Evolution and palaeobiology of pterosaurs

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The first scientific description of a pterosaur was published in 1784 by Cosimo Alessandro Collini, a former secretary of Voltaire and at that time curator of the natural history cabinet of Karl Theodor, Elector of Palatinate and Bavaria. The specimen came from one of the main sources of such fossils, the Late Jurassic lithographic limestones of northern Bavaria, and Collini, after much deliberation, interpreted it as the skeleton of an unknown marine creature (Collini 1784).

In 1801, Georges Cuvier, on the basis of Collini's description and figure, identified the mysterious animal as a flying reptile (Cuvier 1801), for which he later coined the name 'Ptero-Dactyle' (Cuvier 1809). Cuvier's basically correct interpretation of the 'winged finger' marked the beginning of the study of pterosaurs as an extinct group of flying reptiles.

In the two centuries which have elapsed since those first efforts to understand what have been considered bizarre fossils, the study of pterosaurs has developed enormously. Some of the basic questions about them have long been solved: pterosaurs were neither birds, nor bats, as was suggested by various authors of the early nineteenth century, but a peculiar group of vertebrates which acquired the ability to fly in an original way, using a membrane attached to a single finger of the hand. From the few fossils from the Bavarian lithographic limestones known to Cuvier and his contemporaries, the number of pterosaur specimens has increased enormously, starting with the Early Jurassic specimens from Lyme Regis found by Mary Anning in the 1820s and first described by Buckland (1829), to the present day, when more than 60 genera have been found all over the world (see the review by Wellnhofer 1991). It has now become obvious that pterosaurs, although built on a fairly uniform basic type, showed considerable diversity in terms of size and adaptations. However, despite considerable advances in our knowledge of pterosaurs, many questions and problems remain. The aim of this volume is to bring together papers which attempt to shed some light on various aspects of pterosaurs as fossil organisms, with special emphasis on their evolution and palaeobiology.

A first and important aspect is that the fossil record of pterosaurs is far from being completely known. No fossil record can be known entirely, of course, but that of the pterosaurs is still conspicuously incomplete, because it is strongly influenced by the existence of *Konservat-Lagerstätten*, fossil localities with exceptional preservation, which have led to the preservation of the fragile, hollow-boned skeletons of these flying reptiles. The Late Triassic bituminous limestones of northern Italy, the Liassic bituminous shales of southern Germany, the Late Jurassic lithographic limestones of Bavaria, the Early Cretaceous nodules of Brazil, and the fine-grained Late Cretaceous chalk of the central United States are well-known examples of formations which have yielded a wealth of well-preserved pterosaur specimens. In rocks formed under more usual conditions, pterosaur specimens tend to be scanty and fragmentary. As a result, the evolutionary history of pterosaurs is still full of gaps, or time intervals, during which the group is poorly represented, separating periods during which good material was preserved under more or less exceptional taphonomical conditions. Things, however, are changing rather fast, as new specimens are being found both in newly discovered *Konservat-Lagerstätten*, such as the Early Cretaceous Yixian Formation of northeastern China, and in other formations, in which pterosaur fossils may be more fragmentary but are nonetheless important. Some of the papers in this volume are thus descriptions of new pterosaur fossils from various parts of the world and from various stages of the Mesozoic: the Late Triassic of Austria (**Wellnhofer**); the Late Jurassic of the western United States (**Carpenter *et al.***); the Early Cretaceous of Brazil (**Frey *et al.***) and Venezuela (**Kellner & Moody**); and the Late Cretaceous of Morocco (**Pereda-Suberbiola *et al.***) and Romania (**Buffetaut *et al.***).

One of the main problems about pterosaurs is their origin and early evolutionary history. Triassic pterosaurs in particular have been known only for the last 30 years, and yet these early forms, although already fully fledged pterosaurs, are of obvious importance for our understanding of the beginnings of the group. Both a report of a new find from Austria (**Wellnhofer**) and a review of Triassic pterosaurs (**Dalla Vecchia**) address this question in the present volume. More generally, it is only recently that the evolutionary history of pterosaurs has begun to be

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investigated using the modern concepts of phylogenetic systematics. Two papers in this volume (**Kellner; Unwin**) propose alternative comprehensive phylogenies of the Pterosauria, which will undoubtedly serve as a basis for further discussions.

Besides their phylogeny, an enduring problem has been pterosaur biology. Because they have no real equivalent in the present living world, the mode of life of pterosaurs has been the subject of much speculation ever since it was recognized that they were flying animals. A detailed analysis of various aspects of their skeletal anatomy is a prerequisite to an understanding of the way in which they functioned, as illustrated by a study of the morphological evolution of their pectoral girdle (**Bennett**), obviously a fundamental part of the anatomy of any flying vertebrate. As discussed, much of what we know about pterosaurs depends on preservation, and even taxa which have been known for a long time can yield remarkable new information, particularly when good specimens are prepared using modern techniques, as exemplified by the description of axial pneumaticity in *Rhamphorhynchus* (**Bonde & Christiansen**), a taxon first described by Hermann von Meyer in 1847. Careful and painstaking preparation of exquisitely preserved specimens has also contributed immensely to our knowledge of the soft parts of pterosaurs, which are of obvious importance for our understanding of the biology and biomechanics of animals in which the flying apparatus consisted of a wing membrane, which in most instances has not been preserved. As described in one of the papers (**Frey *et al.***), anatomical details as delicate as blood vessels have sometimes been preserved and shed unexpected light on various aspects of pterosaur biology.

Ever since Cuvier realized that pterosaurs were winged reptiles, their locomotion, both in the air and on the ground, has been the subject of much controversy. The flight of pterosaurs can be investigated mainly on the basis of their skeletal anatomy, but comparisons with man-made flying machines can lead to interesting conclusions about the existence of various types of flight adaptations in this group of extinct vertebrates (**Frey *et al.***). Locomotion on the ground is a different matter, and totally divergent interpretations have been put forward on purely morphological grounds, with some authors supporting a bipedal gait, while others favoured a quadrupedal stance. The matter has largely been solved by the discovery and study of pterosaur footprints and trackways, in many parts of the world, which provide direct evidence as to how these animals moved when on the ground. A new discovery of pterosaur footprints from the Late Cretaceous of Mexico is described here (**Rodriguez-de la Rosa**), and a detailed analysis based on the remarkable trackways from the Late Jurassic of Crayssac (southwestern France) clearly illustrates the quadrupedal locomotion of pterodactyloid pterosaurs (**Mazin *et al.***). Pterosaurs were, however, not only able to fly and walk; they could also swim, as shown by ichnological evidence from the Late Jurassic of North America (**Lockley & Wright**), which also provides clues as to their feeding behaviour. Pterosaur trackways have been the subject of much controversy and their parataxonomy has become considerably entangled, hence the need for a critical review advocating drastic simplification (**Billon-Bruyat & Mazin**).

A further way to explore the palaeobiology of pterosaurs is the study of their bone histology. Interestingly, this approach was pioneered as early as the mid-nineteenth century by the British researchers James Bowerbank (1848) and John Quekett (1849*a*, *b*). Some of Quekett's thin sections have survived until the present day (despite the bombing of the Royal College of Surgeons, where they were kept, during the Second World War), and they are redescribed and reinterpreted here (**Steel**). Pterosaur fossils from the Brazilian *Konservat-Lagerstätten* are excellent material for histological investigations, as illustrated by a study on differential growth rates based on such specimens (**Sayão**).

Much indeed can be learned from pterosaur fossils, and the description of a new ornithocheirid taxon from Brazil also includes an interesting piece of forensic palaeontology that provides convincing evidence as to the cause of death of what is now the type specimen (**Frey *et al.***).

Although they are not very common fossils, pterosaurs were an important group of vertebrates during the Mesozoic, and their unusual and interesting adaptations are attracting the attention of a growing number of palaeontologists. The aim of the present volume is to give an idea of the diverse topics addressed by researchers working on these fascinating animals and to encourage further research and discussion.

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