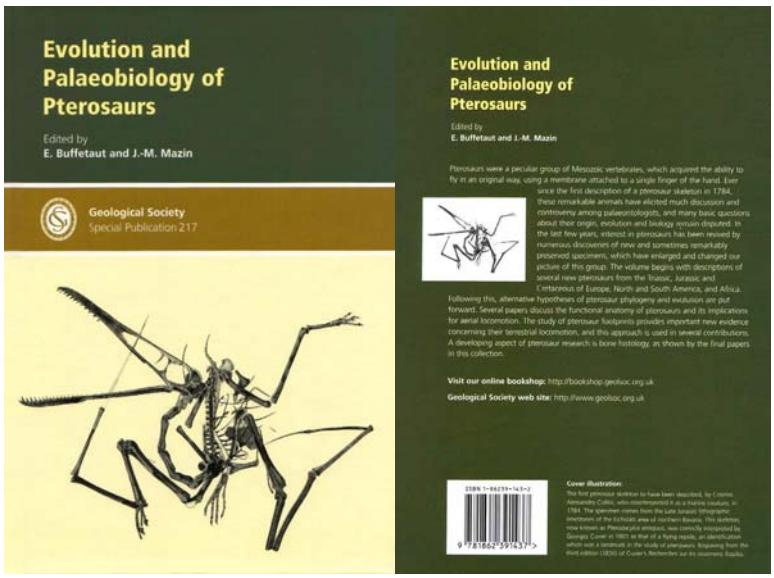
Buffetaut, E. & J.-M. Mazin. Eds. 2003. Evolution and palaeobiology of pterosaurs. - London, Geological Society (Special Publications 217)

Book review by A.J. Veldmeijer & M. Signore



One of the most mysterious prehistoric creatures are the pterosaurs. These contemporaries of the dinosaurs were the first vertebrates able to fly and their long evolution indicates their success. The fossil record however, is scanty and many of the known fossils are of poor quality. Due to the nature of the pterosaur skeleton (hollow, extremely thin walled bones), the skeletons do not easily fossilise and are easily crushed. The commercial trade in fossils often results in fraud and hasty preparation and reconstruction works. This practice also accounts for the lack of detailed information on their locality. Despite these problems, there are enough indications of the great variation, established by their adaptive abilities and lack of co-occurrence, making pterosaurs an important group of Mesozoic vertebrates.

Research on these animals started in 1784 with the description by Collini (who interpreted the animal as a marine creature) of the pterosaur on the cover. The book reviewed here presents the scientific papers of the symposium in Toulouse, France in 2001 (of which the abstracts have been published in 2001), named 'Two hundred years of pterosaurs. A symposium on the anatomy, evolution, palaeobiology and environments of Mesozoic flying reptiles'. The title is slightly confusing because the 'two hundred years' actually are, to be precise, 216 years. However, the editors refer to the 200-year-anniversary of the fact that Cuvier was the first to identify this fossil as a flying reptile (this was in 1801; he published the name Ptero-Dactyle in 1809). So, the study of pterosaurs is older than 200 years but the recognition of them as a flying reptiles is exactly 200 years old.

The book is a collection of individual papers of varying content. There are papers dealing with phylogenetic systematics, trackways, descriptions of new material and morphological studies. We will refrain from a too detailed discussion on the various problems surrounding (the study of) pterosaurs, also noticed in some of the papers and only touch these in passing.

Let us start with some general comments. It strikes us that few among the palaeontologists that contributed to this volume published various, and perhaps too many, papers. Besides this, some also have been reviewing other papers, thus putting a big mark on the publication. Some others do not refer to papers published in the same volume when they should, mentioning research done years before. In addition, some pictures, as a result, have been included twice. Notably, there are differences in the nomenclature of some animals (*e.g.* some conodont genera are listed with two different generic names in two different papers about the same geological setting), and the stratigraphic setting suffers of the same lack of editing as well. Surprisingly few papers are concerned with palaeobiology. Admittedly, few papers do include this topic, but, as is seen often with pterosaurs, they only concern flight. Terrestrial locomotion is discussed on the basis of trackways but not included are studies on the possible life these animals lived on land; almost no attention has been given to the hindlimbs. Particularly annoying are the many (editing) mistakes and incorrect references, among which the worst is the wrong running title (Alexander W.A. Kellner is referred to as A.W.A. Alexander in his chapter with John M. Moody on a scapulocoracoid from Venezuela). Most of the pictures are of high quality, although made according to different criteria (*e.g.* compare Unwin's phylogeny paper with Bennett's myology paper). However, there are

exceptions; especially the illustrations in the paper by Buffetaut, Grigorescu & Csiki on the giant azhdarchid pterosaur from Romania are of lesser quality. The drawings are faint and the pictures, cut out and inserted, give a non-professional impression. Some of the bones are not in their total length in the figure (figure 8, p. 101). Striking is that various works lean heavily on previous published papers. Instances are the chapter on the giant azhdarchid pterosaurs from western Romania by Buffetaut, Grigorescu & Csiki (the description of this material is an elaborate version of Buffetaut, Grigorescu & Csiki, 2002; nevertheless a diagnosis lacks in the systematic part), the phylogeny chapter of Kellner (a slightly extended version of his PhD thesis (Kellner, 1996) as remarked by the author) and parts of the paper 'New pterosaur specimens with soft parts' by Frey *et al.* have been published as well (Frey & Tischlinger, 2000). A final general remark is the lack of reference to (recent) papers, which is partly due to the publication timescale.

Interesting is the discussion about the Triassic pterosaurs. The two papers presenting new material are certainly intriguing; nonetheless, they add very little to the knowledge of Triassic pterosaurs. The paper by Wellnhofer ('A Late Triassic pterosaur from the Northern Calcareous Alps (Tyrol, Austria)') may be an interesting note on a new very fragmentary specimen of *Eudimorphodon*, but surely lacks any reference to palaeobiology or evolution (as suggested in the title of the book). Dalla Vecchia, on the other side, lists a lot of genera in his paper ('New morphological observations on Triassic pterosaurs') and the whole work is maybe among the most useful in the book, except that he seems to ignore the stratigraphy presented in the paper of Wellnhofer (which appears exactly before Dalla Vecchia in the volume). As remarked before, the lack of uniformity in the identification of both genera (*e.g* the same conodont genus is referred to as *Mockina* in Wellnhofer and *Epigondolella* in Dalla Vecchia) and stratigraphy of the Upper Triassic in the two papers confuse more than clarify the stratigraphic significance of the first pterosaur fossils. Moreover, Dalla Vecchia and Wellnhofer seem to be unaware of each other's contribution to the volume.

Carpenter *et al*. present a paper ('A new scaphognathine pterosaur from the Upper Jurassic Morrison Formation of Wyoming, USA') which adds very little to the knowledge of both evolution and palaeobiology of pterosaurs, by erecting a new genus on the basis of a fragmentary rostrum. To the paper they add the description of a mandible, which in one of the figures in the text is clearly assigned to another species as specified both in the text (p. 46) and in the figure 2 (f, g); but in figure 4 (p. 50) the reconstruction of the skull of *Harpactognathus* appears with a lower jaw, which is the one mentioned in figure 2 and marked as *not* belonging to this genus. A bit of confusion? Further specimens should be examined before assigning a partial rostrum to a new genus.

The paper 'A new crested ornithocheirid from the Lower Cretaceous of northeastern Brazil and the unusual death of an unusual pterosaur' by Frey *et al.* presents a new pterosaur. This pterosaur, *Ludodactylus sibbicki,* has a Pteranodon-like crest at its skull; a feature not seen before in pterosaurs form the Araripe Basin. We only mention the most important points of discussion; a more detailed discussion on the many problems surrounding the toothed pterosaurs from Brazil is in preparation. A diagnosis of a fossil should only list the diagnostic features. Here, Frey *et al.* include a discussion and an explanation, which should be reserved for the text proper. It is known that the teeth of various pterosaurs extend posteriorly as far as mid-point of the nasopreorbital fenestra. Although the research is still in progress, preliminary results show that the pattern of teeth size can be used as a diagnostic tool to distinguish between different pterosaur taxa, indicating various problems with the revision by Unwin (2001). The dentition is not used by Campos & Kellner (1985) in their diagnosis of *Anhanguera blittersdorffi* as stated by Frey *et al.* (p. 59). There are various pterosaurs genera without premaxillary crests (for instance *Cearadactylus* and *Brasileodactylus*); hence the presence of a premaxillary crest can hardly be used as a diagnostic feature as it does not distinguish this specimen from others. A foramen lacrimale is found in many pterosaurs and seems, at first sight without having examined the specimen carefully, not to be unlike the holotype of *Anhanguera blittersdorffi* Campos & Kellner, 1985. Such caudally protruding lacrimal processes have been noted in various other pterosaurs as well but the extension and curvature as reported for *Ludodactylus* is new. The mandible shows anteriorly a very slight increase in depth, but there is doubt whether this is a true mandibular crest as seen with so many other mandibles. As the authors state (p. 59) "Unfortunately the status and diagnosis of the Ornithocheiridae and other Cretaceous tooth-bearing pterosaur groups is confused" and the diagnosis of *Ludodactylus* is not an exception to this 'rule'. Most remarkable however, are the comments regarding the mandible of *Brasileodactylus araripensis* Kellner, 1984. The mandible of *Brasileodactylus* differs considerably from all other mandibles (position of teeth, dorsally flattened anterior part), including *Anhanguera* and *Coloborhynchus.* Furthermore, the authors mention the difference in height of the mandibular crest in *Anhanguera piscator* and *Brasileodactylus* but the latter has no mandibular crest! The explanation of the supposed difference as the result of ontogeny, sexual dimorphism or variation cannot be proven, mainly due to the scanty fossil record (most of the species are represented by only one (published) specimen, often consisting only of parts of the skull). The fossils should therefore be treated as a different species unless proven (and not just suggested) otherwise. Surprisingly, Frey *et al.* consider *Anhanguera* and *Coloborhynchus* as belonging to the same genus because according to them the dorsal deflection of the

premaxillae in *Anhanguera* is an ontogenic or dimorphic (although not mentioned, we assume they mean 'sexual dimorphic') feature. For comments see the previously made remarks on ontogeny and sexual dimorphism. Although this has been suggested before (Veldmeijer, 2003), Veldmeijer was aware of the difficulty in proving this and therefore refrained from synonymising. The clearly different configuration of the pre-crest part in *Anhanguera* is only seen in *Anhanguera* and coincides with the rather posteriorly positioned premaxillary crest (*contra* the anteriorly terminating crest in *Coloborhynchus*). *Tropeognathus robustus* was referred to *Coloborhynchus* as early as 1998 (Veldmeijer, 1998).

The second paper by these authors ('A new species of tapejarid pterosaur with soft-tissue head crest') presents the skulls of two tapejarid pterosaurs housed in the collection of the Staatliches Museum für Naturkunde, Karlsruhe. The specimens with large soft-tissue crests clearly differs from the two known species of *Tapejara* and have been assigned new species.

The paper 'Pterosaur (Pteranodontoidea, Pterodactyloidea) scapulocoracoid from the Early Cretaceous of Venezuela' by Kellner & Moody presents the first record of pterosaurs from Venezuela and mainly has its importance in the fact that its "[…] occurrence extends the pterosaur record to the northern part of the South American portion of Gondwana.") (p. 73).

Pereda Suberbiola *et al*, ('A new azhdarchid pterosaur from the Late Cretaceous phosphates of Morocco') describes a new, incomplete and badly damaged cervical vertebrae as a new species and genus. Although we are not working with azhdarchid pterosaurs, the establishment of a new genus on the basis of very incomplete and damaged material seems to lack support.

Some remarks regarding the paper 'Giant azhdarchid pterosaurs from the terminal Cretaceous of Transylvania (western Romania)' by Buffetaut *et al.* have been presented above. Some points regarding the contents however, need attention as well. First, the authors state in the abstract (p. 91) that "[…] the giant azhdarchid *Hatzegopteryx thambema*, the holotype of which […] is described in detail." However, there is no diagnosis offered in the systematic part; instead, the reader is referred to an earlier publication (on this see above as well), which is very inconvenient. But later on page 98, the diagnosis is cited from Buffetaut *et al.* (2002). The remark that it is unusual in pterosaurs that the occipital condyle is larger than the foramen magnum is remarkable, not in the least because the authors themselves present three 'exceptions'. The comparison of the occiput is found wanting of published specimens such as *Criorhynchus mesembrinus* (Wellnhofer, 1987) and *Thalassodromeus sethi* Kellner & Campos, 2002 although the publication of the latter did not include a detailed description and illustration of the occiput.

The phylogenetic views of Kellner ('Pterosaur phylogeny and comments on the evolutionary history of the group') and Unwin ('On the phylogeny and evolutionary history of pterosaurs') have been different for years, resulting in two schools of thought in the realm of the pterosaur-phylogeny. The different points of view, with their emphases on different features, are subject to much discussion and debate, making it a good decision to put both researches in the publication and next to each other. Bennet's paper on the pectoral myology of pterosaurs is very interesting, and the author also suggests a sort of 'phylogeny of structures' in his palaeobiological interpretation of muscle scars and bone movement in *Campylognathoides* and *Anhanguera.* This paper is of particular interest for scholars working on the functional morphology.

The Bonde & Christiansen paper ('The detailed anatomy of *Rhamphorhynchus*: axial pneumaticity and its implications') is also well done, although it seems that *Rhamphorhynchus* becomes almost an excuse to present the authors' ideas about pneumaticity in dinosaurs, giving the impression of a 'misplaced paper' in this case. The specimen is very well-prepared, but the pictures published do no justice to it at all. The conclusions the authors reach about the possibilities of a bird-like respiratory system in pterosaurs imply that aerial sacs evolved at least twice in the vertebrate history if we assume that pterosaurs are not related to dinosaurs at all.

The paper by Frey *et al.* (the same three authors as the previous and next discussed papers, but supplemented with a fourth author) 'New specimens on Pterosauria (Reptilia) with soft parts with implications for pterosaurian anatomy and locomotion' presents various extremely well-preserved fossils. The paper offers a detailed description of all soft-tissue features, which is accompanied with many photographs and drawings. A drawback is the comparison with unpublished material (SMNK PAL 3855). A comparison with *Thalassodromeus sethi* is lacking as well as the paper in which the new *Tapejara navigans* is described. For comments on the remark that taxa have been wrongly diagnosed on the basis ofhte shape of the crest (which are according to the authors probably ontogenetic stages or sexual dimorphs) see above (discussion on the description of *Ludodactylus*).

In the last paper by Frey *et al.* ('Middle- and bottom-decker Cretaceous pterosaurs: unique designs in active flying vertebrates'), the compared material is largely unpublished (it is used for comparison in this paper only but has not been described and published separately, making scientific checking largely impossible), which is strange considering the fact that these parts of the pterosaur body have been published by other authors.

The pterosaur tracks and anatomy are interestingly tackled in Rodriguez de la Rosa's paper, although we would have liked a more detailed analysis of both tracks and osteology of the manus/pes in these animals. The

paper by Mazin *et al.* seems promising in that it illustrates a comparison between crocodilian and pterosaurian trackways, but this kind of comparison has been done before (*e.g.* Unwin, 1996 [note that this paper has been referred to as Unwin, 1997] and references therein) and they add very little to this subject. On the contrary, the good illustrations and a good description in this paper add knowledge of a trackway site, which can be interesting for palaeoichnologists.

Lockely & Wright address several aspects of the palaeobiology of pterosaurs using trackways, and it results in a sort of introduction to the problems involved in this area of palaeobiology. The paper is more of a review of several aspects that have to be investigated than an advancement in any of the fields implied in the title of the book. It must be pointed out that the quality of pictures in this paper varies dramatically from very good drawings to pixellated pictures.

Even more interesting for a palaeoichnologist is the paper by Billion-Bruyat & Mazin, which redefines *Pteraichnus* and all the nomenclature and difficulties associated to pterosaur trackways.

Steel's paper ('The John Quekett sections and the earliest pterosaur histological studies') has some interesting notes for those who work in the field of history of museology and is for the scope of the publication of minor importance.

In conclusion, the book 'Evolution and palaeobiology of pterosaurs' is meant for the professional palaeontologist working with pterosaurs and is therefore a must, because as scientist you cannot simply neglect publications. However, the content is often disappointing; considering this, together with the remarks made on more general topics (editing, references and the like) reading the book is not such a pleasure as one is inclined to think at first sight. Furthermore, the book is expensive.

Buffetaut, E. & J.-M. Mazin. Eds. 2003. Evolution and palaeobiology of pterosaurs. – London, Geological Society (Special Publications 217). 354 pp. ISBN 1-86239-143-2. Price £ 85.00/$ 142.00 (hardback).

Cited literature

Buffetaut, E., D. Grigorescu & Z. Csiki. 2002. A new giant pterosaur with a robust skull from the latest Cretaceous of Romania. – Naturwissenschaften 89: 180-184.

Campos, D.A. & A.W.A. Kellner. 1985. Panorama of the flying reptiles study in Brazil and South America. – Anais Academia Brasileira de Ciências 57, 4: 453-466.

Collini, C.A. 1784. Sur quelques Zoolithes du Cabinet d'Histoire naturelle de S.A.S.E. Palatine et de Bavière, à Mannheim. – Acta Academia Theodoro-Palatinae Mannheim 5: 58-103 (pars physical).

Cuvier, G. 1801. Extrait d'un ouvrage sur les expèces de quadrupèdes don ton a trouvé les ossmens dans l'intérieur de la terre. – Journal de Physique, de Chimie et d'Histoire Naturelle 52: 253-267.

Cuvier, G. 1809. Mémoire sur le squelette fossile d'un reptile volant des environs d'Aichstedt, que quelques naturalistes ont pris pour un oiseau, et dont nous formons un genre de Sauriens, sous le nom de Ptero-Dactyle. – Annales du Muséum national d'Histoire Naturelle 13: 424-437.

Frey, E. & H. Tischlinger. 2000. Weichteilanatomie der Flugsaurierfüße und Bau der Scheitelkämme: Neue Pterosaurierfunde aus den Solnhofener Schichten (Bayern) und der Crato-Formation (Brasilien). – Archaeopteryx 18: 1-16.

Kellner, A.W.A. 1984. Ocorrência de uma mandibula de Pterosauria (*Brasileodactylus araripensis* nov.gen.; nov.sp.) na formação Santana, Cretáceo da chapada do Araripe, Ceará-Brasil. – 33 Anais Congresso Brasileiro de Geologia, Rio de Janeiro 2: 578-590.

Kellner, A.W.A. 1996. Description of new material of Tapejaridae and Anhangueridae (Pterosauria, Pterodactyloidea) and discussion of pterosaur phylogeny. – Ann Harbor, University Microfilm's International/ProQuest.

Kellner, A.W.A. & D.A. Campos. 2002. The function of the cranial crest and jaws of a unique pterosaur from the Early Cretaceous of Brazil. – Science 297: 389-392.

Mazin, J.-M., J.-P. Billon-Bruyat, E. Buffetaut, F. Duranthon, M. Bilotte and J. Le Loeuff. Eds. 2001. Two hundred years of pterosaurs. A symposium on the anatomy, evolution, palaeobiology and environments of Mesozoic flying reptiles. Toulouse, France, September 5-8, 2001. – Strata 1, 11.

Unwin, D.M. 1996. Pterosaur tracks and the terrestrial ability of pterosaurs. – Lethaia 29: 373-386.

Unwin, D.M. 2001. An overview of the pterosaur assemblage from the Cambridge Greensand (Cretaceous) of Eastern England. – Mitteilungen Museum für Naturkunde Berlin, Geowissenchaftliche Reihe 4: 189-221.

Veldmeijer, A.J. 1998. The Leiden specimen of *Coloborhynchus* (Pterosauria). In: **Jagt, J.W.M., P.H. Lambers, E.W.A. Mulder & A.S. Schulp. Eds. 1998.** Third European workshop on vertebrate palaeontology. Programme and abstracts. Field guide. – Maastricht, Natuurhistorisch Museum Maastricht: 69.

Veldmeijer, A.J. 2003. *Coloborhynchus spielbergi* sp. nov. (Pterodactyloidea) from the Albian (Lower Cretaceous) of Brazil. – Scripta Geologica 125: 35-139.

Wellnhofer, P. 1987. New crested pterosaurs from the Lower Cretaceous of Brazil. – Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie 27: 175-186.