

剪断翼龙的翅膀：对于翼展估计和多样性的评论

Clipping the Wings of Giant Pterosaurs: Comments on Wingspan Estimations and Diversity

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Giant azhdarchids are perhaps the most spectacular pterosaurs known and, although they lack the elaborate headcrests or striking dentition that adorn other charismatic pterosaurs, the sheer enormity of their proportions has drawn a wealth of popular and scientific interest. Their remains, however, are so fragmentary that only limited interpretations of their anatomy and taxonomy can be made with certainty. Here, we report on recent investigations into giant azhdarchid taxonomy and size estimates that suggest both may be over-inflated.

Proportions

It is almost poetic that, as with many other giant fossil animals, the remains of giant pterosaurs are relatively tiny fragments of once immense creatures (Fig. 1). This has caused some controversy over wingspan estimates in the past (e.g. Greenewalt 1975), but the proportions of azhdarchids are now sufficiently known that estimating the sizes of the largest taxa should be reasonably reliable. It is now generally accepted, for instance, that the isolated humerus of *Quetzalcoatlus northropi* Lawson, 1975 predicts a wingspan of between 10 – 11 m (Langston 1981; Chatterjee and Templin 2004), but claims for pterosaurs spanning up to 2 m more are less well constrained. While these differences may seem relatively trivial, adding 2 m to the wingspan of an 11 m span pterosaur predicts a mass increase of almost 60 per cent: given how important mass estimations are to accurately modelling so many physiological, mechanical and ecological parameters of extinct animals, it is imperative that size estimations of giant forms are as precise as possible.

The cervical vertebra that represents *Arambourgiania philadelphiae* Arambourg, 1959 has been suggested to represent a form spanning 11 – 13 m (e.g. Frey and Martill 1996), but the scaling methods used in these estimations assume isometric growth across

the entire pterosaur skeleton. There is good evidence that many aspects of pterosaur skeletons grew with pronounced allometry, however, with the cervical vertebrae of long-necked ctenochasmatooid pterosaurs developing with positive allometry relative to body and wing elements (Wellnhofer 1970). This is consistent with other long necked forms (e.g. sauropods, plesiosaurs, giraffes) and it is likely that azhdarchid necks grew in the same fashion. The *Arambourgiania* vertebra provides some support for this, matching predictions that it should be proportionately much longer than the equivalent vertebra from a smaller azhdarchid. The elongate *Arambourgiania* vertebra almost certainly reflects pronounced allometric neck growth and, accordingly, size estimates assuming a relatively short neck are too high. We do not doubt, however, that the size of the vertebra indicates that *Arambourgiania* was a ‘giant’ pterosaur, but we lack sufficient azhdarchid neck scaling data to reliably estimate its wingspan at present.

The fragmentary humerus of *Hatzegopteryx thambema* Buffetaut et al. 2002, appears to represent an animal spanning around 12 m (Buffetaut et al. 2002), an apparent contradiction given that the humeral head and deltopectoral crest of the same specimen are of comparable size to that of *Q. northropi*. The deltopectoral crest of the *Hatzegopteryx* humerus appears to have been dorsally deflected through post-depositional distortion, however, altering the distal profile to suggest that the diaphysis was wider than it actually was in life (see figure, D). As such, the palmar-posterior diaphysis width reported by Buffetaut et al. (90 mm) actually records the anterodorsal-posteroventral diaphysis diameter and, once corrected for, the diaphysis measures 80 mm across. This value is identical to that of *Q. northropi* and suggests that *Hatzegopteryx* had an equivalent wingspan. Accordingly, spans of 10 – 11 m are the largest reliable size estimate for the giant pterosaurs at present.

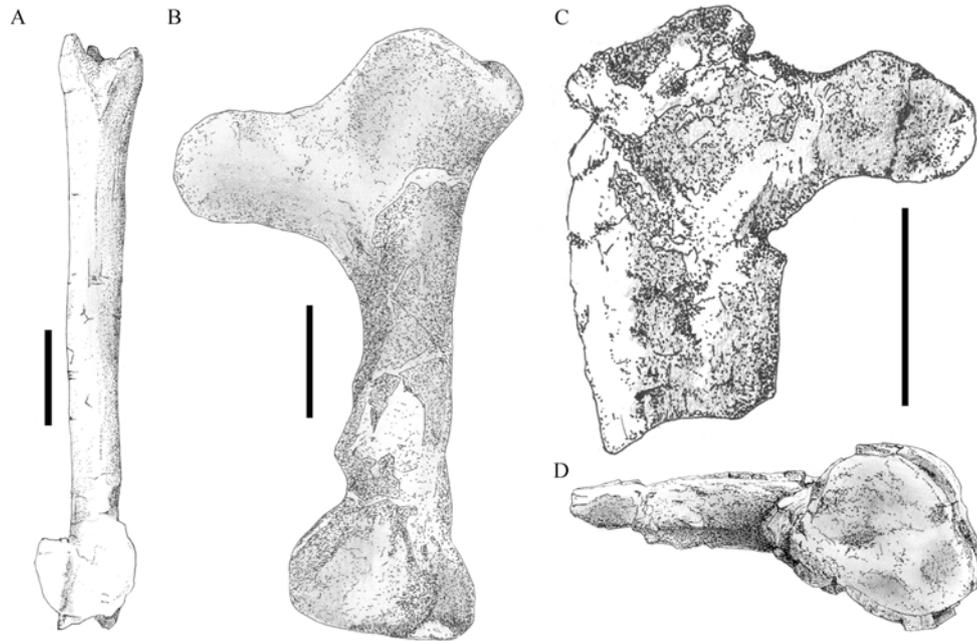


Fig. 1 Giant azhdarchid material used in size estimations. **A**, *Arambourgiania philadelphiae* cervical vertebra, dorsal view (after Frey and Martill 1996); **B**, *Quetzalcoatlus northropi* humerus, dorsal view (after Wellnhofer 1991); **C** and **D**, *Hatzegopteryx thambema* partial humerus, ventral (**C**) and distal (**D**) views. Scale bars represent 100 mm

Giant pterosaur taxonomy

The scanty remains of the three named giant azhdarchids (*Q. northropi*; *A. philadelphiae* and *H. thambema*) bear enough azhdarchid synapomorphies to be confidently referred to Azhdarchidae, but they are otherwise taxonomically problematic. There are several aspects to the taxonomic confusion of this group, with their representation by remains that are typically considered undiagnostic for pterosaurs (cervical vertebrae, limb bone fragments) is a core issue, as is their general incomparability with each other. Although comparisons of giant material can be made with smaller pterosaurs, most features that distinguish them (e.g. the elongate, deep centrum of the *Arambourgiania* cervical; the robust extremities of the *Hatzegopteryx* and *Q. northropi* humeri) probably reflect scaling and mechanical influences rather than phylogenetic differences. Moreover, recently described azhdarchid material shows wider distribution of features once considered diagnostic for some giant forms. The taxonomic ambiguity that surrounds *Quetzalcoatlus* is another key issue: the type species of this genus, *Q. northropi*, has not been diagnosed (save for a problematic and generally ignored attempt by Nesov 1991) and it has not been demonstrated that the referral of other material to this taxon (*Q. sp.*) has been done so reliably. This, in turn, confuses comparisons between the humeri of *Hatzegopteryx* and *Q. northropi*: so far as can be determined, the humeri of these forms are virtually identical (see above) and, if *Q. northropi* can be distinguished from other azhdarchids, *Hatze-*

gopteryx should be synonymised with this form. The quadrate of *Hatzegopteryx*, however, has been distinguished from that of *Q. sp.*, but the uncertain affinities of this taxon question the meaning of this comparison. We refrain, however, from making further judgements on the status of *Quetzalcoatlus* and *Hatzegopteryx* until the former is described in more detail: the information currently available on all *Quetzalcoatlus* material is not adequate to make an informed decision on its taxonomic status at present. It is notable, however, that the existence of these giant azhdarchid taxa in approximately coeval deposits and the potential for such large flying animals to disperse with relative ease over vast distances makes it plausible that they are congeneric (Habib, pers. comm. 2009), providing yet another reason to regard giant azhdarchid taxonomy with caution.

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