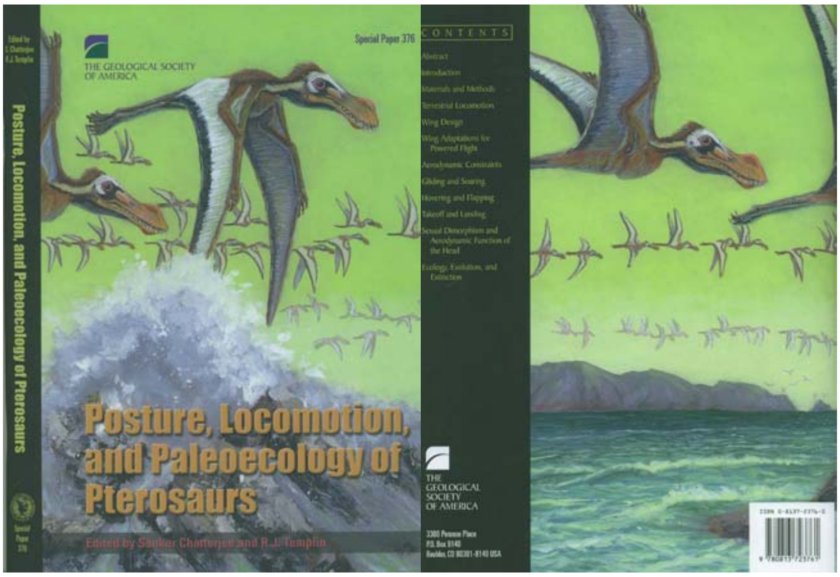
Chatterjee, S. & R.J. Templin. 2004. Posture, locomotion, and paleoecology of pterosaurs. – Boulder, Geological Society of America (Special Paper 376)

Book review by H.J.M. Meijer



S. Chatterjee, Paul Whitfield Horn Professor of Geology at Texas Tech University, and R.J. Templin, retired head of the Canadian National Research Council's Aerodynamics Laboratory, have joined their forces in 'Posture, locomotion and paleoecology of pterosaurs'. Pterosaur fossils have been found for more than 200 years, but very little is known about their locomotion, posture and palaeobiology. In this paper, the authors investigate the posture, locomotion and palaeobiology of pterosaurs based on anatomy, biomechanics and aeronautical engineering. For their investigations, ten genera of pterosaurs were taken representing 160 million years of pterosaur evolution.

The first chapter of this paper focuses on terrestrial locomotion. The posture and gait of pterosaurs is highly debated; traditional reconstructions infer a quadruple gait as several trackways found suggest that both the manus and pes are used in terrestrial locomotion. An alternative view is the theropod model, assuming that pterosaurs were bipedal cursors like theropods and birds. The authors explore both models with a three dimensional cast of *Anhanguera*; inferences of the experimental range in joint motion suggest that both models are partially correct: pterosaurs used quadrupedal locomotion during slow walking, whereas they used bipedal locomotion for take off and landing. However, experimental joint motion does not necessary reflect the actual motion of the joints *in vivo* as joints have ligaments, tendons and several layers of connective tissue that prevents them from dislocating. The presence of such structures limits the joint's range of motion as inferred from the skeletal elements by the authors and will change their model of pterosaur locomotion. The authors do not mention whether or not this has been incorporated in their analysis. A stick diagram is used to show the bipedal and quadrupedal poses in *Anhanguera*. As *Anhanguera* is a medium-sized pterosaur, it would have been interesting to see how the stick diagrams for quadrupedal and bipedal locomotion would have looked like for smaller and larger pterosaurs. Especially large species like *Quetzalcoatlus* have a very large wing to fold back; what are the effects of wing size on quadrupedal walking abilities?

The next series of chapters are preparatory for the aerodynamic analysis in that they discuss the anatomical adaptations and constraints of the wings for flight. Concerning wing design, a morphological comparison is made with bat and bird wings and clearly points out the similarities and differences between these flying vertebrates. Based on wing planform, the authors make a distinction between the 'rhamphorynchoids'; pterosaurs with the wing membrane attached to the ankle, and 'pterodactyloids'; with their wing membranes attached at the knee. In both types of pterosaurs, the wing membranes are stiffened by actinofibrils. Not only do these actinofibrils maintain the membrane's camber, but they might also help in folding the wing. Pterosaur wing morphology and its aerodynamic performance are discussed in comparison to the wing morphology of seabirds, showing a good example of convergent evolution. In the next chapter, 'Wing adaptations for powered flight', the authors discuss the adaptations for powered flight found in pterosaurs. Although the authors give an elaborate analysis of the shoulder and wing kinetics, again no mention is made on the possible effects of the ligaments, tendons and fascia on the range of joint motion.

In the chapter 'Aerodynamic constraints' Chatterjee & Templin use the previously discussed anatomical features to come to an analysis an aerodynamic performance for the selected species. Although I think that such an integration of palaeontology and biomechanics is badly needed, the mathematical illustration of the aerodynamic analysis on pages 34–38 should have been placed within an appendix. Putting it into the text does not improve the readability of the paper, as not all palaeontologists are equally skilled in biomechanics. However, as this chapter shows that combining palaeontological information with biomechanics provides us with new and very useful insights, some points of criticism can be raised. For instance, the difference in wing planform between rhamphorhynchoids and pteranodontids that is not incorporated in the analysis will have had an effect on their flight performance. The chapters 'Gliding and soaring' and 'Hovering and flapping' continue within this biomechanical framework when considering the different modes of flying that require different adaptations to the anatomical apparatus. The same holds for 'Takeoff and landing', although it seems that the authors have been making too many (but sometimes unavoidable) assumptions in this chapter. For the estimation of maximal anaerobic power output, data on muscle physiology are used from birds and humans. Between these two groups of warm-blooded vertebrates, this ratio already differs by a factor 2 (birds 2–2.5, humans 5). There is no evidence to assume that pterosaurs muscles are anything like avian or human muscles; it is even highly likely that pterosaur muscles were very different (for instance, air oxygen saturation was higher during certain periods in the Mesozoic). Therefore, this estimation should be considered as a provisional one. In addition, it is assumed that the legs play a role in takeoff and landing by the use of an elastic tendon that lies at the back of the lower leg and ankle. The generation and release of such elastic energy is dependent on the contraction of the muscle attached to the elastic tendon. The authors do not mention whether evidence (muscle scars, processes, etc.) for such a muscle has been found. Another worrying thing is the slender built of the legs in most pterosaur; it would have been interesting to see if the legs are able to resist to the large impacts involved during landing and takeoff.

After this extensive and detailed section on aerodynamic performance, the authors continue with a discussion on cranial morphology. The title on page 53 ('Sexual dimorphism and aerodynamic function of the crest') suggests an aerodynamic analysis of the head, the cranial crest in particular, in relation to flight performance, similar to the analyses in the previous chapter. Unfortunately, only one single sentence is written (p. 54, second column) on the possible increased horizontal drag due to a downward tilt of the head in *Anhanguera*, in addition to some assumptions about the involvement of the head in aerial turning. The cranial crest displays a wide variety in size and shape; sexual dimorphism is a very likely explanation for this diversity. The presence of such a (large) cranial crest changes the outline of the body significantly. Differences in aerodynamic performance in relation to size and shape of the cranial crest are to be expected. For instance, what is the relation between crest size and L/D ratio? Is flight performance related to the position of the crest on the skull (anteriorly or posteriorly located?). How does crest location relate to the different types of flight in pterosaurs (*e.g.* gliding or hovering)? This section would have been the perfect opportunity to explore these questions, but unfortunately the authors do not pay any attention to this.

The final chapter of the book, 'Ecology, evolution and extinction', reviews and summarises some theories and general ideas on pterosaur evolution and palaeobiology. However, no new ideas are presented here and therefore, this chapter would have been more appropriate as an introductory chapter to this quite specific article on pterosaur locomotion.

In conclusion, this paper provides a detailed and in-depth biomechanical and aerodynamic analysis of pterosaur locomotion, both terrestrial and aerial. Chatterjee & Templin certainly deserve credit for this. Although some features were not included in the analysis, it shows us that applying biomechanics to fossils can be a very interesting and rewarding thing to do as it answers several questions. However, it raises many more at the same time. The information obtainable from fossils is limited and because of this lack of sometimes-vital information of the in vivo situation, erroneous assumptions are easily made. Biomechanics is a great tool to study animal locomotion, but certainly in combination with fossils, we must be cautious not to overestimate the value of the model.

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