Historical Biology: An International Journal of Paleobiology
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/ghbi20


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Published online: 06 Mar 2014.


To link to this article: http://dx.doi.org/10.1080/08912963.2014.882099

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BOOK REVIEW


Mark Witton’s Pterosaurs is an enormous, lavishly illustrated encyclopaedia of all things pterosaur. Scholarly but highly readable, fully referenced throughout, and featuring hundreds of excellent photos, diagrams and beautiful, colour life restorations, this volume is a must-own, whatever your interest in pterosaurs. And there are not that many books devoted to pterosaurs to begin with, so another one on the market can only be good. The volume is properly titled Pterosaurs: Natural History, Evolution, Anatomy. However, this title does not appear anywhere on the cover (or spine).

Pterosaurs is a large book, featuring 26 chapters spread over more than 280 pages. Early chapters review the history of our ideas about pterosaurs, the evolutionary relationships and origin of the group, and what we know of pterosaur anatomy (bony and soft).

Many issues covered here remain controversial. The consensus opinion supported by the majority of recent phylogenetic studies is that pterosaurs are crown-archosaurs, close to dinosaurs (note that the clade Ornithodira exists no matter where pterosaurs fall within Diapsida) (Sereno 1991; Benton 1999; Brusatte et al. 2010; Nesbitt 2011). This is the idea that Witton favours, which is fair enough since there are unpublished studies showing that the crown-archosaur hypothesis is supported even when oddball taxa considered close to pterosaurs by some (Peters 2000) are included in the analysis too. Nevertheless, the crown-archosaur idea does look odd given that we lack taxa that appear in any way transitional between pterosaurs and other ornithodirans (Faxinalipterus minima – published in 2010 as a possible sister-taxon to the rest of Pterosauria – is not a pterosaur, nor obviously close to pterosaurs at all (Soares et al. 2013)).

Witton follows the honourable tradition of inventing hypothetical proto-pterosaurs that bridge the gap between Scleromochlus-like ornithodirans and known, early pterosaurs. I am not entirely sold on his use of the innovative term HyPtA (meaning Hypothetical Pterosaur Ancestor) for these creatures – the acronym is not exactly sexy – but his invention of the creatures themselves is not all that bad: invoking an anatomy and lifestyle for an ancestral organism involves the formulation of a set of hypotheses that will be supported or knocked down by future finds.

And there are other proto-pterosaurs out there in the literature, just as there are proto-birds and proto-bats.

Chapter 6 – ‘Flying reptiles’ – summarises current thinking on pterosaur aerodynamics and launch behaviour, one of Witton’s most interesting contentions being that pterosaurs have consistently been made too lightweight by previous authors. This has some impact on wing loading and hence flight style. As is familiar to pterosaur workers, Witton’s revised mass estimates and wing loadings make pterosaurs more comparable to the birds that they otherwise resemble in planform (Witton 2008; Witton and Naish 2008) – a satisfying picture that has been bolstered by conclusions from some other workers (but, of course, not all of them; this is pterosaur science we are talking about).

More innovative is Chapter 7 (‘Down from the skies’), devoted to terrestrial locomotion. Witton’s pterosaurs can bound, swim, climb and most of them walk with narrow gaits (though these generalisations do not apply across the whole of Pterosauria, of course). The pterosaurs of the prior literature have been imagined as inelegant sprawlers, slow, clumsy and lame on the ground, unable even to resist light gusts of wind (recall how the terrestrial locomotion depicted for the Walking With Dinosaurs ornithocheirids was based on shuffling people, walking on crutches) (Wellnhofer 1988; Unwin 1988, 1997, 2005).

In fact, data from trackways, pelvic and limb morphology, limb bone thickness and bending strength (Fastnacht 2005), and inferred hindlimb and forelimb posture (Fujisawa and Hutchinson 2012) indicate very strongly that pterodactyloid pterosaurs at least were far more proficient on the ground than people have previously given them credit for. Witton weaves all these lines of evidence together in a compelling narrative and can be said to be leading a revolution on the terrestrial abilities of pterosaurs. I agree with him: it now seems that pterodactyloids were proficient and agile on the ground, though non-pterodactyloids likely were not.

Readers may also be surprised to see several Witton illustrations that show pterosaurs swimming and even diving. Some trackways seemingly show that some pterosaurs foraged in shallow water, their bodies afloat and their long forelimbs being used as punting tools. Given the aquatic habits of many pterosaur species, it is hard to believe that they were incapable of at least some aquatic behaviour: despite claims made here and there about pterosaurs being too pneumatic to swim or dive, or with a wing form or body shape that would prevent swimming or
diving, there are no obvious or compelling reasons disallowing such behaviour, and Witton proposes that taxa like _Pteranodon_ might routinely have floated and dived.

Yes, there are frigatebirds (which _can_ swim, if they really have to, but generally avoid doing so), but hardly any pterosaurs are as specialised for a dedicated aerial existence as they are (nyctosaurids are the probable exception). Hone and Henderson (2013) have since used digitally simulated floating models to test the floating abilities of pterosaurs.

Chapter 8 – ‘The private lives of pterosaurs’ – reviews several areas that will be unfamiliar to the majority of non-specialists: what do we know about pterosaur prey items, pathology, parasites, sex lives and growth strategies? The honest answer is ‘not much’, but we know enough to at least give us an insight into all of these areas. As is the case throughout the book, diagrams and life reconstructions depict the key evidence or show re-enactments of things that really must have happened.

The meat and proverbial potatoes of the book are formed by reviews of all pterosaurian groups. Each group (each ‘family’, if you like) gets its own chapter. Once upon a time, popular books would have given you the impression that pterosaur diversity consisted of _Dimorphodon_, _Rhamphorhynchus_, _Pterodactylus_ and _Pteranodon_ and not much else. But things have boomed in recent decades, such that the chapters here on wukongopterids, boreopterids, lonchodectids, chaoyangopterids, thalassodromids, and not much else. But things have boomed in recent decades, such that the chapters here on wukongopterids, boreopterids, lonchodectids, chaoyangopterids, thalassodromids, and others will be wholly novel to some readers.

On that note, it is well known that views on the phylogeny, systematics and nomenclature of pterosaurs vary quite considerably from one study to the next (though note that members of particular research communities do tend to converge on similar results). Witton notes this and the arrangement he favours – in general, it is the phylogenetic scheme recovered by Lü et al. (2010) – is of course not the one favoured by all pterosaur experts. But when you are doing a book you have to come up with an arrangement of some sort.

Anyway, each of these chapters introduces us to the group in question, reviews and discusses what we know of its anatomy, discusses the probable flight and grounded, terrestrial behaviour of the group’s members and, finally, provides an overview of palaeoecology. The last chapter – the discussion of palaeoecology – is one of the most novel within the book. Tradition and convention would have it that pterosaurs flew over the surface of the sea and caught fish, or flew close to watery places and caught dragonflies and other flying insects. Admittedly, this ‘samey’ view of pterosaurs was challenged by the idea that dsungaripterids might have eaten shelled molluscs (Wellnhofer 1991) and that tapejarids were perhaps frugivorous (Wellnhofer and Kellner 1991). But, otherwise, the overwhelming impression has always been that pterosaurs caught fish or insects while flying on the wing.

In fact, details present across the pterosaur skeleton show, Witton argues, that all those different pterosaur groups were doing different things – sometimes subtly different, sometimes strikingly different. As an example, let us briefly consider the long-snouted, long-winged ornithocheirid-type pterosaurs (istiocactusids, boreopterids, ornithocheirids, nyctosaurids and pteranodontids), virtually all of which possess proportionally small, relatively weakly muscled hindlimbs. These pterosaurs all look more or less alike, and, yes, the general view has been that they pretty much all did the same thing – they _flew over the surface of the sea and grabbed fish_.

But when all of their anatomical nuances, proportional differences and so on are examined, a case can be made that we are, in fact, seeing groups of species that, even within this one group, perhaps did such diverse things as scavenge from vertebrate carcasses in terrestrial environments, grab fish from the sea surface, float or swim and ‘cage’ mouthfuls of small, planktonic prey, float and make short surface dives, and live a frigatebird-like life that really does involve flying over the water surface and grabbing fish.

In short, Witton’s view of pterosaurs is exciting and refreshing in its diversity, complexity and plausibility. Think of modern animal groups, whether they be gulls, seals or anoles: anatomical differences reflect different feeding and foraging strategies, nuances and niche-specific behaviours are everywhere, and no two species are ever really alike. This sort of thing was surely true of extinct animals – I am _sure_ it was, we all are. But this is the first time that we have seen this many ideas on pterosaur behaviour and lifestyle.

I personally think that more ideas of this sort are needed – so long as, that is, that they are internally logical, incorporate data from all available lines of evidence and appear grounded in a good understanding of biomechanics, ecology and the anatomy, behaviour, diversity and functional morphology of living animals. As should be obvious from the fact that I co-author with him (Witton and Naish 2008, 2013), I think that Mark is very good at this sort of thing (certainly better than those palaeontologists who take just one or two features and concoct an unrealistic and unlikely behavioural hypothesis) and I generally find myself agreeing with his conclusions and hypotheses.

However, it is important to note that, at the moment, many of the ideas that Witton discusses and explores are, indeed, just ideas: typically proposed here for the first time ever, they now require investigation using rigorous, quantitative techniques. But you have to start somewhere. Mark knows this and his hypotheses should serve as an inspiration for future studies.

If there is anything that becomes a take home with regard to this book, it is that pterosaurs are more diverse in anatomy and proportions that has been made obvious
before. Without naming names, the general impression created by some pterosaur workers is that pterosaurs are basically all alike, only with different skulls. As is made clear, not only through the text, but also thanks to those standardised reconstructions, pterosaurs actually exhibit notable and significant differences in the length and form of the neck, in wing length, in hindlimb size and in, well, everything, really.

The pace of pterosaur research means that, needless to say, many new things have appeared since *Pterosaurs* appeared. There are quite a few new, recently named taxa that would have warranted discussion or mention including the *Tupuxuara*-like azhdarchoid *Caupedactylus*, the small azhdarchid *Vectidraco*, the Patagonian azhdarchid *Aerotitan* and a raft of new Cambridge Greensand taxa. Witton’s scepticism about the alleged azhdarchoid identity of *Aurorazhdarcho* (he has it wrongly spelt *Aurozhdarcho* [sic]) has since been confirmed by Bennett’s (2013) paper on *Pterodactylus* and *Ardeadactylus*, and then there is the whole awkward situation involving *Lonchodraco* and Lonchodraconidae. New studies on pterodactyloid limb posture have appeared (Fuijiwara and Hutchinson 2012; Costa et al. 2013), and so on.

Overall, the style of the text is friendly and conversational, even witty and vernacular. There are definitely places where I feel that it needed to be a bit tighter though, and I get the impression that better copy-editing was needed. On other negative points, one or two of the illustrations look a bit rushed (I do not much like the theropod on p. 102) and I am not sure that the curly lines used in a few of the diagrams (Figures 7.8 and 9.2) – they look like something out of a Tim Burton movie – fit with the rest of the book. However, these are exceptions in an otherwise glorious tour-de-force.

As if it is not clear enough from what I have already said, Witton’s *Pterosaurs* is a remarkable visual feast, packed full of novel art as well as excellent photographs that the author clearly worked hard to obtain. There are, in fact, illustrations of some sort on virtually every single page – you will never get bored of looking at this book. A major Wittonian innovation is the invention of a consistent pose for pterosaurian reconstructions (both skeletons and life restorations). Reminiscent of Greg Paul’s lateral-view dinosaurs, they make it easy to compare and contrast the many taxa Witton illustrates. And look out for the nods and references to *Batman Begins*, the arthropod-filled gorges of Skull Island, and what, exactly, is that marking on the lonchodectid’s wing?

If you like or are even vaguely interested in pterosaurs, you really need this book. I dearly hope that it inspires others to produce similar, spectacularly well-illustrated volumes on other tetrapod groups.

References


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