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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.

A new approach to determining pterosaur body mass and its implications for pterosaur flight

By
Mark P. Witton*

*Palaeobiology Research Group, School of Earth and Environmental Sciences, University of Portsmouth,
Burnaby Building, Burnaby Road, Portsmouth, PO1 3QL, UK*

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Abstract

Efforts to establish the masses of pterosaurs have been attempted for almost a century, but the methods employed are often as problematic as their conclusions that pterosaurs are unusually lightweight. Historically, most pterosaur masses have been determined through geometric modelling of pterosaur bodies and extrapolation of body densities from modern birds. However, both ecology and flight style are known to induce variation of body density across modern bird species, casting doubt on this frequently used method. Here, a new approach to mass estimation is attempted that requires no assumption of soft tissue density or distribution: following observations that the relationship of dry skeletal mass to body mass is essentially identical in ecologically and phylogenetically disparate modern birds and mammals, the skeletal masses of 19 pterosaur taxa have been estimated and their body masses regressed from the relationship between skeletal mass and body mass in modern forms. Masses derived from this method are up to three times greater than those estimated in previous studies with the largest pterosaur in this investigation (wingspan 10 m) found to have a mass of 250 kg. Reappraisal of pterosaur masses shows that lightweight pterosaur mass estimates are considerably lower than those of similarly sized birds and bats, requiring inordinate amounts of pneumaticity (up to 90 per cent for the lowest estimates of the largest forms) and are wholly unrealistic in light of the enormous sizes achieved by some pterosaurs. Combining heavier mass data with restorations of pterosaur wings based on preserved wing membranes permits assessment of basic pterosaur flight characteristics. Preserved wing membranes suggest that ankle-attached brachiopatagia are the best supported pterosaur wing model, and distinctions in forelimb/hindlimb ratios produce a range of wing shapes despite a standardised brachiopatagia configuration. Plotting greater masses and ankle-attached wings into a principal component analysis of aspect ratio and wing loading demonstrates that pterosaurs had a range of flight styles similar to those seen

in modern volant vertebrates. A broad spectrum of pterosaur flight styles are predicted including marine and thermal soars, adaptive generalists and forms for which flight is energetically costly and expensive.

Key words: Pterosaurs, mass estimation, wing ecomorphology, palaeoecology.

Zusammenfassung

Versuche, die Masse von Pterosauriern festzustellen können schon fast ein Jahrhundert zurückverfolgt werden, allerdings sind die angewandten Methoden oftmals genau so problematisch wie die daraus resultierende Schlussfolgerung, dass Pterosaurier generell Leichtgewichte gewesen sind. Geschichtlich gesehen wurde der überwiegende Teil der Masse-Berechnungen auf der Basis geometrischer Modellerstellungen von Pterosaurierkörpern und durch Extrapolation der Körpedichte an Hand neuzeitlicher Vögel bestimmt. Allerdings tragen Ökologie und Flugstil nicht unerheblich dazu bei, dass die Körpedichte bei verschiedenen Vogelspezies sehr unterschiedlich sein kann; dies stellt diese häufig benutzte Methode in Frage. In dieser Arbeit stellen wir eine neue Methode zur Massebestimmung vor, die weder eine Vorabeinschätzung der weichen Gewebematerialien noch deren Distribution erfordert. Auf der Basis der Beobachtung, dass das Verhältnis zwischen trockener Skelettmasse und Körpermasse im Wesentlichen identisch ist in ökologisch und phylogenetisch disperaten Vögeln und Säugetieren, wurde die Skelettmasse von 19 Pterosaurier Taxa kalkuliert, und deren Körpermasse wurde geschätzt unter Verwendung des Verhältnisses zwischen Skelettmasse und Körpermasse bei heutigen Tieren. Massen, die durch diese Methode ermittelt wurden sind, sind bis zu drei Mal höher als solche Massen, die in früheren Studien ermittelt wurden. Der größte Pterosauier (Spannweite 10 Meter), den wir in unserer Untersuchung modelliert haben, hatte demnach eine Masse

*E-mail: Mark.Witton@port.ac.uk

von 250 kg. Die Neuabschätzung der Pterosaurier Massen zeigt, dass Pterosaurier, wenn man sie als Leichtgewichte interpretiert, eine erheblich geringere Körpermasse gehabt haben müssen, als ähnlich große Vögel und Fledermäuse und dass sie erhebliche Pneumatisierung (bis zu 90 % für die niedrigste Schätzung der größten Form) erfordern, um flugfähig zu sein. Dies belegt, dass die Rekonstruktion dieser Tiere als Leichtgewichte unrealistisch ist angesichts der enormen Größen, die von manchen Pterosauriern erreicht wurden. Die Kombination von Massen-Daten mit der Rekonstruktion von Pterosaurier Flügeln, welche auf fossil erhaltenen Flügelmembranen basieren, erlaubt eine Einschätzung der fundamentalen Pterosaurier Flugmerkmale. Die Flügelmembranen deuten darauf hin, dass Brachiopatagia, die am Fußgelenk angebracht sind, die am Besten belegten Pterosaurier-Flügelmodelle sind, dass aber Unterschiede im Verhältnis der Vorder- zu den Hinterextremitäten trotz einer standardisierten Brachiopatagia-Konfiguration eine Anzahl von Flügelformen produziert haben. Eine graphische Darstellung von größeren Massen und am Fußgelenk angebrachter Flügel in einer PCA mit Flügelstreckung und Tragflächenbelastung zeigen, dass die Pterosaurier Flugstile hatten, die denen neuzeitlicher fliegender Wirbeltiere ähnlich sind. Die Diversität von Pterosaurier Flugstilen wurde prognostiziert mit Marin- und Thermalgleitern; anpassungsfähige Generalisten und Formen, für die der Flug energieverbrauchend und kostspielig ist.

Schlüsselwörter: Pterosaurier, Massebestimmung, Flügel-Ökomorphologie, Paläökologie

1. Introduction

Body mass is an important physical attribute of any organism, affecting both physiological and biomechanical properties of individuals and influencing broader ecological and evolutionary trends (SCHMIDT-NIELSEN 1984). However, while the masses of modern animals can be obtained with relative ease, estimating the masses of extinct taxa – even those with close extant relatives – can be challenging due to uncertainties over soft tissue densities and the incomparability of estimated masses with those of modern animals (e.g. CASINOS 1996; BIKNEVICIUS 1999). In spite of these difficulties, numerous studies have attempted to calculate the masses of pterosaurs in an effort to understand their locomotory methods. Studies into animal locomotion rely on use of body mass figures to estimate structural loading of skeletal components, movement speeds and, in the case of volant animals such as pterosaurs, flight characteristics (e.g. COOMBS 1978; CAMPBELL & TONNI 1983; CASINOS 1996; HENDERSON 1999; CHATTERJEE et al. 2007). Without knowing the mass of a flying object even basic aerodynamic data such as weight, wing loading and glide performance cannot be calculated: given that flight was apparently the principle locomotory method employed by pterosaurs, estimating their mass is crucial to understanding their locomotory capability.

Many authors have concluded that pterosaurs were extremely lightweight for their size (e.g. HANKIN & WATSON 1914; BROWN 1943; BROWER & VEINUS 1981; CHATTERJEE & TEMPLIN 2004) and several workers have calculated that pterosaurs were

considerably lighter than comparably sized Recent fliers (BROWER & VEINUS 1981; HAZLEHURST & RAYNER 1992; CHATTERJEE & TEMPLIN 2004). However, there is little agreement on the specific mass of even the best known and studied pterosaurs (Tab. 1). This is highlighted particularly well through the genera *Pteranodon* and *Quetzalcoatlus*, the masses of which are frequently scrutinised because of their relative completeness and gigantic size. The mass of a 6–7 m span *Pteranodon* has most frequently been reported at less than 17 kg (e.g. BRAMWELL 1970; BRAMWELL & WHITFIELD 1974; STEIN 1975; BROWER & VEINUS 1981; WELLNHOFER 1991a; HAZLEHURST & RAYNER 1992; CHATTERJEE & TEMPLIN 2004), but has been suggested to be as low as 10 kg (HANKIN & WATSON 1914; BROWN 1943). Higher estimates were given by KRIPP (1941), who suggested a mass of 30 kg for a *Pteranodon* with a wingspan of 7 m. HEPTONSTALL (1971), JERISON (1973) and PAUL (2002) echoed these figures with 20–25 kg estimates for a *Pteranodon* of 6–7 m span, and as much as 50 kg for an 8 m span (PAUL 2002).

Mass estimates for a 10–11 m span *Quetzalcoatlus* have been even more variable. Most workers have suggested masses

Table 1: Previously estimated masses of *Pteranodon* and *Quetzalcoatlus*.

Authors	Wingspan (m)	Mass (kg)
<i>Pteranodon</i>		
HANKIN & WATSON 1914	6.4	9.1
KRIPP 1941	7.0	30
BROWN 1943	6.7	11.34
BRAMWELL 1970	7.62	11.3 – 25
BRAMWELL 1971	8.2	18
HEPTONSTALL 1971	6.8	22.7
JERISON 1973	6.95	20
STEIN 1975	7.2	15
BRAMWELL & WHITFIELD 1974	6.95	12.8 – 23.8
BROWER & VEINUS 1981; BROWER 1983	6.95	14.9
WELLNHOFER 1991a; HAZLEHURST & RAYNER 1992; CHATTERJEE & TEMPLIN 2004	6.95	16.6
PAUL 1991, 2002	6.0	20 – 25
	8.0	50
<i>Quetzalcoatlus</i>		
BROWER & VEINUS 1981	11.43	75
LANGSTON 1981	11.0 – 12.0	86
PADIAN 1984	11.0	65
PAUL 1987	11.0	113
WELLNHOFER 1991a	11.0 – 12.0	< 86
PAUL 1991, 2002	11.0	200-250
MARDEN 1994	10.4	250
SHIPMAN 1998	12.0	127
ATANASSOV & STRAUSS 2002	unspecified	90-120
CHATTERJEE & TEMPLIN 2004	10.39	70
UNWIN 2005	11.0	50
WITTON 2007	10.0 – 11.0	70 – 85

between 70–85 kg (LANGSTON 1981; BROWER & VEINUS 1981; WELLNHOFER 1991a; CHATTERJEE & TEMPLIN 2004; WITTON 2007), but masses of 50–60 kg have also been proposed (PADIAN 1984; UNWIN 2005). SHIPMAN (1998) and ATANASSOV & STRAUSS (2002) estimated heavier masses of 90–127 kg, while MARDEN (1994) and PAUL (2002) suggested 200–250 kg. Note that the highest mass estimate for *Pteranodon* is three-times that of the lower, while a factor of five distinguishes the highest *Quetzalcoatlus* mass estimate from the lowest. This contention is compounded by differing opinions on the aerodynamic feasibility of heavier estimates: some workers have suggested that a quarter-tonne *Quetzalcoatlus* would be incapable of becoming airborne and prefer lower mass estimates for this reason (CHATTERJEE & TEMPLIN 2004), but others have determined that a pterosaur of this mass could achieve flight with no difficulty (MARDEN 1994).

Much of the discrepancy over pterosaur mass reflects alternative approaches to its calculation and the inherent difficulties in modelling the masses of extinct animals. Many methods have been employed to calculate mass for extinct forms, including regression of body parameters from closely related extant taxa (e.g. CAMPBELL & TONNI 1983; EGI 2001), determining body volume from water displacement (e.g. ALEXANDER 1985) and digital reconstructions (e.g. HENDERSON 1999; GUNGA et al. 2007). Pterosaur mass has traditionally been estimated through geometric modelling of body components, finding their volume and multiplying them by a suitable body density (HEPTONSTALL 1971; BRAMWELL & WHITFIELD 1974; BROWER & VEINUS 1981; BROWER 1983; HAZLEHURST & RAYNER 1992; CHATTERJEE & TEMPLIN 2004). These geometrically determined masses have recently been extrapolated to model the masses of a range of pterosaurs through multivariate analyses (e.g. HAZLEHURST & RAYNER 1992; ATANASSOV & STRAUSS 2002; CHATTERJEE & TEMPLIN 2004). However, despite its wide use, the accuracy of geometrically modelling pterosaur mass is debateable. Along with requiring accurate reconstructions of the extent of pterosaur soft-tissues, the employment of a suitable body density is paramount and, despite good evidence of pneumatisation in pterosaur bones (e.g. HANKIN & WATSON 1914; BRAMWELL & WHITFIELD 1974; WELLNHOFER 1985; BONDE & CHRISTENSEN 2003; STEEL 2004; O'CONNOR 2006), the extent of pneumatic structures in their soft-tissues is not known in any quantifiable measure. Several workers have extrapolated bird body densities as proxies for pterosaur density (e.g. BRAMWELL & WHITFIELD 1974; BROWER & VEINUS 1981; BROWER 1983; CHATTERJEE & TEMPLIN 2004), but detailed research into bird body densities has yet to be performed. There is little agreement, for example, on the 'average' body density of a bird: WELTY (1975) gave a value of 0.6 g/cm³ for the specific gravity of a duck; BROWER & VEINUS (1981) and BROWER (1983) suggested an average value of 0.9 g/cm³ for all birds based on a plucked duck, HAZLEHURST & RAYNER (1992) and CHATTERJEE & TEMPLIN (2004) cited 0.73 g/cm³, while PAUL (1988) reported 0.8 g/cm³. In actuality, such figures are misleading as bird density has been proven to be dependant on ecology (e.g. LOVVORN et al. 1991; LOVVORN & JONES 1994; SEAMANS et al. 1995) and, critically for investigations into pterosaur flight, reflective of particular flight styles. Birds employing long-distance, soaring flight have lower densities (c. 0.6 g/cm³) than short-range, high energy fliers (0.8–0.9 g/cm³; see SEAMANS et al. 1995). This variation

brings the reliability of estimating pterosaur body density from an 'average' bird body density into question, requiring either the predisposition of a similar lifestyle for all pterosaurs or undervaluing body density as a flight adaptation. Furthermore, the appropriateness of extrapolating density from modern birds is particularly questionable when applied to larger pterosaurs: the largest modern birds (wingspans of c. 3 m) fall short of even moderately-sized pterodactyloids, let alone the largest. Extrapolating density from these comparatively small forms ignores the potentially important role that density may have played in reducing overall body mass in giant pterosaurs. Extrapolation of body densities from even the largest modern birds to giant pterosaurs is therefore suggested to be highly presumptuous and potentially highly erroneous.

Few other methods have been employed to assess pterosaur mass. KRIPP (1941) scaled attributes of an engineless Horten V, one of a series of tailless aircraft developed by the Horten brothers between 1933 and 1945, to a 7 m span *Pteranodon* to deduce its mass and wing characteristics. With the 16 m wingspan of the 825 kg Horten V being 2.29 times that of the pterosaur, the mass of *Pteranodon* was calculated through:

$$1. \quad m_{bm} = 825/2.29^4$$

where m_{bm} is body mass. KRIPP (1941) deserves recognition as one of the first workers to approach the issue of pterosaur mass methodologically, but his estimate relies on the Horten V being a suitable modern pterosaur analogue and the appropriateness of this is questionable. JERISON (1973) employed a univariate equation based on the bird skull and body lengths to estimate the mass of *Pteranodon*:

$$2. \quad W = 0.5l^2$$

where W = body weight (g) and l = is the head and body length (cm). However, clear morphological distinctions between the two groups are not factored into this equation and the values obtained from this method reflect the masses of pterosaur-proportioned birds, not the pterosaurs themselves. STEIN (1975) extrapolated the mass of *Pteranodon* from the wing loading of the free-tailed molossid bats *Eumops perotis* and *Molossus ater*. This method assumes that the flight styles of *Pteranodon* and molossid bats are essentially identical and is reliant on accurately modelling the *Pteranodon* wing planform for precise comparison with those of the molossids. However, the incompleteness of most preserved pterosaur wing membranes do not permit sufficiently accurate reconstructions of pterosaur wings for such comparisons. Moreover, extrapolating *Pteranodon* mass from a predetermined flight model assumes strong convergence between pteranodontians and molossid bats in all attributes affecting wing morphology (e.g. foraging method, wing structure, habitat).

1.1 A new approach to pterosaur mass estimation

Here, an alternative method of estimating pterosaur mass is employed that uses skeletal mass to calculate total body mass. Work performed by PRANGE et al. (1979) reveals that, contrary to the popularly held belief that birds have relatively

lightweight skeletons compared to non-volant animals, the relationship between dry skeletal mass and body mass is consistent across birds and mammals irrespective of phylogeny, ecology or size. Amongst birds ranging from 0.0031–80.92 kg, this relationship is:

$$3. \quad m_{sk} = 0.065(m_{bm})^{1.071}$$

where m_{sk} is skeletal mass. The same analysis with mammals (ranging from 0.0063–6600 kg) shows a relationship between dry skeletal mass and body mass of:

$$4. \quad m_{sk} = 0.061(m_{bm})^{1.09}$$

In both cases the relationship is strongly supported with r^2 values of 0.993 in the avian dataset and 0.992 in the mammalian. This suggests the highly pneumatised skeletons of birds are, relatively, just as heavy as those of non-volant mammals. The broad ecological and phylogenetic distinctions between these groups suggest it might be possible to establish the masses of many fossil forms from their dry skeletal mass, including pterosaurs. Such a method avoids the pitfalls of estimating soft-tissue pneumaticity because only bony mass needs to be determined and this can be estimated from fossil data with far more confidence than body density can be extrapolated from any modern animal. Furthermore, there is no requirement to determine the dimensions of soft tissues on a fleshed-out pterosaur and, because the skeletons used by PRANGE et al. (1979) had all bone marrow removed in the drying and skeletonisation process, the mass of this tissue does not have to be estimated. This method therefore avoids many of the uncertainties that introduce doubt over previous mass estimates. Nineteen pterosaur genera (Tab. 2) were modelled using this technique (two morphs of *Pteranodon*, the larger with proportions 60 per cent greater than the smaller, were modelled in reflection of the presumed sexual dimorphism of this form [see BENNETT 1992] and brings the total number of modelled individuals to 20). To compare the results this method with those of other pterosaur mass studies and assess their implications for pterosaur flight, principal component analysis of basic aerodynamic attributes were performed following techniques outlined by NORBERG & RAYNER (1987), RAYNER (1988) and HAZLEHURST & RAYNER (1992).

2. Methods

2.1 Mass estimation

The masses of pterosaur skeletons were established through geometric modelling of skeletal components using dimensions derived from relevant literature (Tabs 2 and 3). Long bone lengths were obtained across the longest axis of the bone shafts, while diameters were taken from three averaged measurements across their diaphyses. More complicated elements (e.g. pelvis, skulls) were modelled using maximum bone dimensions and typically broken down into simpler components to more accurately assess their mass (Tab. 3). Attempts were made to represent the spectrum of pterosaur phylogeny and size, and each major pterosaur clade of UNWIN (2003) is represented

Table 2: Taxa used in mass estimation and sources of osteological data.

Taxon	Source of osteological data
Basal pterosaurs	
<i>Preondactylus buffarinii</i>	WILD 1984
<i>Dimorphodon macronyx</i>	OWEN 1870; PADIAN 1983
<i>Eudimorphodon ranzii</i>	WILD 1978
<i>Rhamphorhynchus muensteri</i>	WELLNHOFER 1975
<i>Sordes pilosus</i>	WELLNHOFER 1991a
<i>Anurognathus ammoni</i>	WELLNHOFER 1975; DALLA VECCHIA 2002
Pterodactyloids	
<i>Nurhachius ignaciobritoi</i>	ANDRES & JI 2006; WANG et al. 2005
<i>Anhanguera piscator</i>	WELLNHOFER 1991b; KELLNER & TOMIDA 2000
<i>Pteranodon longiceps</i>	BENNETT 2001
<i>Nyctosaurus gracilis</i>	WILLISTON 1902a; BENNETT 2003a
<i>Pterodactylus antiquus</i>	WELLNHOFER 1970
<i>Ctenochasma gracile</i>	WELLNHOFER 1991a
<i>Pterodaustro gui azui</i>	SANCHEZ 1973
<i>Huanhepterus quingyangensis</i>	DONG 1982
<i>Dsungaripterus weii</i>	YOUNG 1964, 1973
<i>Sinopterus dongi</i>	WANG & ZHOU 2002
<i>Huaxiapterus corollatus</i>	LU et al. 2006
<i>Zhejiangopterus linhaiensis</i>	CAI & WEI 1994
<i>Quetzalcoatlus northropi</i>	KELLNER & LANGSTON 1996; WELLNHOFER 1991a; CAI & WEI 1994

by at least one taxon. The number of modelled components ranged from 71 to 79 across different taxa. The volumes of these elements were multiplied by two to reflect bone density (2.0 g/cm³; HEPTONSTALL 1971; CURREY 2002) and determine bone mass. All component masses were then summed to calculate total skeletal mass and, using the relationship between avian skeletal mass and body mass determined by PRANGE et al. (1979), total body mass was computed. The avian regression was used due to the closer phylogenetic and ecological affinities of pterosaurs to birds than mammals, but the mammalian regression can be employed with negligible effects on the overall results.

2.1.1 Pneumacity

The pneumatic nature of pterosaur bone has been noted by many authors (e.g. SEELEY 1901; EATON 1910; BRAMWELL & WHITFIELD 1974; BONDE & CHRISTENSEN 2003; STEEL 2004; O'CONNOR 2006) but has not yet been quantified across the pterosaur skeleton. Estimating the pneumaticity of the pte-

Table 3: Geometric shapes used in skeletal modelling and equations used to model their volume. l, length; w, width; h, height; r, radius.

Component	Shape	Equation	Component	Shape	Equation
Cranial material			Ribs	Hollow cylinder	$(\pi r_1^2 l - (\pi(r_1 - r_2)^2 l)) * 0.75$
Skull	Half pyramid	$1/3(0.5wh)l$			
Mandibular symphysis	Half pyramid	$1/3(0.5wh)l$	Forearm		
Mandibular rami	Cuboid	lwh	Humerus	Cylinder	$\pi r^2 l$
Vertebrae			Ulna	Cylinder	$\pi r^2 l$
Atlas axis	Cylinder	$\pi r^2 l$	Radius	Cylinder	$\pi r^2 l$
Cervical 3	Cylinder	$\pi r^2 l$	Carpals	Cylinder	$\pi r^2 l$
Cervical 4	Cylinder	$\pi r^2 l$	Pteroid	Cone	$1/3(\pi r^2 l)$
Cervical 5	Cylinder	$\pi r^2 l$	Metacarpal 4	Cylinder	$\pi r^2 l$
			MC 4 Ph1	Cylinder	$\pi r^2 l$
Cervical 6	Cylinder	$\pi r^2 l$	MC 4 Ph2	Cylinder	$\pi r^2 l$
Cervical 7	Cylinder	$\pi r^2 l$	MC 4 Ph3	Cylinder	$\pi r^2 l$
Cervical 8	Cylinder	$\pi r^2 l$	MC 4 Ph4	Cone	$1/3(\pi r^2 l)$
			Digit 1	Cone	$1/3(\pi r^2 l)$
Dorsals	Cylinder	$\pi r^2 l$	Digit 2	Cone	$1/3(\pi r^2 l)$
Sacrals	Cylinder	$\pi r^2 l$	Digit 3	Cone	$1/3(\pi r^2 l)$
Caudals	Cone	$1/3(\pi r^2 l)$			
Pectoral girdle			Hindlimb		
Sternum	Prism	$0.5lwh$	Femur	Cylinder	$\pi r^2 l$
			Tibia	Cylinder	$\pi r^2 l$
Scapula ramus	Cuboid	lwh	Fibula	Cylinder	$\pi r^2 l$
Coracoid ramus	Cuboid	lwh	Tarsals	Cylinder	$\pi r^2 l$
Glenoid	Cylinder	$\pi r^2 l$	Digit 1	Cone	$1/3(\pi r^2 l)$
Pelvic region			Digit 2	Cone	$1/3(\pi r^2 l)$
Pubis	Prism	$0.5lwh$	Digit 3	Cone	$1/3(\pi r^2 l)$
Prepubis	Prism	$0.5lwh$	Digit 4	Cone	$1/3(\pi r^2 l)$
			Digit 5	Cone	$1/3(\pi r^2 l)$

rosaur skeleton is integral for modelling pterosaur skeletal mass, but variation of bone cortex thicknesses and concentrations of trabeculae and spongiosa across single bones (STEEL 2004) renders modelling of this attribute difficult. WEDEL (2005) noted similar difficulties in estimating the pneumaticity of sauropod dinosaur vertebrae and employed CT scan sections to determine average void space within these bones. Here, a regression analysis of bone wall thickness to bone diameter was used to estimate pneumaticity in pterosaur bones, employing data from 27 bone sections in STEEL (2004) and, to provide greater resolution for larger pterosaurs, three cortex thicknesses from a cast of UJ VF1, the large cervical vertebrae of *Arambourgiania philadelphiae* housed in the collections of the University of Jordan (see MARTILL et al. 1998 for further details):

$$5. \quad B_w = 0.043B_d^{-0.524}$$

where B_w equals the bone wall thickness and B_d is the diaphysis diameter (Fig. 1). The cortex thickness was then subtracted from the dimensions of the geometrically modelled bone and the volume of the pneumatic cavity calculated. This figure was then subtracted from the overall bone-shape volume to generate an estimate of pneumatised bone mass. Bone wall thicknesses were calculated for all elements of the

modelled skeletons: non-pneumatised bones are treated as hollow to account for the space occupied by bone marrow, the mass of which does not factor into the equations of PRANGE et al. (1979). Trabeculae and spongiosa are not specifically accounted for in this model, however, due to a lack of sufficient data on their distribution and concentration in pterosaur skeletons. Unfortunately, cortex thickness data for the smallest and largest pterosaurs is wanting and the histology regression is predominantly modelled on moderately sized forms. However, comparisons between modelled cortex thicknesses and measured cortex demonstrates an accuracy of ± 0.03 mm, indicating reasonable precision in predicting bone wall thicknesses.

2.1.2 Accuracy of mass estimation

The skeletal masses of 9 bird long bones, 4 pectoral elements and 5 skulls were modelled to assess the accuracy of mass determination method employed here. Typically, bone masses were found to lie ± 10 per cent of actual values, although three bones were calculated to be 15 per cent above (pelican ulna, *Rynchops* skull) or below (albatross humerus) actual masses. Across all modelled bones, average masses were predicted to be 5 per cent higher than measured values. Limb bone masses were the most accurately predicted elements and, when averaged across the sample, showed negligible differences from actual values. Skull

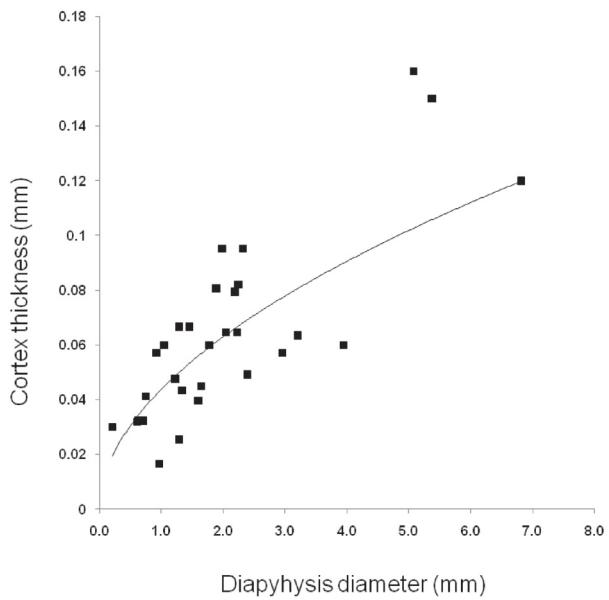


Figure 1: Bone histology regression calculated from data in STEEL (2003) and from UJ VF1.

masses were generally predicted to be 7 per cent greater than actual values, while pectoral element masses were 2 per cent lower. It is thought that the poorer accuracy of these latter figures reflects the greater complexity of these bones compared to the relatively simple shapes of avian limb bones. The use of numerous components in reconstructing the skeletal masses and the predominance of long bones in the pterosaur skeleton dilutes the effects of such discrepancies, and the general proximity of the estimated avian bone masses to those measured from actual bones suggests the pterosaur skeletal masses estimated here approximate real figures.

2.2 Aerodynamic calculations

Wing area (S) and wingspan (b) are required to calculate basic aerodynamic attributes such as wing loading (Q) and aspect ratio (A). Wing area was digitally measured by the standard convention as the combined area of both wings and portion of the body between them. Wingspan was measured from reconstructed pterosaur profiles (see below). Aspect ratio and wing loading were then derived using:

$$6. \quad A = b^2/S$$

$$7. \quad Q = m_{bg}g/S$$

where g is equal to acceleration due to gravity (9.81).

2.2.1 Wing area reconstructions

Pterosaur profiles were reconstructed in dorsal view using the same limb proportions as those employed in mass estimations. These reconstructions were digitised and their wing area measured using the freeware program ImageJ (version 1.8). Standardised extensions of the fore- and hindlimb joints were used to make wing morphology as comparable as possible bet-

ween taxa. Basal pterosaurs (Tab. 2) were restored with elbow and wrist extensions at 155° based on reported extensibility of these joints in *Rhamphorhynchus* (WELLNHOFER 1975). Pterodactyloids (Tab. 2) were given greater extension (165°) in the same joints following the recorded extensibility of the *Santanadactylus* wrist (WELLNHOFER 1985). In accordance with wing finger extensibility reported for *Rhamphorhynchus* and *Santanadactylus* (WELLNHOFER 1975, 1985), most pterosaurs were restored with wing fingers extended 165° from the metacarpal. However, wing finger extension was increased to 175° for pteranodontians (*Pteranodon longiceps* and *Nyctosaurus gracilis*) following the reported extensibility of the *Pteranodon* wing finger (BENNETT 2001). Wingspan was derived by measuring the distance between the wingtips when held in their respective configurations: these values are typically smaller than those derived from wing-bone lengths alone (such as the methods outlined in BENNETT 2001: 117–118) due to the effect of the limb bones being angled relative to the wingspan measurement. In all forms, femora were arbitrarily angled at 45° from the acetabulum and tibiae aligned parallel to the vertebral column.

Although the osteology of pterosaur wings can be reconstructed with some certainty, the extent of their wing membranes remains controversial. Contention is primarily focused in two areas: orientation of the pteroid and subsequent depth of the propatagium, and attachment of the brachiopatagium to the hindlimb. A full discussion of pteroid orientation is beyond the scope of this work, but alternate reconstructions of this controversial element can be found in BRAMWELL & WHITFIELD (1974); FREY & RIESS (1981), PENNYCUICK (1988), BENNETT (2006) and WILKINSON et al. (2006). In light of recent work suggesting that broader propatagia increased the lift generated by pterosaur wings (WILKINSON et al. 2006), most pterosaurs modelled here have been restored with pteroids projecting anteromedially from the wing metacarpal to form a broad propatagium. This membrane was reconstructed as extending from the shoulder to tip of the pteroid and across to the distal wing metacarpal. The peculiar pteroid morphology of nyctosaurs (see WILLISTON 1902b and BENNETT 2003a) has been suggested to reflect a narrow forewing (FREY et al. 2006) and has been accordingly modelled here.

Similarly controversial is the attachment site of the posterior margin of the brachiopatagium to the hindlimb. Because this element is only rarely and often ambiguously preserved, alternate models of pterosaur brachiopatagia can be found throughout the 200 year history of pterosaur research (see UNWIN 1999 for a brief review). Among studies modelling pterosaur flight, ‘broad-chord’ brachiopatagia attached at the ankle are most common (HEPTONSTALL 1971; BRAMWELL & WHITFIELD 1974; STEIN 1975) and were used for basal pterosaurs by CHATTERJEE & TEMPLIN (2004). Conversely, BROWER & VEINUS (1981) and BROWER (1983) modelled all pterosaurs with ‘narrow-chord’ wings attaching at the pelvis without any hindlimb incorporation at all. An intermediate condition, where the brachiopatagia attaches at the knees, was used to model the wing area of pterodactyloids by CHATTERJEE & TEMPLIN (2004). Acknowledging the controversy over pterosaur wing shape, HAZLEHURST & RAYNER (1992) modelled pterosaurs with ankle, thigh and pelvis-attached wings. Note that these studies have assumed that an ankle-attached brachiopatagia can only

produce a deep, broad wing and, conversely, only a thigh- or pelvis-attached membrane can produce a narrow planform. This dichotomy between ‘broad’ or ‘narrow’ wings is almost certainly an oversimplification of pterosaur wing shape and ignores the potential for differential chord dimensions along the extent of the wing (Hone, personal communication, 2007).

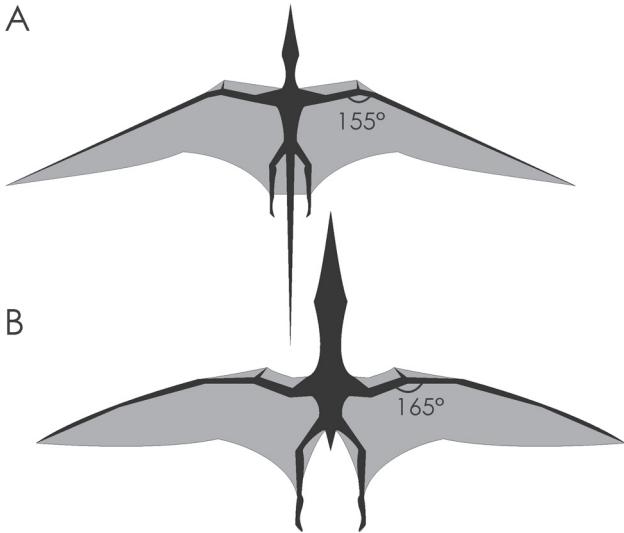


Figure 2: Wing planforms of basal and pterodactyloid pterosaurs used in this study. A, planform of *Rhamphorhynchus muensteri*; B, planform of *Dsungaripterus weii*. Note distinctions in uropatagia and extendibility of the wing finger.

As the brachiopatagium comprises the majority of wing area, accurately modelling its extent is paramount to understanding pterosaur flight. Several recent fossil discoveries have provided additional insights into pterosaur wing shape and suggest that broad-chord, ankle-attached brachiopatagial models may be most accurate. Previously, the best evidence for this wing shape came from a specimen of *Sordes pilosus* from the Karabastau Formation of Kazakhstan (SHAROV 1971), a fossil almost inarguably demonstrating attachment of the membrane at the ankle (UNWIN & BAKHURINA 1994). Complementing this are fossils of a campylognathoidid (WILD 1993; BAKHURINA & UNWIN 2003), anurognathids (WANG et al. 2002; BENNETT 2007a), rhamphorhynchid (FREY et al. 2003), ctenochasmatid (LÜ 2002) and azhdarchoid (FREY & TISCHLINGER 2000; FREY et al. 2003) that demonstrate brachiopatagial attachment at the ankle. Given that these taxa represent the broad range of pterosaur phylogeny (UNWIN 2003; KELLNER 2003) and phylogenetically bracket almost all pterosaur taxa, it is most parsimonious to conclude that all pterosaurs had broad, ankle-attaching wings. Furthermore, this wing configuration is the only model supported well by fossil evidence: wings with posterior margins meeting the pelvis (*sensu* PADIAN 1979) are not demonstrated in any pterosaur specimen and knee-attaching brachiopatagia can only be seen (ambiguously) in *Pterodactylus* specimens from the Solnhofen limestone (see WELLNHOFER 1991a), a deposit that often preserves distal wing soft tissues far more readily than proximal. As such, although some workers have cast doubt on the ankle-attached pterosaur wing model (e.g. DYKE et al.

2006), this configuration is both best supported by fossil data and the most parsimonious model phylogenetically. In the pterosaur reconstructions made here, a standardised wing shape was derived from the ‘dark-wing’ *Rhamphorhynchus* specimen (JME SOS 4784, housed at Jura-Museum Eichstätt, Germany) and fitted to each pterosaur profile (Fig. 2). Reconstructing the wing profile in this manner leads to a superficially bird-like planform with a rounded trailing margin rather than the tapering wings of other pterosaur wing reconstructions (e.g. BRAMWELL & WHITFIELD 1974; STEIN 1975; BROWER & VEINUS 1981; BROWER 1983; HAZLEHURST & RAYNER 1992; CHATTERJEE & TEMPLIN 2004).

The third wing membrane, the uropatagium, was not modelled by BROWER & VEINUS (1981), BROWER (1983) or HAZLEHURST & RAYNER (1992) but is a potentially important variable of pterosaur wing anatomy and should be included in wing area assessments. Specimens of *Sordes*, *Eudimorphodon* and *Jeholopterus* demonstrate a broad uropatagium extended between their hindlimbs supported by elongated fifth pedal digits (BAKHURINA & UNWIN 1992, 2003; WILD 1993; UNWIN & BAKHURINA 1994; WANG et al. 2002). By contrast, specimens of *Pterodactylus* suggest that pterodactyloids had reduced urpatagia extending along the posterior margin of the hindlimb between the pelvis and ankle and bore no support from any digits (WELLNHOFER 1970). Among pterosaur taxa modelled here, those with elongate membrane-supporting fifth digits were modelled with the expansive *Sordes*-style urpatagia, while those with truncated fifth digits were given the reduced *Pterodactylus*-style variant.

3. Results

3.1 Mass estimation

Pterosaur body masses were found to range from 0.035 kg (*Anurognathus*, $b = 0.352$ m) to 259 kg (*Quetzalcoatlus*, $b = 9.64$ m), giving the largest form over 6000 times the magnitude of the smallest (Tab. 4). As may be expected, a strong correlation between mass and wingspan is demonstrated (Fig. 3):

$$8. \quad m_{bm} = 0.551b^{2.516}$$

with mass increasing disproportionately to wingspan. Several taxa are atypically heavyset or lightweight for their wingspan: *Dimorphodon* ($b = 1.01$ m, $m_{bm} = 1.24$ kg), *Dsungaripterus* ($b = 2.51$ m, $m_{bm} = 9$ kg) and *Quetzalcoatlus* are 117, 54 and 43 per cent heavier than projected for their wingspans, while *Rhamphorhynchus* ($b = 0.894$, $m_{bm} = 0.263$ kg), *Anhanguera* ($b = 4.01$ m, $m_{bm} = 11.98$ kg) and *Nyctosaurus* ($b = 2.04$ m, $m_{bm} = 2.66$ kg) have masses 63 (former two cases) and 77 per cent of their expected figures. At 36.68 kg (large morph, $b = 5.96$ m) and 10.53 kg (small morph, $b = 3.7$ m), *Pteranodon* is over 30 per cent lighter than expected. Stronger allometry is seen in the relationship between mass and wingspan of basal pterosaurs than is seen in pterodactyloids:

$$9. \quad m_{bm} = 0.681b^{2.807} \text{ (basal pterosaurs)}$$

$$10. \quad m_{bm} = 0.519b^{2.550} \text{ (pterodactyloids)}$$

This discrepancy is best highlighted between the 1.24 kg of *Dimorphodon* compared to 0.91 kg in *Sinopterus* ($b = 1.14$ m): despite a similar wingspan, the basal pterosaur is 20 per cent more massive than the pterodactyloid. The consequence of these scaling relationships suggests that any basal pterosaur with a wingspan over 0.35 m will have a greater mass than an equivalently sized pterodactyloid.

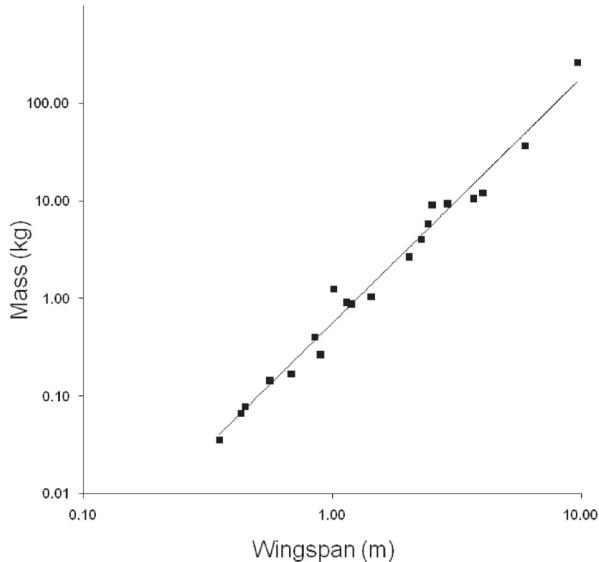


Figure 3: Pterosaur masses estimated in this study plotted against wingspan.

3.2 Aspect ratios and wing loading

Despite the standardised brachiopatagial configuration used in this investigation, aspect ratios are notably different between taxa (Tab. 4). Aspect ratios range from 6.6 in *Preondactylus* to 22.9 in *Nyctosaurus*, and a clear distinction can be made between the aspects of basal pterosaurs and pterodactyloids. Proportionally, basal pterosaurs have greater wing areas and correspondingly lower aspect ratios, but their wing shapes are more restricted with aspects ranging by 5.16 compared to 14.95 in pterodactyloids. Generally, forelimb/hindlimb ratios (taken as lengths of humerus + ulna carpal + wing metacarpal + flight phalanges/femur + tibia) correlate positively with lower aspect ratios, although this relationship looses among pterosaurs with higher aspects and limb ratios (e.g. *Rhamphorhynchus*, *Pteranodon*, *Nyctosaurus*). Over half of the taxa modelled here fall into a tight cluster of low aspect/low limb ratios ($A = 7.3\text{--}10.4$; limb ratio = 2.7–3.7), with pterodactyloids showing greater correlation between increasing limb ratios and aspect. In accordance with the size disparity of the animals modelled here, wing loading varies considerably. The lowest is that of *Anurognathus* (22.39 N/m²), whilst the highest is seen in *Quetzalcoatlus* (223.66 N/m²). Wing loading is proportionally lower in basal pterosaurs than in pterodactyloids, but this attribute does not correlate with aspect ratio or limb ratios in either group.

4. Discussion

4.1 The realism of pterosaur masses

The pterosaur body masses estimated here are far higher than previously cited values, with the 36 kg *Pteranodon* and 259 kg *Quetzalcoatlus* more than twice as massive as most published figures for these genera (Tab. 2). Comparing the scaling relationship of this study with those of previously calculated wingspan/mass regressions demonstrates this distinction well:

11. $m_{bm} = 0.1833b^{2.4823}$ (BROWER & VEINUS 1983)
12. $m_{bm} = 0.206b^{2.3329}$ (HAZLEHURST & RAYNER 1992)
13. $m_{bm} = 0.1863b^{2.4767}$ (CHATTERJEE & TEMPLIN 2004)

The exponent of this analysis (2.516) is similar to those produced in earlier studies and suggests some consensus on the relative scaling between body mass and wingspan. However, while the proportionality coefficients of these studies show relatively little variation (0.0227, average of 0.191), this figure strongly contrasts with the proportionality coefficient of this study which, at 0.551, is up to three times greater than those modelled by previous workers (Fig. 4). This difference demands investigation into the accuracy of these contrasting estimates: can volant animals really have masses as high as suggested here, could heavyweight pterosaurs really fly, and, conversely, are lightweight pterosaur masses really feasible?

4.1.1 Comparison with modern fliers

A dataset of 96 modern birds, representing the suite of bird phylogeny and size, ($b = 0.089\text{--}3.5$ m; data from SAVILLE 1957; McGAHAN 1973; PENNYCUICK 1971, 1972, 1983, 1987; PENNYCUICK et al. 2000; TOBALSKE & DIAL 1996; HERTEL & BALANCE 1999; ROSÉN & HEDENSTRÖM 2001; HEDENSTRÖM & ROSÉN 2001) reveals that they share a similar relationship between mass and wingspan with the heavyset pterosaurs of this analysis (Fig. 4):

$$14. \quad m_{bm} = 0.623b^{2.346}$$

Analysis of the same relationship between wingspan and mass in 102 modern bats ($b = 0.16\text{--}1.3$ m; data from NORBERG & RAYNER 1987; NORBERG et al. 2000) reveals that smaller bats ($b \leq 0.3$ mm) are generally lighter than birds of equivalent size but scale with greater allometry so that larger forms are of equivalent mass to comparably spanned birds (Fig. 4):

$$15. \quad m_{bm} = 0.5088b^{3.0294}$$

Small bats also have lower masses than comparably sized pterosaurs modelled in this study, but larger bats are like birds in conforming well to the heavier pterosaur estimates offered here. In both cases, the proportionality coefficient of this study conforms well to those of modern fliers, whereas the lightweight pterosaur estimates of other analyses have proportionality coefficients half that of bats and one third that of birds. Hence, although modern forms cannot suggest whether the predicted masses of the largest pterosaurs are feasible, cor-

Table 4: Mass, wing morphology and principal component analysis results of this study.

Taxon	Wingspan (m) <i>b</i>	Skeletal mass (kg)	Mass from scaling equation (kg) <i>M</i>	Weight (Mg) <i>N</i>	Wing area (m ²) <i>S</i>	Aspect ratio ($\delta^2/S/A$)	Wing loading (N/m) <i>Q</i>	Q1	Q2	Q3	Limb ratio
<i>Preondactylus</i>	0.45	5.43	0.08	0.77	0.030	6.59	25.27	-0.312	-0.398	-0.392	3.02
<i>Dimorphodon</i>	1.01	86.43	1.24	12.18	0.153	6.68	79.76	0.990	0.802	-1.028	3.28
<i>Anurognathus</i>	0.35	2.46	0.04	0.35	0.016	8.01	22.39	-0.740	-0.413	0.496	3.47
<i>Eudimorphodon</i>	0.85	27.89	0.40	3.93	0.079	9.21	50.00	0.533	-0.053	0.350	4.38
<i>Rhamphorhynchus</i>	0.89	18.33	0.26	2.58	0.068	11.75	37.99	0.443	-0.783	1.273	5.71
<i>Sordes</i>	0.56	10.04	0.14	1.41	0.044	7.14	32.23	0.001	-0.251	-0.271	3.72
<i>Nuriachius</i>	2.28	278.40	4.00	39.23	0.361	14.39	108.61	1.807	-0.032	1.286	4.52
<i>Anhangüera</i>	4.01	833.91	11.98	117.51	0.964	16.68	121.88	2.525	-0.627	1.476	4.99
<i>Pteranodon</i> (large)	5.96	2553.54	36.68	359.84	1.980	17.85	180.82	3.101	-0.401	1.424	4.97
<i>Pteranodon</i> (small)	3.70	732.97	10.53	103.29	0.765	17.90	135.02	2.404	-0.348	1.769	4.97
<i>Nyctosaurus</i>	2.04	185.21	2.66	26.10	0.182	22.92	143.72	1.503	0.459	3.035	7.81
<i>Pterodactylus</i>	0.43	4.62	0.07	0.65	0.018	10.10	35.55	-0.490	0.136	1.161	3.25
<i>Huanhepterus</i>	2.42	404.94	5.82	57.06	0.735	7.97	77.65	2.087	-0.505	-0.892	3.00
<i>Ctenochasma</i>	0.68	11.72	0.17	1.65	0.051	9.22	32.65	0.159	-0.611	0.556	3.50
<i>Pterodaustro</i>	1.19	60.70	0.87	8.55	0.128	11.03	66.61	0.958	-0.013	0.769	4.93
<i>Dsungaripterus</i>	2.51	627.02	9.01	88.36	0.624	10.09	141.58	2.141	0.536	-0.136	3.23
<i>Sinopterus</i>	1.14	63.23	0.91	8.91	0.146	8.91	61.08	0.979	0.015	0.015	3.16
<i>Huaxiapterus</i>	1.43	71.63	1.03	10.09	0.209	9.77	48.23	1.202	-0.848	0.263	3.08
<i>Zhejiangopterus</i>	2.90	646.60	9.29	91.12	1.027	8.19	88.69	2.344	-0.494	-0.923	2.80
<i>Quetzalcoatlus</i>	9.64	18034.65	259.06	2541.40	11.363	8.18	223.66	4.132	-0.253	-1.804	2.81

relation between the masses of modern fliers and equivalently sized ‘heavyweight’ pterosaurs suggests that at least the smaller pterosaurs of this study are not unrealistically burdened. By contrast, for lightweight estimates to be accurate, pterosaurs would require adaptations for mass reduction far beyond that of any modern volant vertebrate.

4.1.2 Aerodynamic modelling of pterosaur flight

Several models of pterosaur flight have assumed that pterosaurs had to be lightweight to become airborne: CHATTERJEE & TEMPLIN (2004), for instance, suggested that a quarter-tonne *Quetzalcoatlus* was far too massive to take off and fly. Conversely, STEIN (1975) and MARDEN (1994) found no difficulty with a heavyset *Pteranodon* and quarter-tonne *Quetzalcoatlus* becoming airborne. These contradicting conclusions highlight the pitfall of basing mass estimates on assumptions used in modelling pterosaur flight. Pterosaur anatomy is too poorly understood to back-calculate mass from results of aerodynamic calculations: it is currently difficult to distinguish the effects of greater masses on failed pterosaur flight models from incorrect assumptions of wing shape, flight energetics or takeoff mechanics. Whether a quarter-tonne pterosaur could fly can only be answered definitively when all other values in pterosaur flight equations have been certified, suggesting that it is highly presumptuous to favour either heavy or lightweight pterosaur masses from aerodynamic equations alone.

4.1.3 Body size and soft tissue composition

The discrepancy between the masses of modern flying vertebrates and lightweight pterosaurs calls into question the accuracy of soft tissue reconstructions in geometric modelling: are lightweight pterosaurs supplied with realistic amounts of body tissues? PAUL (2002) suggested that a 7 m span *Pteranodon* would have a total cubic volume of 40 litres, thereby requiring *Pteranodon* to have been over 60 per cent pneumatic to achieve the sub-16 kg estimates proposed by many pterosaur workers. The low mass estimates for a giant *Quetzalcoatlus* require even more substantial pneumatisation: a 1/10th clay model of a 10 m span *Quetzalcoatlus* constructed to the same proportions as those used in the geometric skeleton model suggests its volume can be estimated at 500 litres. For an animal of 500 litres to have a mass of 50 kg, 90 per cent of the body has to be pneumatised and its density becomes 0.1 g/cm³. Moreover, even the relatively high 127 kg estimate of ATANASSOV & STRAUSS (2002) requires a body density of 0.25 g/cm³, while the quarter-tonne estimates of MARDER (1994), PAUL (2002) and this study produce a density of 0.5 g/cm³. Densities of 0.1–0.25 g/cm³ are impossibly low: even if the volume of *Quetzalcoatlus* has been overestimated by 30 per cent, a body with 65–85 per cent pneumaticity would still be required to achieve masses of 50–127 kg. By contrast, although a density of 0.5 g/cm³ is lower than any reported figures for modern birds, it remains possible that the largest pterosaurs were less dense than modern volant forms in order to combat the exponential effects of increasing size on body mass. Alternatively, if the volume of *Quetzalcoatlus* has been overestimated by 30 per cent, then the body density of a 250 kg individual rises to 0.7 g/cm³, a value consistent with many modern birds (see SEAMANS et al. 1995).

Further problems with low masses become apparent when differential tissue masses are considered. Subtracting the *Quetzalcoatlus* skeletal mass determined in this study (18 kg) from lightweight *Quetzalcoatlus* mass estimates leaves between 32–107 kg of mass to account for all remaining soft tissues. The lowest of these figures is almost half of the estimated flight

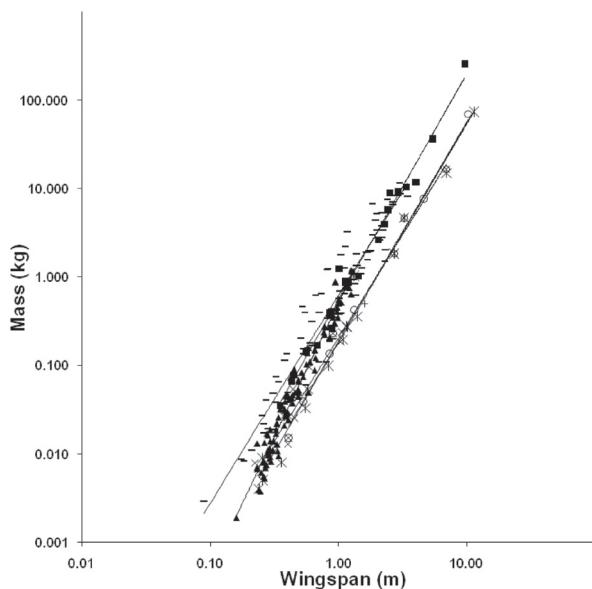


Figure 4: Comparative datasets of estimated pterosaur masses and known masses of extant forms. Closed squares, this study; open circles, CHATTERJEE & TEMPLIN (2004); crosses, HAZLEHURST & RAYNER (1992); stars, BROWER & VEINUS (1981); horizontal lines, extant bird masses; closed triangles, extant bat masses. See text for bird and bat data references.

muscle mass attributed to *Quetzalcoatlus* by MARDEN (1994) and recalls observations by PAUL (2002) that such masses would not permit sufficient muscle mass to fill the space occupied by flight muscles on the *Quetzalcoatlus* humerus, let alone any other soft tissues. By contrast, heavier masses leave over 200 kg for allocation to other soft tissues.

Finally, the size of the animals under consideration needs to be acknowledged: 200–250 kg is a remarkably low mass for an animal that would stand nearly 2.5 m tall at its shoulder. To put this size into context, consider that similarly proportioned giraffes (*Giraffa camelopardalis*, Fig. 5) have masses between 636–1395 kg (HALL-MARTIN 1977). A quarter-tonne pterosaur of this magnitude still conforms to the notion that pterosaurs were lightweight, just not one that deserves the title of an “ultralight airbeings” as described by PAUL (1991). The idea of pterosaurs being extremely lightweight appears to have grown from observations of their extensively pneumatized skeletons and anecdotal mass figures cited by early workers (e.g. WILLISTON 1902b; HANKIN & WATSON 1914; BROWN 1943) with no methodological details. This, combined with a consensus that pterosaurs were little more than delicate, weather-dependant gliders (e.g. WILLISTON 1902b; KRIPP 1941; BRAMWELL 1970; NESOV 1984; CHATTERJEE & TEMPLIN 2004) apparently entrenched the idea that pterosaurs were atypically lightweight. The evidence that pneumatized bird skeletons occupy just as much mass as those of un-pneumatized mammalian skeletons implies that pneumaticity does not necessarily reduce overall mass (PRANGE et al. 1979) and that these early observations regarding pterosaur mass were in error. Instead, pneumatized bones may be a consequence of

mass redistribution, allowing for relatively heavy flight-related structures such as feathers, wing membranes or developed forearm muscles (PRANGE et al. 1979; also see SEAMANS et al. 1995 for relative feather masses), and a similar explanation can be hypothesized for the extensive pneumatization of pterosaur skeletons. The ability of pterosaurs to redistribute the mass of their skeletons more extensively than any other vertebrates may explain their attainment of tremendous sizes while retaining volant abilities.

4.2 Pterosaur masses and body proportions

A comparison between the masses of pterosaur body elements highlights the diversity of pterosaur anatomy, reflecting differences in relative wing length along with distinctions in development of skeletal components across different taxa. The relatively low masses of ornithocheiroids and *Rhamphorhynchus* correlate with higher aspect ratios: *Nyctosaurus* has the highest aspect of any pterosaur modelled here (22.92) with *Anhanguera* and *Pteranodon* essentially joint second (16.68 and 17.85, respectively). *Rhamphorhynchus* has the highest aspect of any basal pterosaur (11.753). High aspect ratios are indicative of long, narrow wings, and this observation is also borne out in the limb ratios of these animals, a relationship established through the incorporation of both fore- and hind-limbs into the flight membrane. Hence, it is unsurprising that the pterosaurs with the most disproportionate limb ratios (e.g. 5.7 in *Rhamphorhynchus*, 4.99 in *Anhanguera*) also have the highest aspect ratios, and these figures demonstrate that the lower masses of these pterosaurs are a consequence of having disproportionately long wings for their body size.

Conversely, *Dimorphodon* and *Dsungaripterus* have unusually high masses. BROWER & VEINUS (1981) also found *Dimorphodon* to be unusually heavy with an estimated mass almost three-times the value predicted by their regression analysis. The aberrant masses of these forms appear to reflect a relatively massive build for their wingspans, with the hindlimbs of both atypically robust and *Dimorphodon* also bearing an atypically weighty skull. Similarly, *Quetzalcoatlus* is also 111 kg greater than the relationship between mass and wingspan predicts, but several more factors affect this overestimate than those of *Dimorphodon* and *Dsungaripterus*. Chiefly, the sparse fossil record of giant azhdarchids suggests caution be exercised over any estimate of their mass: until more complete specimens are found, mass estimates of giant pterosaurs can only be derived by scaling up closely related smaller forms. However, on the assumption that the morphology of giant pterosaurs reflects that of their smaller brethren, the discrepancy between the predicated mass of a 10 m span azhdarchid and the actual figure is noteworthy. This result may be a consequence of the small number of large pterosaurs modelled in this study: the average wingspan from the 20 pterosaurs modelled here is 2.3 m, casting some uncertainty over the relationship between wingspan and mass in taxa four times this dimension. Of further significance is that the next largest pterosaurs in this study are all ornithocheiroids: the disproportionately elongate wings and small bodies of these forms generate relatively low masses for their wingspans and contrast with the robust build of azhdarchids. Azhdarchids combine long necks, elongate hindlimbs and large bodies with short wings and subsequently have relatively

high masses for their wingspans. This is demonstrated well by the mass of the 2.9 m span *Zhejiangopterus* compared to the 4 m span *Anhanguera*: despite having a wingpan 28 per cent larger than *Zhejiangopterus*, *Anhanguera* only masses 23 per cent greater when the relationship between wingspan and mass predicts a mass increase of 126 per cent. These distinctions in form tell a cautionary tale about regressing masses of giant pterosaurs from datasets of smaller forms or those with disparate anatomy (e.g. BROWER & VEINUS 1981).

4.3 Wing shape

Despite the uniform application of an ankle-based brachiopatagia in this investigation, a broad suite of aspect ratios were found across pterosaur taxa in this study with a range of 16.32. This compares relatively well with the aspect range of 15 found by BROWER & VEINUS (1981) but is much greater than the 10.14 of CHATTERJEE & TEMPLIN (2004) and 10.3 of HAZLEHURST & RAYNER (1992; note that this and subsequent discussion of the wing shape used by these authors refers to the broad wing model of these authors for greater comparability with the wing morphology used in this study). The aspect range produced here achieves values comparable with the highest aspects of other authors (even those using pelvis or knee-based attachment sites for the brachiopatagium: see BROWER & VEINUS 1981; CHATTERJEE & TEMPLIN 2004) and the lowest aspect wings modelled by HAZLEHURST & RAYNER (1992). This range makes the pterosaur aspects of this study far more comparable to the aspect range of modern birds, which range from 4.5–18 (e.g. SAVILLE 1957) and contrasts with the relatively limited planforms of other investigations. Recently, DYKE et al. (2006) suggested that differences in limb disparity between different pterosaurs may reflect differential attachment of the brachiopatagium, but the diversity of wing shape produced here with a standardised brachiopatagium demonstrates that skeletal proportions alone can account for tremendous diversity in planform without the need for distinct brachiopatagial configurations. The plasticity of form in pterosaur brachiopatagia may explain why ankle-attached wings appear to be consistent across the phylogenetically diverse range of pterosaur specimens showing well-preserved brachiopatagia.

Assessment of wing shape in this study reveals that basal pterosaurs generally have lower aspect ratios than those of pterodactyloids, but the differences in uropatagial morphology in these forms has little overall effect on aspect. Removal of the uropatagia in *Rhamphorhynchus* and *Preondactylus*, forms with the highest and lowest aspects of all basal pterosaurs, only raises the aspect by 0.5 and 0.65, respectively. Rather, attributes such as hindlimb length and extendibility of forearm bones are far more important in wing shape: with their relatively restricted wing metacarpal extension, basal pterosaurs project the distal wing tips posteriorly to form lower aspect, broader chord wings than pterodactyloids. Conversely, greater extension of the wing metacarpal in pterodactyloids produces a wing with greater lateral projection and increased tapering towards the wing tip. This condition is most developed in pteranodontians with the additional 10° extension in the wing finger that produces higher aspect wings than any other pterosaurs. The disproportionately short hindlimbs and torsos of

these forms reduce the depth of the wing and exaggerate this condition further.

4.4 Implications of higher masses and ankleattached brachiopatagia on pterosaur flight

The higher masses suggested in this study have several consequences for our understanding of pterosaur flight. Increasing mass exponentially heightens induced flight power requirements and minimum flight speeds (NORBERG 1995), the effects of which would be experienced most during takeoff. The launch capabilities of pterosaurs have been said to be limited by peculiarities of pterosaur anatomy or reliant on headwinds and topography (e.g. BRAMWELL & WHITFIELD 1974; STEIN 1975; CHATTERJEE & TEMPLIN 2004), but note that many of these studies assumed pterosaurs had very limited terrestrial abilities. Recent reappraisals of pterosaur terrestrial locomotion (e.g. MAZIN et al. 2003) suggests they had adept terrestrial capabilities that would lend themselves well to assisting takeoff, providing strong propulsive forces for stationary launches or permitting running to aid reaching minimum flight speeds. It is unlikely that basal pterosaurs were as proficient at terrestrial locomotion as pterodactyloids however, and their comparatively limited sizes may reflect selective pressures to minimise launch costs.

The range of masses and aspect ratios modelled here suggest a broader array of flight styles among pterosaurs than previously modelled. Modern volant forms demonstrate that wing loading and aspect ratios correlate directly with flight style and ecology (e.g. NORBERG & RAYNER 1987; RAYNER 1988), and principle component analysis of these attributes in birds and bats can compare and categorise flight styles independently of mass (see NORBERG & RAYNER 1987; RAYNER 1988 and HAZLEHURST & RAYNER 1992 for methodological details). This method has been used to assess the flight characteristics of lightweight pterosaurs (HAZLEHURST & RAYNER 1992) and corroborated the long held view that almost all pterosaurs were marine soarers, best suited to gently gliding long distances through exploitation of updrafts, thermals and wind currents (e.g. HANKIN & WATSON 1914; HEPTONSTALL 1971; BRAMWELL 1971; BRAMWELL & WHITFIELD 1974; STEIN 1975; BROWER & VEINUS 1981; BROWER 1983; HAZLEHURST & RAYNER 1992; CHATTERJEE & TEMPLIN 2004). Plotting the loading and aspect ratios of other datasets dealing with pterosaur flight into the principal component analysis of HAZLEHURST & RAYNER (1992) also shows support for this conclusion: the pterosaurs of BROWER & VEINUS (1981), HAZLEHURST & RAYNER (1992) and CHATTERJEE & TEMPLIN (2004) plot almost exclusively on the margins of the ‘marine soarer/aerial predator’ adaptive zones (Fig. 6). However, this limited ecology contrasts with the diversity of pterosaur anatomy: it is unlikely that the short-winged, massively skulled and heavyset *Dimorphodon* flew and foraged in the same manner as a long winged, pincer-jawed ornithochirid, for example. Applying the greater range of wing areas and body masses of pterosaurs calculated in this study into the same principal component analysis suggests a much broader spectrum of flight characteristics than previously anticipated and, most notably, the pterosaurs modelled in this study plot within the same ecomorphospace as that occupied by birds

and bats. This contrasts with the datasets of lightweight, narrow-winged pterosaurs of other studies that typically plot around the lowest-loading margins of the bird and bat adaptive zones (Fig. 6). Furthermore, few pterosaurs in this study were found to be strongly shorebird-like and none demonstrated wing ecomorphology comparable with that of frigate birds. As with previous studies, however, no pterosaurs were found to have flight characteristics comparable with diving birds or water birds.

Some caution should be applied to interpreting the precise placement of the pterosaur data within this model: the margins of error that accompany any mass or wing area estimates of this kind mean data plots are almost certainly somewhat imprecise, but broad conclusions regarding flight characteristics can be drawn. Azhdarchids and *Huanhepterus* have the low loading and aspects of modern static soarers (e.g. vultures, raptors, storks), a flight style that correlates with both their abundance in continental settings (e.g. LAWSON 1975; DONG 1982) and functional morphology (WITTON & NAISH, in review). Ornithocheiroids and *Rhamphorhynchus*, by contrast, have the moderate loading and high aspect wings of marine soarers, a lifestyle that conforms to the elongate, presumably

glide-efficient wing morphology of these pterosaurs. The two *Pteranodon* morphs modelled here plot in approximately the same region of the graph, albeit with the larger (wingspan 5.96 m) demonstrating slightly higher aspect than the smaller (wingspan 3.7 m). A continuum of other pterosaur taxa is seen between these forms, with forms such as *Pterodaustro* and particularly *Pterodactylus* approximating the position of wading charadriiformes and other shorebirds, a position that correlates well with the wading-adapted feet of these taxa (see WELLNHOFER 1970; SANCHEZ 1973 for examples of such foot morphology). The plotting of *Anurognathus* amongst fast, manoeuvrable fliers such as Hirundinidae, Apodiformes and Falconiformes is also intriguing in light of the reported adaptations of anurognathids to aerial insectivory (e.g. WELLNHOFER 1991a; BENNETT 2003b, 2007a). Several pterosaur taxa, including three basal forms and several derived pterodactyloids, show ‘average’ wing loading and aspects that correlate with strong, albeit unspecialised fliers in modern birds (RAYNER 1988). The plotting of numerous, chronologically disparate pterosaurs in this cluster suggests that this niche remained important throughout pterosaur evolution. The presence of forms like *Preondactylus* and *Eudimorphodon* in this group

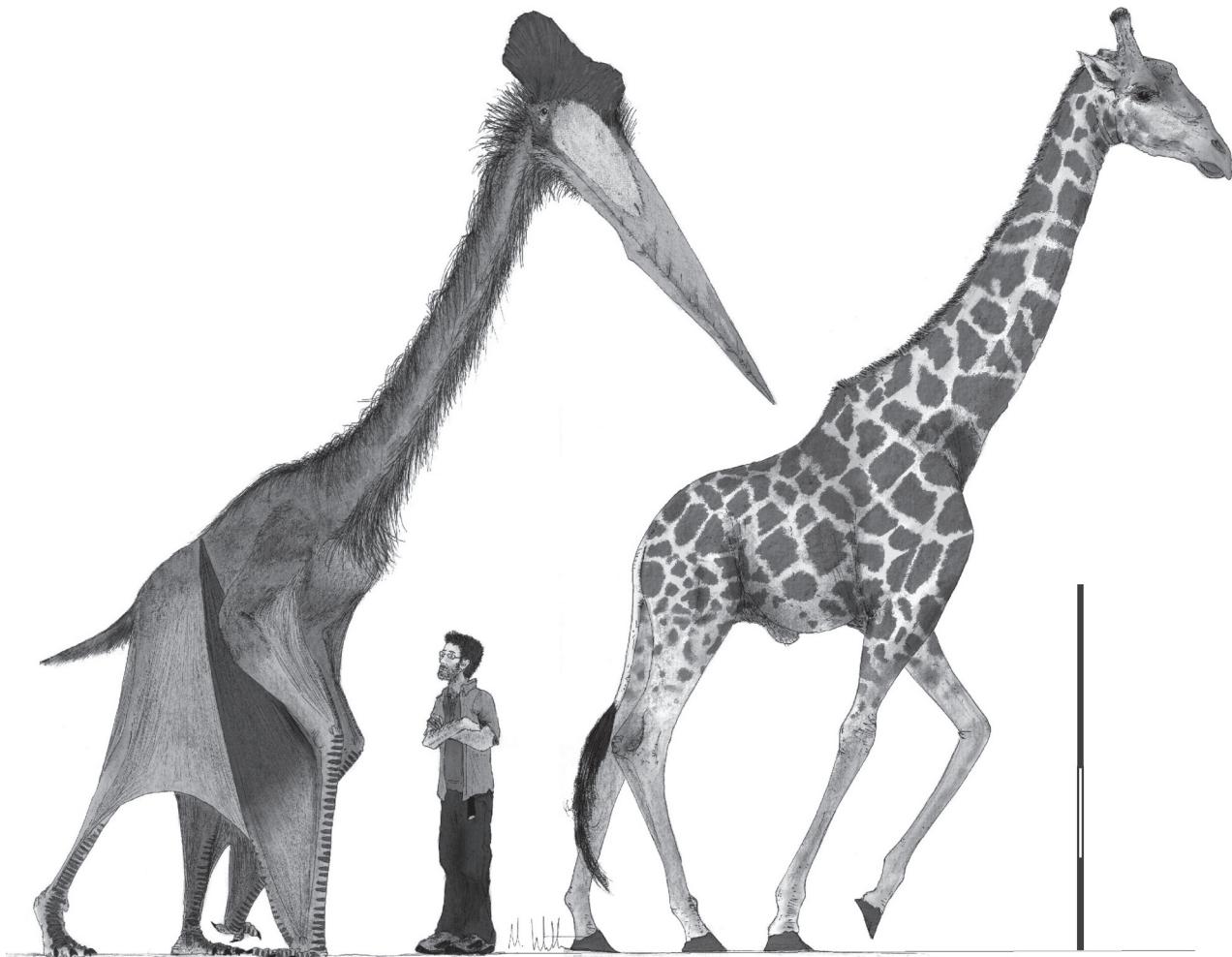


Figure 5: Comparative sizes of *Quetzalcoatlus northropi* (2.5 m tall at shoulder; 250 kg estimated mass); the author (1.75 m total height, 65 kg measured mass) and *Giraffa camelopardalis* (2.75 m tall at shoulder; measured mass 636–1395 kg). Scale bar represents 2 m.

suggests that early pterosaurs were less specialised fliers than later forms, with the development of specialist static- and dynamically-soaring forms occurring later. The plotting of *Dimorphodon* among birds which have atypically high flight costs such as rails, pheasants and tinamous, or fly in high-energy bursts of limited duration (woodpeckers, jacanas), provides an alternative view of pterosaur flight and raises the possibility that not all pterosaurs were adept, high performance fliers. The strong hindlimbs and manus of *Dimorphodon* (e.g. Padian 1983; Unwin 1988) may correlate with its apparent poor flight performance may reflect a more arboreal or terrestrial lifestyle than other pterosaurs. *Dimorphodon* may have been a relatively

reluctant flier that only utilised flight for travelling quickly over short distances or for evading predators.

5. Conclusions

Analyses of pterosaur mass have suffered from a rather blinkered approach to methodology and achieved a subsequently narrow set of conclusions. It appears that anecdotal figures of pterosaur mass were transcribed to quantitative estimates without consideration for the grounding of such results: little attention appears to have been given to the often

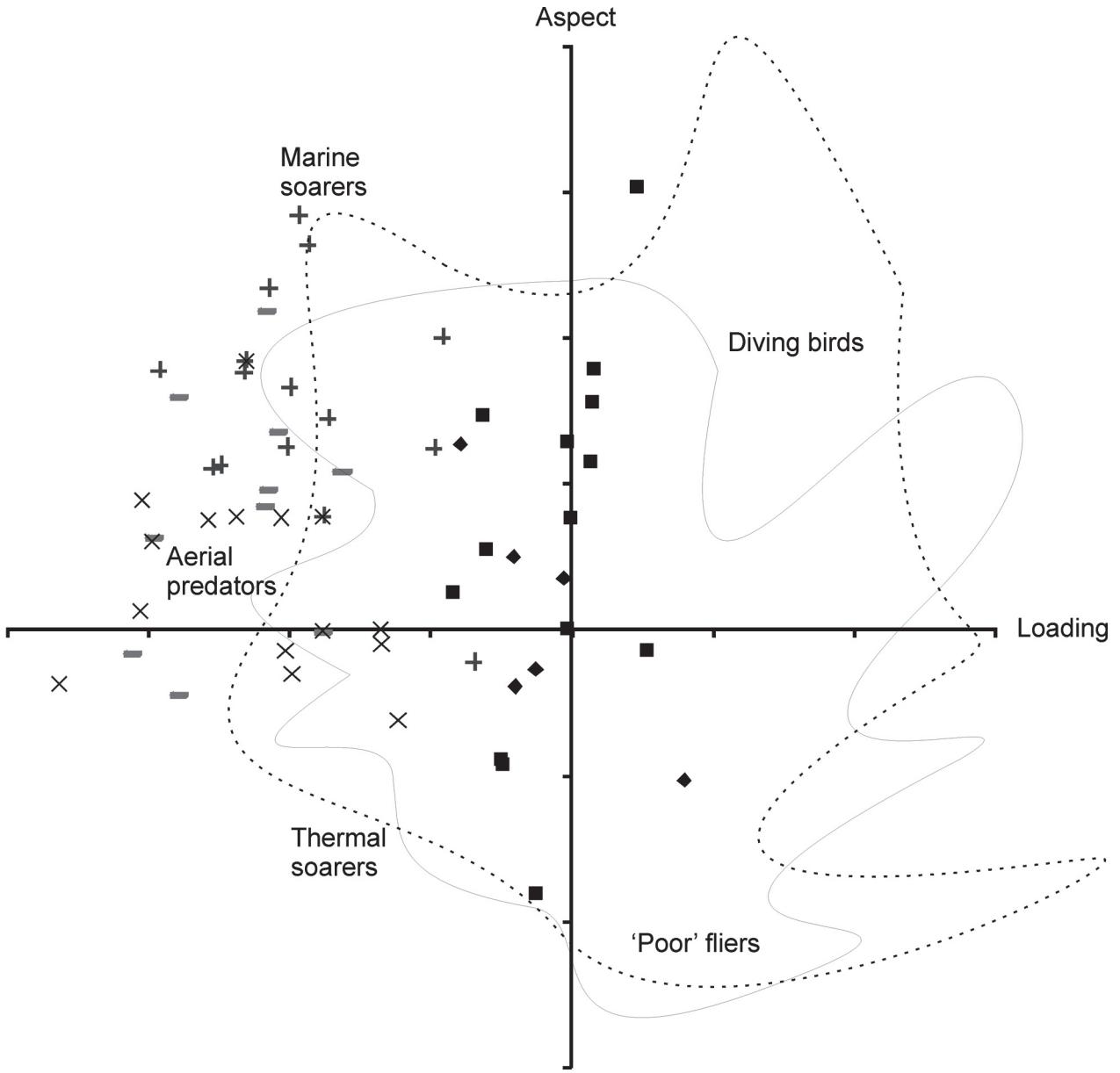


Figure 6: Comparative principal component analysis of wing loading (Q2 of Tab. 4) to aspect ratio (Q3) of pterosaur wings. Closed squares, pterodactyloids (this study); closed diamonds, basal pterosaurs (this study); crosses, wing data from Brower & Veinus (1981); oblique crosses, wing data from Hazlehurst & Rayner (1992); horizontal lines, wing data from Chatterjee & Templin (2004). Dotted lines indicate ecomorphospaces of modern volant vertebrates. Heavy dashed line, bat wing ecomorphospace (after Norberg & Rayner 1987); light dashed line, bird wing ecomorphospace (after Rayner 1988). Bird flight style labels taken & Rayner (1988) and Hazlehurst & Rayner (1992). See Norberg & Rayner (1987), Rayner (1988) and Hazlehurst & Rayner (1992) for further details on methodology.

gigantic proportions of the animals involved, the discrepancy of estimated masses with modern volant forms or the degree of pneumaticity required to meet some mass estimations. The work performed here demonstrates the need for alternative methodologies to test the results of others and highlight potential flaws in methods and conclusions, in this case being the unfeasibly low mass estimations of pterosaurs. However, the geometric technique used here to restore pterosaur skeletal and body mass is a relatively crude approach to what could, if developed further, be a useful tool for estimating the mass of all extinct vertebrates. Being largely comprised of tubular bones, pterosaur skeletons lend themselves well to the relatively simple geometric method used here, but digitisation of skeletons and an increased understanding of bone histology could provide far greater accuracy of skeletal masses than the methods used here and allow for truly complex bone shapes to be modelled accurately. CAT scanning of complete, undistorted fossils may provide the most accurate means through which to do this.

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Postscript

Recent work by BENNETT (2007b) suggests that medially-directed pteroids have greater anatomical support than the anteromedially-directed pteroids employed, but this work was brought to the author's attention too late for appropriate changes to the study and manuscript to be made. However, note that a medially-directed pteroid has only a slight impact on overall wing area, decreasing the estimated planform areas of *Rhamphorhynchus*, *Pteranodon*, *Dsungaripterus* and *Quetzalcoatlus* by 3, 9, 6 and 2 per cent, accordingly. These changes do not have a significant impact on the conclusions drawn about pterosaur wing ecomorphology, but aspect ratios and wing loading will be marginally greater than stated with this wing configuration.

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