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巨型翼龙类能够飞行吗？

The Volancy, or Not, of Giant Pterosaurs

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Many pterodactyloids had wingspans that vastly exceed those of any other flying animals, living or extinct. Ornithocheiroids and neoazhdarchidans were particularly large pterosaurs that regularly attained wingspans over 4 m. Certain members of these groups – Pteranodontia and Azhdarchidae – attained the largest wingspans of any pterosaurs, making them the largest flying animals known. The flight of giant pterosaurs has been modeled repeatedly over the last century (e.g. Hankin and Watson 1914; Bramwell and Whitfield 1974; Brower and Veinus 1981; Chatterjee and Templin 2004) and researchers have invariably concluded that they were capable of powered flight. Some recent studies, however, suggest that a reappraisal of giant pterosaur flight is called for. Applying a dataset of albatross flapping frequencies to giant pterosaur-sized animals has suggested that pterosaurs spanning over 5.1 m and massing over 41 kg would struggle to flap sufficiently to takeoff and sustain flight (Sato et al. 2009), rendering all large and giant pterosaurs flightless. This echoes sentiments expressed by Chatterjee and Templin (2004) that suggested pterosaurs with masses over 70 kg would be incapable of flight. If the 'high' mass estimates recently proposed for pterosaurs are accurate (Paul 1991, 2002; Witton 2008), this limit would also ground all large pterosaurs.

While such claims may seem almost heretical to pterosaur workers, it is worth considering that contemporarily relevant considerations of giant pterosaur flight abilities are lacking and, in some respects, the claims of Sato et al. and Chatterjee and Templin are quite progressive. The long research history of giant pterosaur flight (e.g. Hankin and Watson 1914; Kripp 1941; Bramwell and Whitfield 1974; Brower and Veinus 1981) is strongly biased towards the 7 m span ornithocheiroid *Pteranodon*, so the consideration of the flight ability of large azhdarchids by the latter authors is commendable. In addition, almost all pterosaur flight analyses have assumed that pterosaurs were extremely lightweight for their size. Recently, however, strong arguments for 'high' pterosaur masses - essentially suggesting pterosaurs massed the same as equivalently-sized modern flying animals - have been published (Paul 1991, 2002; Marden 1994; Witton 2008). If correct, these estimates suggest that the conclusions of flight analyses using 'low' masses are of limited use in contemporary research. The consideration of 'high' masses by Sato et al. and Chatterjee and Templin is, again, therefore quite laudable. However, just as the low mass estimations and taxonomic bias of older studies may bring their modern utility into question, there are numerous limitations in the methodologies and rationales behind the Sato et al. and Chatterjee and Templin studies. Here, we outline apparent flaws in their work and report osteological and scaling data that strongly suggests that even the largest pterosaurs were capable of flight.

The problems of pterosaur/bird interchangeability

Both Sato et al. (2009) and Chatterjee and Templin (2004) assume, to varying degrees, that pterosaur and bird mechanics can be treated interchangeably. Both studies predict that pterosaurs launched in an avian-like, bipedal fashion, and Sato et al. also use procellariiform masses and flapping frequencies to estimate the same attributes for pterosaurs. Pterosaur femoral scaling trends reveal that they were unlikely to have taken off bipedally, however (Habib 2008), because, unlike birds, pterosaur hindlimb bones do not scale with sufficient allometry to withstand the bending stresses incurred during bipedal launches. Their forelimb bones, however, scale with pronounced allometry and, even taking safety factors into account, would be capable of supporting twice the body mass of a given pterosaur during takeoff. It is therefore more likely that pterosaurs used quadrupedal launches to become airborne (Habib 2008). Their utilisation of strong flight musculature – massing up to 50 kg in the largest forms (Marden 1994) - for this purpose may partially explain why pterosaurs could become so large while flighted birds, by comparison, seem limited to masses of 70 kg or less. Similarly, differences between bird and pterosaur wing and body proportions mean that applying flapping frequencies or extrapolating body masses between them is questionable. While we admire the empirical approach of such methods, we find the morphological differences between birds and pterosaurs too great to place much confidence in these findings. Accordingly, we do not consider them convincing evidence for pterosaur flightlessness.

Evidence for volant habits in giant pterosaurs

By contrast, giant pterosaur volancy is strongly supported by numerous lines of evidence. Giant individuals of *Pteranodon* are known to bear every anatomical hallmark of flight seen in smaller pterosaurs (e.g. complex and robust shoulders and proximal forearms, but slender, hypertrophied distal regions) and, so far as can be seen from their fragmentary fossils, giant azhdarchids exhibited the same (e.g. Buffetaut et al. 2002). It is notable that the largest fully grown giant pterosaurs would have outgrown the limits of flight proposed by Sato et al. and Chatterjee and Templin by up to six times the proposed flight mass limit, prompting questions as to why they should appear so flight ready if so much of their growth had taken place under grounded conditions. Indeed, scaling regimes have resulted in the flight anatomy of giant pterosaurs becoming even more conspicuous than that of their smaller brethren, a paradoxical development if giant pterosaurs were incapable of flight. Such scaling trends have resulted in giant pterosaur skeletons that are particularly strong, a consequence of their expanded diameters and extensive pneumatisation. Although there is conflicting evidence regarding the purpose of pneumatisation (mass reduction *vs*. mass redistribution), the beneficial effects it brings to increasing bone strength:weight ratios and increasing linear bone dimensions without additional mass are well documented: it is probably no coincidence that the most pneumatised pterosaurs are also the largest (Claessens et al. 2009). These findings contradict thoughts that pterosaur skeletons were lightweight, delicate structures: for their mass, pterosaurs are probably some of the most mechanically resilient creatures known.

The terrestrial abilities of allegedly flightless pterosaurs must also be considered. Pteranodontids have some of the most disproportionate forelimb/hindlimb ratios of any pterosaurs and were probably relatively poor terrestrial locomotors. By contrast, reconstructed pteranodontid flight anatomy has been repeatedly found to work efficiently in flight (e.g. Bramwell and Whitfield 1974; Chatterjee and Templin 2004; Witton 2008), and their frequent occurrences in open marine sediments despite lacking swimming adaptations corroborates these observations. Azhdarchids, by contrast, were recently proposed to be particularly adept at terrestrial locomotion (Witton and Naish 2008), suggesting a habitually grounded lifestyle is more tenable in these forms. However, the expanded bones of pterosaur skeletons – and particularly those of azhdarchids - surpass the mechanical requirements of purely grounded habits by some margin: their humeral diameters and lengths are similar to some of the largest and heaviest extant artiodactyls but, with their overall mass being a fraction of comparatively-sized mammals, their strength:weight ratios are far higher. In addition, like pteranodontids, the azhdarchid bauplan has been predicted to work well in flight (Marden 1994; Chatterjee and Templin 2004; Witton 2008; Habib and Witton, this volume) and there is, therefore, good reason to assume that azhdarchids were proficient volant animals as well as terrestrial. The most parsimonious interpretation of giant pterosaur anatomy, scaling trend and mechanics seems, therefore, to be that they were volant animals. Any claims to the contrary have to explain why grounded animals should have invested so many resources into retaining many obvious and mechanically tenable volant characteristics.

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