



The new giant pterosaurs: novel anatomies and habits in the largest flying animals

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Abstract

Azhdarchid pterosaurs, a derived group of Cretaceous pterodactyls, are among the most famous of all flying reptiles. Instrumental to this fame is the attainment of giant proportions by several azhdarchid species, such as *Quetzalcoatlus northropi* and *Hatzegopteryx thambema*, which are the largest flying animals known with estimated wingspans of 10 m (Figure 1B). Giant size does not characterise all azhdarchids, however, with the 14 other known azhdarchid species attaining varying body wingspans down to 2.5 m (Figure 1A). Azhdarchid anatomy is strikingly distinctive and characterised by elongate, toothless jaws; long, stiff necks comprised of hypertrophied, tube-like cervical vertebrae; elongate forelimb elements with proportionally short wing fingers; small and robust extremities, and long femora. Giant azhdarchids and their relatives were one of the most successful pterosaur groups known, with an evolutionary lineage sustaining at least 80 million years, spreading to all continents except Antarctica, and dominating the closing stages of pterosaur evolution (Witton, 2013). Despite their fame, the relative abundance of their fossil remains and reputation as some of the most spectacular pterosaurs known, many details of azhdarchid anatomy and palaeobiology have historically been poorly understood and controversial. As recently as five years ago, azhdarchids were generally perceived as incredibly lightweight, seabird-like animals which operated on the very limits of flight and viable soft-tissue: body volume ratios, and were of highly uncertain lifestyles (e.g. Kellner and Langston, 1996; Chatterjee and Templin, 2004).

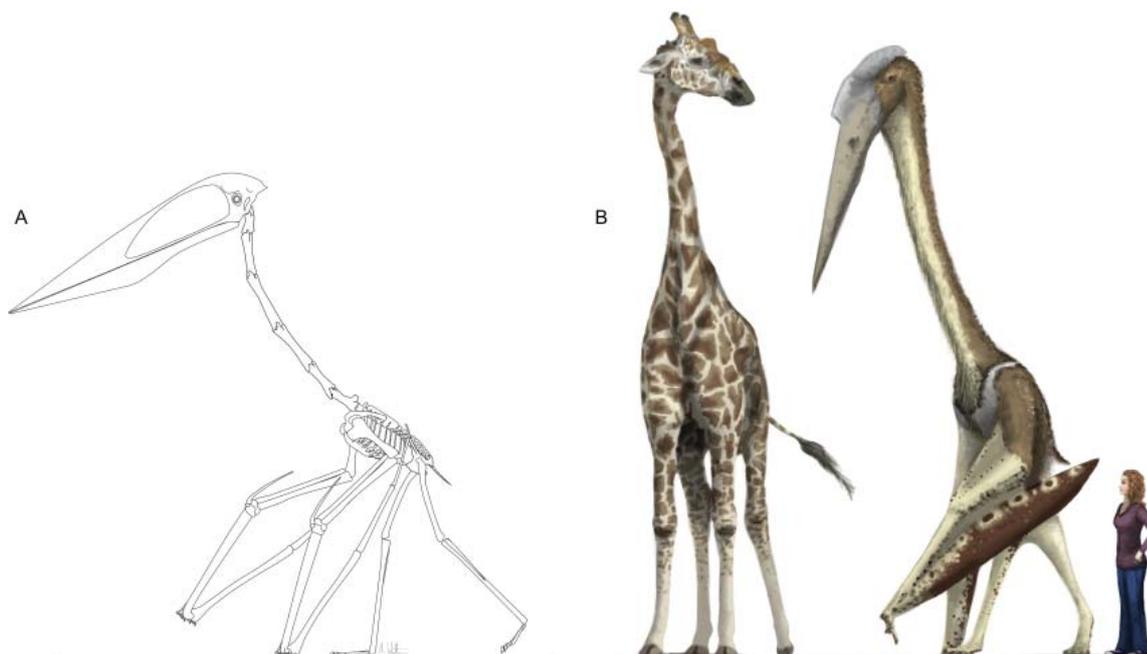


Figure 1. Skeletal reconstruction of the 3 m wingspan azhdarchid *Zhejiangopterus linhaiensis* in walking posture; B, life reconstruction of the giant azhdarchid *Arambourgiania philadelphiae* alongside a bull Masai giraffe (*Giraffa camelopardalis tippelskirchi*).

Recently, a series of studies into azhdarchid anatomy, palaeoecology and biomechanics have offered fresh insights into the diversity and lifestyles of these animals. Much of the confusion surrounding their palaeobiology seems to reflect limited research into the specifics of their functional morphology and *a priori* assumptions about pterosaur lifestyles and locomotory methods. These studies have drawn particularly startling conclusions

about the palaeobiology of the largest azhdarchids, including new considerations of their likely body masses (e.g. Witton, 2008; Henderson, 2010; Witton and Habib, 2010). Pterosaurs have been traditionally considered to have extremely low body masses to facilitate flight at large wingspans, leading to suggestions that giraffe-sized azhdarchids massed no more than a svelte male human, 70 kg (e.g. Chatterjee and Templin, 2004). Appraisals of giant pterosaur body volumes and skeletal mass indicate that such masses are unrealistically low and require unreasonable amounts of airspace within giant azhdarchid soft-tissues. They are also inconsistent with mass/wingspan relationships seen in modern volant tetrapods. Several independent lines of evidence indicate pterosaur masses were, on average, three times greater than most previously estimated 'lightweight' values, suggesting masses of 200-250 kg were likely for the largest azhdarchid species (e.g. Witton, 2008; Henderson, 2010; Witton and Habib, 2010).

The likelihood of heavier masses in giant azhdarchids has prompted reappraisal of their flight abilities. Several authors (e.g. Chatterjee and Templin, 2004; Sato et al., 2009; Henderson, 2010) proposed that these pterosaurs were flightless, being too heavy to take off or sustain flight, assuming – as per tradition – that pterosaurs attained flight using a bird-like, bipedal launch mechanism. The first detailed appraisals of pterosaur launch strategies found substantial evidence for their utilisation of quadrupedal takeoff mechanisms however, in which most of their launch energy is attained from powerful flight musculature in a manner akin to some bats (Habib, 2008). Modelling of giant azhdarchid humeral strength indicates that they were capable of withstanding launch loads of multiple bodyweights at even 'heavy' masses, which is consistent with their use in quadrupedal launch (Witton and Habib, 2010). This, combined with the well-developed wing anatomy known from several giant azhdarchid fossils, is good evidence that even the largest known azhdarchids were flightworthy. Models of giant pterosaur flight mechanics suggest they were powerful fliers, capable of sustained speeds of 90 kph, bursts of 173 kph, and single flights spanning 16,000 km (Witton and Habib, 2010).

Additional investigations have challenged ideas that azhdarchids were Mesozoic analogues of seabirds. Azhdarchid anatomy seems well adapted for terrestrial locomotion and indicative of an ecology like that of terrestrially-foraging birds, such as ground hornbills and storks (Witton and Naish, 2008; Carroll et al., 2013). Many unusual features of azhdarchid anatomy – their long limbs, compact extremities, long and stiff necks, and jaw morphology preclude many proposed azhdarchid lifestyles including skim-feeding, dip-feeding, pelican-like 'scoop-feeding', habitual scavenging and sediment probing. However, azhdarchid limb anatomy is well suited to sustained bouts of terrestrial locomotion (Witton and Naish, 2008; Carroll et al., 2013), a finding supported by the efficient limb carriage and cushioned extremities recorded in azhdarchid trackways (Hwang et al., 2002). Their elongate jaws and neck anatomy are also ideally suited for foraging on small animals and other grounded foodstuffs. Recent arthrological studies into the azhdarchid cervical series (Averianov, 2013) support its use in fairly undemanding foraging strategies like terrestrial foraging (Witton and Naish, in review). Corroborating evidence for a primarily terrestrial existence for azhdarchids stems from over 50% of azhdarchid-bearing formations representing continental sediments, and 84% of their occurrences – even those in marine basins - being associated with continental Mesozoic faunas. Aspects of azhdarchid wing morphology also suggest they primarily flew within terrestrial environments. Niche-partitioning in azhdarchid species has been identified through disparate body size in conspecific taxa, as well as jaw morphology (Vremir et al., 2013).

It is not only perceptions of azhdarchid lifestyles and locomotion which are changing. Recently discovered giant azhdarchid material from Maastrichtian deposits of Transylvania suggests that giant azhdarchids were more anatomically diverse than previously anticipated. These new remains, some of which are reported by Vremir (2010), include an enormous and robust, but proportionally short posterior azhdarchid cervical vertebra which is likely of the same approximate size and congeneric with, or at least very closely related to, the near-contemporary, 10 m wingspan Transylvanian azhdarchid *Hatzegopteryx thambema*. This vertebra appears to belong to a relatively short neck, with its estimated cervical III-VII length only 1.39 m. This dimension is comparable to the neck lengths of azhdarchids with 50% smaller wingspans, and contrasts markedly with the 2.3 m cervical III-VII length predicted for the giant azhdarchid *Arambourgiania philadelphiae*. This find complements other observations that azhdarchid anatomy is not as uniform as often perceived (Witton, 2013; Vremir et al., 2013), which may indicate that the group was also not constrained ecologically. Azhdarchids

with shorter, more robust necks, for instance, may represent bauplans adapted for predating larger prey than azhdarchids with longer and more slender necks.

These hints of unprecedented diversity in Azhdarchidae suggest the significance of azhdarchids in Late Cretaceous ecosystems and the nature of their extinction may warrant reevaluation. The discovery of powerful, robust azhdarchid species in well-sampled depositional Transylvanian units devoid of large predators suggests giant azhdarchids may have operated as apex predators in some Cretaceous ecosystems. Azhdarchids operating in environments with larger predators, by contrast, likely operated in lower predator niches, even when attaining large body sizes. It seems possible that at least Maastrichtian azhdarchids were a more diverse and healthier lineage than previously considered, and that the extinction of azhdarchids – which almost exclusively represent Pterosauria in the Maastrichtian – at the K-Pg interval was a more significant event than suggested by some authors (e.g. Unwin, 2005; Witton, 2013). Further discoveries of giant azhdarchids, along with those of their smaller relatives, are sorely needed to shed light on the nature of their extinction, as well as other components of the increasingly complicated palaeobiological landscape of these pterosaurs.

Keywords: Pterosauria, Azhdarchidae, anatomy, palaeoecology, flight

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