, with previous size estimates ranging from 70 kg (CHATTERJEE & TEMPLIN 2004) to 200 kg (PAUL 2003). Most recently, Witton (this volume) has made a strong argument for a body mass near 250 kg in *Q. northropi*. Considering the overall dimensions of the largest azhdarchids, this is a reasonable figure. However, at such sizes, the ability to launch using hindlimb leaping or running would, more than likely, be very limited. Under the model of CHATTERJEE & TEMPLIN (2004), which utilized a running, hindlimb dominated launch cycle, *Q. northropi* could barely launch even at the unreasonably low mass of 70 kg. That analysis is quite informative, because it demonstrates the intense size limits that pterosaurs would face if limited to hindlimb-dominated launch cycles. A hindlimb dominated, running launch was probably not feasible for large-bodied pterosaurs. This becomes increasingly apparent when more realistic estimates of body mass and wing loading are utilized. By contrast, a quadrupedal launch would allow much greater leaping forces by including the musculature of the flight apparatus, such as the coracobrachialis and pectoralis muscles, and thus produce high launch speeds. A high speed, leaping launch in pterosaurs would not only allow the animals to reach their take-off window more rapidly, but it would also enable them to switch to a higher speed gait early in the flight cycle, perhaps immediately. Given that high-speed gaits require lower flapping amplitudes, a high velocity, leaping launch has the distinct advantage of allowing for greater spans, in addition to higher body masses.

4. Conclusions

The comparative approach presented here does not provide information on the specific kinematics of pterosaur launch. However, a comparative approach does provide evidence for a unique launch dynamic in pterosaurs that future research can build upon using specific, mechanical models. Given our current knowledge of pterosaur anatomy, terrestrial gait, and bone strength relationships, a quadrupedal launch model for pterosaurs is no less parsimonious than a bipedal launch model. Furthermore, the quadrupedal launch model explains additio-

nal biological trends, such as the discrepancy in size between the largest known pterosaurs and the largest known birds. Quadrupedal take-off models should be seriously considered in future pterosaur research, and bipedal launching (be it by leaping or running) should not remain the default dynamic for pterosaurs. Instead, specific evidence should be used to justify the use of either a bipedal launch or quadrupedal launch when reconstructing pterosaur mechanics and behavior.

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5. References

- ALEXANDER, D. (2002): Nature's Flyers: Birds, Insects, and the Biomechanics of Flight; Baltimore MD (Hopkins University Press), 358 pp.
- ASKEW, G. N. & MARSH, R. L. (2002): Muscle designed for maximum short-term power output: quail flight muscle. – Journal of Experimental Biology, **205**: 2153–2160.
- BENNETT, S. C. (1995): An arboreal leaping origin of flight and the relationships of pterosaurs. – Journal of Vertebrate Paleontology, **15** (Suppl. to no. 3): 19A.
- BENNETT, S. C. (1997): Terrestrial locomotion of pterosaurs: A reconstruction based on *Pteraichnus* trackways. – Journal of Vertebrate Paleontology, **17**: 104–113.
- BIEWENER, A. A., & DIAL, K. P. (1995): In vivo strain in the humerus of pigeons (*Columba livia*) during flight. – Journal of Morphology, **225**: 61–75.
- BLOB, R. W. & BIEWENER, A. A. (1999): In vivo locomotor strain in the hindlimb bones of *Alligator mississippiensis* and *Iguana iguana*: implications for the evolution of limb bone safety factor and non-sprawling limb posture. – Journal of Experimental Biology, **202**: 1023–1046.
- BREWER, M. L. & HERTEL, F. (2007): Wing morphology and flight behavior of pelecaniform seabirds. – Journal of Morphology, **268**: 866–877.
- BROWER, J. C. & VEINUS, J. (1981): Allometry in pterosaurs. – The University of Kansas Paleontological Contributions, **105**: 1–32.
- CAI, Z. & WEI, F. (1994): *Zhejiangopterus linhaiensis* (Pterosauria) from the Upper Cretaceous of Linhai, Zhejiang, China. – Vertebrata PalAsiatica, **32**: 181–194.
- CANALS, M., GROSSI, B., IRIARTE-DÍAZ, J. & VELOSO, C. (2005): Biomechanical and ecological relationships of wing morphology of eight Chilean bats. – Revista Chilena de Historia Natural, **78**: 215–227.
- CARTER, D. R. (1978): Anisotropic analysis of strain rosette information from cortical bone – Journal of Biomechanics, **11**: 199–202.
- CARRANO, M. T. & BIEWENER, A. A. (1999): Experimental alteration of limb posture in the chicken (*Gallus gallus*) and its bearing on the use of birds as analogs for dinosaur locomotion – Journal of Morphology, **240**: 237–249.

- FERRETTI, J. L., CAPOZZA, R. F. & ZANCHETTA, J. R. (1996): Mechanical validation of a tomographic (pQCT) index for noninvasive estimation of rat femur bending strength. – *Bone*, **18**: 97–102.
- GARCIA, G. J. M. & SILVA, J. K. L. (2006): Interspecific allometry of bone dimensions: A review of the theoretical models. – *Physics of Life Reviews*, **3**: 188–209.
- GERE, J. M. & TIMOSHENKO, S. P. (1990): *Mechanics of Materials*; Boston (PWS-Kent), 912 pp.
- GREENEWALT, C. H. (1962): Dimensional relationships for flying animals. – *Smithsonian Miscellaneous Collections*, **144**: 1–46.
- HABIB, M. & RUFF, C. B. (in press): The effects of locomotion on the structural characteristics of avian limb bones. – *Zoological Journal of the Linnean Society*.
- KELLNER, W. A. & TOMIDA, Y. (2000): Description of a new species of anhangueridae (pterodactyloidea) with comments on the pterosaur fauna from the Santana Formation (Aptian-Albian), Northeastern Brazil. – *National Science Museum Monographs* No. 17.
- LANGSTON, W. (1981): Pterosaurs. – *Scientific American*, **1981/2**: 122–136.
- LAWSON, D. A. (1975): Pterosaur from the latest Cretaceous of West Texas: discovery of the largest flying creature. – *Science*, **187**: 947–948.
- MARTIN, D. E., SEVERNS, A. E. & KABO, J. M. (2004): Determination of mechanical stiffness of bone by pQCT measurements: correlation with non-destructive mechanical four-point bending test data. – *Journal of Biomechanics*, **37**: 1289–1293.
- NORBERG, U. M. (1990): *Vertebrate Flight: Mechanics, Physiology, Morphology, Ecology and Evolution*; Berlin (Springer Verlag), 291 pp.
- PADIAN, K. (1983): A functional analysis of flying and walking in pterosaurs. – *Paleobiology*, **9**: 218–239.
- PADIAN, K. (2003): Pterosaur stance and gait and the interpretation of trackways. – *Ichnos*, **10**: 115–126.
- PADIAN, K. & WILD, R. (1992): Studies of Liassic pterosauria, I. The holotype and referred specimens of the Liassic pterosaur *Dorygnathus banthensis* (Theodor) in the Petrefaktensammlung Banz, Northern Bavaria. – *Palaeontographica, Abt A*, **225**: 59–77.
- PAUL, G. S. (2002): *Dinosaurs of the Air*; Baltimore (Johns Hopkins University Press), 460 pp.
- PENNYCUICK, C. J. (1983): Thermal soaring compared in three dissimilar tropical bird species, *Fregata magnificens*, *Pelecanus occidentalis*, and *Coragyps atratus*. – *Journal of Experimental Biology*, **102**: 307–325.
- PENNYCUICK, C. J. (1989): *Bird Flight Performance: A Practical Calculation Manual*. 170 pp.
- POLK, J. D., DEMES, B., JUNGERS, W. L., BIKNEVICIUS, A. R., HEINRICH, R. E., & RUNESTAD, J. A. (2000): A comparison of primate, carnivore and rodent limb bone cross-sectional properties: are primates really unique? – *Journal of Human Evolution*, **39**: 297–325.
- RAYNER, J. M. V. (1988): The evolution of vertebrate flight. – *Biological Journal of the Linnean Society*, **34**: 269–287.
- RAYNER, J. M. V. (1991): Avian flight evolution and the problem of *Archaeopteryx*. – In: J. M. V. RAYNER & R. J. WOOTTON (Eds), *Biomechanics in Evolution*; Cambridge (Cambridge University Press), 183–212.
- RAYNER, J. M. V. (2001): On the origin and evolution of flapping flight aerodynamics in birds. – In: J. GAUTHIER & L. F. GALL (Eds), *New Perspectives on the Origin and Evolution of Birds*; New Haven CT (Special Publication of the Peabody Museum of Natural History), 363–385.
- RISKIN, D. K., BERTRAM, J. E. A. & HERMANSON, J. W. (2005): Testing the hindlimb-strength hypothesis: non-aerial locomotion by Chiroptera is not constrained by the dimensions of the femur or tibia. – *Journal of Experimental Biology*, **206**: 1309–1319.
- RUBIN, C. T. & LANYON, L. E. (1982): Limb mechanics as a function of speed and gait: A study of functional strains in the radius and tibia of horse and dog. – *Journal of Experimental Biology*, **101**: 187–211.
- RUFF, C. B. (2000): Body size, body shape, and long bone strength in modern humans. – *Journal of Human Evolution*, **38**: 269–290.
- RUFF, C. B. (2002): Long bone articular and diaphyseal structure in Old World monkeys and apes, I: Locomotor effects. – *American Journal of Physical Anthropology*, **119**: 305–342.
- SELKER, F. & CARTER, D. R. (1989): Scaling of long bone fracture strength with animal mass. – *Journal of Biomechanics*, **22**: 1175–1183.
- SWARTZ, S. M., BENNETT, M. B. & CARRIER, D. R. (1992): Wing bone stresses in free flying bats and the evolution of skeletal design for flight. – *Nature*, **359**: 726–729.
- UNWIN, D. (2006): *Pterosaurs from Deep Time*; New York (PI Press), 352 pp.
- SCHUTT, W.A. Jr, ALTBACH, J. S., CHANG, Y. H., CULLINANE, D. M., HERMANSON, J. W., MURADALI, F. & BERTRAM, J. E. A. (1997): The dynamics of flight-initiating jumps in the common vampire bat *Desmodus rotundus*. – *The Journal of Experimental Biology*, **200**: 3003–3012.