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古魔翼龙和披羽蛇翼龙的水上起飞能力

Capacity for Water Launch in Anhanguera and Quetzalcoatlus

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Many of the large pterodactyloid pterosaurs come from marine sediments or inland freshwater deposits (Lawson, 1975; Bennett, 1994; Wang et al., 2005; Unwin, 2006). While the feeding ecology of large pterosaurs is still contentious, it is possible that some species entered the water to feed (Bramwell and Whitfield, 1974; Brower, 1983), and even excluding this possibility, many likely took food from the water surface or otherwise flew in close proximity to the water during travel and foraging (Brower, 1983; Unwin, 2006; Witton, 2008). As a result of these behaviors, it is plausible (or even likely) that some large pterosaurs were forced into or onto the water through stochastic events. Unless a water launch was possible for large pterosaurs, such events would presumably be lethal unless shallow water or shoreline was immediately available. For pelagic species, especially, these conditions were unlikely to be met in most circumstances.

Here we present the results of a quantitative and comparative morphological analysis in two large pterosaurs, *Anhanguera santanae* and *Quetzalcoatlus* sp., regarding the capacity for water launch. Our results indicate that both species could launch from calm water, without the assistance of wind or waves, using a form of quadrupedal takeoff. While the capacity for such a behavior is not demonstration that such behavior was utilized, both species possess a wide array of anatomical features that would make water launch both efficient and effective. Prior work has demonstrated that pterosaurs were poorly adapted for a bipedal launch as seen in birds, but were well adapted for a quadrupedal takeoff (Habib, 2008). Similarly, it is unlikely that pterosaurs could accommodate the running, bipedal launch that living water birds utilize for takeoff from the water surface. However, living piscivorous raptors launch from the water using primarily a push from the wings against the water surface (Corvidae et al., 2006). Large pterosaurs such as *Anhanguera* and *Quetzalcoatlus* may have utilized a broadly similar mechanism to free themselves from the water surface. While such pterosaurs were far larger than living raptorial birds, they had the advantage of proportionately less body drag, relatively greater flight muscle mass, and the ability to use both the hind limbs and forelimbs in escape from the water.

In order for any pterosaur to successfully launch from the water surface using a quadrupedal gait, it would need to accomplish two primary mechanical tasks, each of which can be seen as a distinct phase of launch. Firstly, a water-launching pterosaur would need to escape surface resistance and suction (escape phase). Following the escape phase, the animal would need to impart momentum to the water surface primarily at the wing finger joint (MCIV-PHIV joint) sufficient to generate substantial forward acceleration, and ultimately launch velocity (propulsion phase). Effective propulsion against the water in this manner would require that the animal counter slippage of the forelimb sufficiently to generate forward acceleration. Our input parameters are indicated in Table 1. Ranges are given for those data where a minimum and maximum potential value were utilized, in order to accommodate uncertainty of soft tissue anatomy.

Our calculations indicate that escape from the water surface was possible, in both *Anhanguera* and *Quetzalcoatlus*, but that this phase would be slow in comparison to the propulsion phase. For *Anhanguera*,

 Table 1
 Input parameters. FMF: Flight Muscle Fraction (percentage of total body mass). HLMF: Hind limb muscle fraction (percentage of total body mass). Span given in meters. Anaerobic Capacity is given in W/kg.

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	FMF	HLMF	Span	Anaer. Capac.
Anhanguera	20-26%	10-12%	4.01	300-400
Quetzalcoatlus	20-26%	12-14%	4.80	300-400

the initial escape phase could be accomplished with a net remaining acceleration of 17.6 m/s^2 , and an acceleration of up to 39.2 m/s² on the subsequent, unhindered propulsive bound. For Quetzalcoatlus, this phase would be more powerful, with an acceleration of 44.7 m/s^2 if the launch were made in a single propulsive phase, or a lesser acceleration if made in multiple hops. Sufficient contact area to provide a useable propulsion phase would require that the wing finger be opened 15-25 degrees in both animals. This contact area was greatly augmented by the exceptionally broad MCIV-PHIV joint in both species. The escape phase would require exceptional adductor musculature, and we note that both Anhanguera and Quetzalcoatlus appear to have had greatly expanded adductor musculature, though the expansion occurred differently in the two species: in Anhanguera, the orientation and enlargement of *m. subscapularis* appears to be of particular importance, along with the reinforcement of the joint between the scapula and notarium (Bennett, 2009). In Quetzalcoatlus, the enlarged and deflected deltopectoral crest and greater expanded coracoid flange would have been of greater importance in the alignment and expansion of musculature critical for water launch.

Propulsive phase in *Anhanguera* would likely have reached accelerations of 29.4-39.2 m/s², compared to 44.7 m/s² in *Quetzalcoatlus*. Because of the greater proportional musculature in *Quetzalcoatlus*, full launch may have been possible in a single propulsive phase. *Anhanguera*, by contrast, seems to have been adapted for a launch phase using a series of repeated propulsions, which would have occurred as a series of "hops" across the water surface. A similar sequence of multiple hops would also be readily available to *Quetzalcoatlus* with the consequences that launch accelerations and biomechanical stresses would be reduced.

We cannot confirm that either *Quetzalcoatlus* or *Anhanguera* actually utilized a water launch in life. However, both species present a suite of characteris-

tics that would be expected in water-launching pterosaurs, and quadrupedal water launch behavior would help to explain features such as: the expanded scapula (*Anhanguera*), reinforced scapular-notarial joint, expanded deltopectoral crest (and its unusual orientation in both species), expanded coracoid process (*Quetzalcoatlus*), exceptionally broad MCIV-PHIV wing finger joint, limb length disparity (*Anhanguera*), and expanded posterior brachial musculature.

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