New perspectives on pterosaur palaeobiology

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Abstract: Pterosaurs were the first vertebrates to evolve powered flight and occupied the skies of the Mesozoic for 160 million years. They occurred on every continent, evolved their incredible proportions and anatomy into well over 100 species, and included the largest flying animals of all time among their ranks. Pterosaurs are undergoing a long-running scientific renaissance that has seen elevated interest from a new generation of palaeontologists, contributions from scientists working all over the world and major advances in our understanding of their palaeobiology. They have especially benefited from the application of new investigative techniques applied to historical specimens and the discovery of new material, including detailed insights into their fragile skeletons and their soft tissue anatomy. Many aspects of pterosaur science remain controversial, mainly due to the investigative challenges presented by their fragmentary, fragile fossils and notoriously patchy fossil record. With perseverance, these controversies are being resolved and our understanding of flying reptiles is increasing. This volume brings together a diverse set of papers on numerous aspects of the biology of these fascinating reptiles, including discussions of pterosaur ecology, flight, ontogeny, bony and soft tissue anatomy, distribution and evolution, as well as revisions of their taxonomy and relationships.

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Pterosaurs have one of the longest research histories of any extinct vertebrate group and have been studied by some of the most notable names in vertebrate palaeontology, including Georges Cuvier, William Buckland, Richard Owen, O.C. Marsh and Harry Govier Seeley (Wellnhofer 2008). It is widely known that pterosaurs were recognized as flying animals as early as 1801 (Cuvier 1801) thanks to material described by Collini (1784). However, earlier letters between researchers showed that pterosaurs were already in the minds of the scientists of the late 1700s (e.g. Hermann, see Taquet & Padian 2004) and recent works suggest other specimens were at least discovered, if not described, before 1784 (Ösi et al. 2010).

Aside from a notable hiatus in the mid-twentieth century, research into flying reptiles has advanced more or less continuously since their discovery. However, the last four decades have seen a great expansion in interest in pterosaurs from researchers, palaeoartists and laymen (Fig. 1). As evidence of this, the entire twentieth century saw the publication of only three major overviews of pterosaur science (Seeley 1901; Wellnhofer 1978, 1991) while the twenty-first century already has two (Unwin 2005; Witton 2013). Public interest is demonstrated by large exhibitions dedicated to these animals in London, Japan and the USA, as well as plans to construct a pterosaur museum in the Xinjiang Autonomous Region of China. Dedicated, multi-million pound television documentaries and increasingly prevalent roles in popular media are further evidence of pterosaurs occupying a more prominent position in the public’s consciousness.

Pterosaur researchers have typically attributed this interest to the ever-increasing number of pterosaur fossils being discovered, many occurring in Brazilian and Chinese Lagerstätten. It is certainly hard to overstate the impact and scientific excitement associated with these sites, especially considering their discovery within a few decades of each other. In rapid succession they led to the discovery of several major clades, numerous new species, novel details of skeletal and soft tissue anatomy, exquisitely preserved three-dimensional specimens and the first fossils of pterosaur eggs. Collectively, this produced a wealth of new information and helped resolve many longstanding questions about pterosaur biology, as well as prompting many new ones (Hone 2012).

The elevated discovery rates of new pterosaur specimens may have catalysed much of our renewed interest in this group, but it is continued study...
Fig. 1. Illustrations of the British Jurassic pterosaur *Dimorphodon macronyx* showing scientific developments through pterosaur research over two centuries. (a) Detail of a 1829 watercolour by Reverend G.E. Howman depicting *D. macronyx* as a monstrous ‘flying dragon found at Lyme Regis supposed to be noctivagous’ (Martill 2014). (b) An ungainly, bat-like reconstruction in the monograph of Owen (1870). (c) Harry Seeley’s progressive interpretation of *D. macronyx* as an erect-limbed quadruped from his 1901 book; note that an alternative interpretation of *D. macronyx* as a biped also appears in Seeley (1901); (d) The restoration of *D. macronyx* as a highly active, bird-like digitigrade biped by Padian (1983) – a controversial interpretation that nevertheless symbolises the reinvention of pterosaurs in the late twentieth century. (e) Modern interpretation of *D. macronyx* adult and speculative juveniles from the cover of this volume, reflecting contemporary interpretations of pterosaur soft tissues, muscle development and ecology. The flying juveniles reflect the long-awaited twenty-first century discovery of pterosaur embryos and their unexpected flight-ready anatomy.
and the insights provided by applying new palaeontological methods to them that is sustaining, if not increasing, their academic and popular appeal. Modern interest in pterosaurs has proved to be a self-perpetuating discipline within modern palaeontology rather than a scientific ‘fad’.

**International pterosaur symposia**

Recent pterosaur studies have been presented not only in books and research papers, but also in a series of pterosaur-themed volumes based on the now regular international meetings of pterosaur researchers. The meetings as they occur today evolved from a workshop of pterosaur researchers at the 55th Annual Meeting of the Society of Vertebrate Paleontology, held in Pittsburgh, Pennsylvania, USA in 1995 and have now expanded to a regular series with worldwide participation.

A second Society of Vertebrate Paleontology symposium was held in New York in 1996 (*Kellner et al.* 2013) and was followed by a gathering in Toulouse, France in the year 2000, the first meeting to result in an associated published collection of pterosaur papers (*Buffetaut & Mazin* 2003). Next was a small meeting in Bergamo, Italy (*Paganoni* 2003) and then Munich, Germany in 2007. The Munich meeting was the first to be called Flugsaurier, now a recurrent name for pterosaur symposia, and also produced an associated paper volume (*Hone & Buffetaut* 2008). Since then, pterosaur researchers have convened at Flugsaurier 2010 (Beijing, China), Flugsaurier 2012 and Flugsaurier 2015 (Rio de Janeiro, Brazil), resulting in a volume edited by *Kellner et al.* 2015. The most recent event, Flugsaurier 2015, held in Portsmouth, UK, resulted in the current volume.

Based on past successes and the promise of at least one more pterosaur meeting (scheduled for 2018 in Los Angeles, California, USA) it is clear that these congregations are a continued success. The seven meetings have seen more than 200 published abstracts and collectively gathered hundreds of researchers from six continents. The benefits of modern digital communications have doubtlessly increased modern palaeontological science, but they have not superseded the value of bringing together individuals to meet, exchange ideas and examine specimens.

**Proceedings of Flugsaurier 2015**

As is now traditional for pterosaur meetings, a series of papers pertaining to content delivered in posters and talks at Flugsaurier 2015 are presented in this volume, alongside a number of other pterosaur-focused studies. The topics of these papers are broad, with many bringing new specimens, or details of specimens, to light, while others touch on ongoing uncertainties, controversies and issues within pterosaur palaeobiology.

Although the pterosaur record has improved considerably in recent years, enormous gaps in our knowledge still remain. Thus the reports of several new pterosaur specimens in this volume are welcome additions to the literature. They include unpublished material of the giant, Late Cretaceous Jordanian azhdarchid *Arambourgiania philadelphiae*, perhaps even lost elements of the holotype, which are discussed by *Martill & Moser* (2017). Remains of another large, Late Cretaceous pterodactyloid are reported by *Bennett* (2017). This specimen, although fragmentary, is significant for representing a rare American Turonian pterosaur and allows a more complete understanding of pterosaur evolution around the Western Interior Seaway. *Rigal et al.* (2017) describe new pterodactyloid specimens from the British Wealden Group, a Lower Cretaceous unit of historical importance to pterosaur workers, but frustratingly limited with regard to new pterosaur material. Their work has a bearing on the status and content of the controversial clade Longchodeidae and includes the erection of a new genus. *McLain & Bakker* (2017) describe pterosaur material from the Late Jurassic Morrison Formation, which helps to elucidate the taxonomic content of this poorly understood pterosaur fauna. *Leal et al.* (2017) describe new cervical material from Brazil providing further suggestive evidence of chaoyangopterid pterosaurs outside of Chinese deposits. *Lü et al.* (2017) briefly describe a new anurognathid specimen from the Early Cretaceous of Liaoning, which may have a pedal grasping adaptation unlike any other pterosaur.

Pterosaur researchers also remain challenged by the poor documentation of existing discoveries. Such a topic is addressed by *Hone et al.* (2017) for the widely known, but poorly understood, Early Cretaceous Chinese pterosaur *Noripterus complicidens*. This species is represented by excellent material, but poor curation and relatively scant attention from pterosaur workers means that our concept of *Noripterus* requires re-evaluation.

A contentious aspect of pterosaur research is their systematics. Several competing interpretations of their phylogenetic relationships have been published in the last two decades (e.g. *Unwin* 2003; *Kellner* 2003; *Andres et al.* 2014) and much work remains to resolve related nomenclatural, taxonomic and phylogenetic disagreements. In this volume, *Vidovic & Martill* (2017) present a fourth distinct pterosaur phylogeny and challenge recent taxonomic interpretations of the Solnhofen pterodactyloids *Pterodactylus antiquus*, *P. kochi* and *Germanodactylus rhampolinus*. Evidently,
controversies over pterosaur systematics are set to run for some time yet.

Novel insights into pterosaur palaeobiology are reported in several papers. Bennett & Penkalski (2017) discuss unusual, banded growth patterns in the rostrum of the large Late Cretaceous, North American Pteranodon. It is sobering for researchers to consider that Pteranodon – undoubtedly one of the best studied and documented pterosaurs – is still the source of new and unexpected information on pterosaur anatomy. Codorniu et al. (2017) provide a full description of an embryonic specimen of the Cretaceous filter-feeding pterosaur Pterodaustro guinazui, providing one of the most comprehensive insights into pre-hatching pterosaur anatomy to date.

Welcome attempts to reconstruct functional anatomy are also provided. Frigot (2017) performs one of the first detailed assessments of pterodactyloid upper hindlimb myology using the exquisitely preserved holotype pelvis of the Cretaceous Wealden azhdarchoid Vectidraco daisy Morrissiae. Henderson (2017) presents one of the first quantified assessments of pterosaur bite force and skull mechanics using digital skull models, while Palmer (2017) reports the physical modelling of pterosaur wing membrane properties, providing valuable insights into wing anatomy and function.

This volume also provides discussions attempting to further understand pterosaur faunas and ecology. One means of understanding the role of flying reptiles in Mesozoic food webs is via fossils that preserve the gut contents, feeding traces or other evidence of ancient trophic interactions. These are reviewed by Witton (2017), revealing pterosaurs to be both consumers and consumed in Mesozoic ecosystems. O’Sullivan (2017) comments on the pterosaur assemblage of the Oxford Clay Formation from the UK and examines the status of the neglected taxon ‘Rhamphorhynchus jessoni’. Dalla Vecchia (2017) describes a wing metacarpal from the Late Cretaceous of Italy and discusses its implications for the changing picture of pterosaur diversity at the end of the Mesozoic. Unwin & Martill (2017) revise the identity of a Jurassic specimen from Thailand, which has been identified as azhdarchoid, but might be better considered to be rhamphorhynchid.

The unfamiliar nature of pterosaurs and their sparse fossil record render them a challenging group to understand. However, as demonstrated here, perseverance in the study of these flying reptiles rewards researchers with new insights and ideas about their evolution and palaeobiology. This volume represents only the latest thinking in a long history of pterosaur research: we look forward to the scientific discussion and increased understanding that these papers will inspire.

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