

THE ILLUSTRATED ENCYCLOPEDIA OF PTEROSAURS, by Peter Wellnhofer. 1991. Crescent Books, New York. 192 pp. \$19.95 (hardcover).

The pterosaurs were the first vertebrates to develop fully powered flight. They have long enjoyed a moderate popularity with the public but pterosaurs have almost always been upstaged by the dinosaurs and have had to take second billing in popular works. Now with the publication of Peter Wellnhofer's book that situation is remedied. The book is the first written solely about pterosaurs since Harry Govier Seeley's remarkable "Dragons of the Air." Like Seeley, Peter Wellnhofer is an acknowledged expert on pterosaurs, having studied them for 25 years. The notes on the dust jacket state that the book is intended to be a popular reference book about pterosaurs and a companion volume to David Norman's "Illustrated Encyclopedia of Dinosaurs." It is patterned on Norman's book, and one cannot help but compare the two. The book is profusely illustrated with photographs of specimens, diagrams, old reconstructions, and many new reconstructions by Wellnhofer and John Sibbick, the artist who also illustrated Norman's book. The new reconstructions are excellent and present pterosaurs as entirely believable animals, neither bird- nor bat-like, but wholly their own. The text is easy to read and includes much historical information about the people and specimens involved in the discovery and interpretation of pterosaurs. There are occasional digressions that stray rather far from the subject (e.g., a section on dragon myths), but the text is easy to follow and the historical information makes it enjoyable to read.

The book begins with a brief introduction to pterosaurs, followed by a long and detailed review of the history of the study of pterosaurs, from the discovery of the first specimen of *Pterodactylus antiquus* up to the present. Next there is a discussion of the two competing hypotheses of the origin of pterosaurs and the relationship of pterosaurs to other diapsids: pterosaurs are the sister-group of dinosaurs (Padian, 1984a; Gauthier and Padian, 1985); pterosaurs descended directly from eosuchians (Wild, 1983). Wellnhofer seems to reject the hypothesis that dinosaurs and pterosaurs are sister-groups because he rejects Padian's arguments for a terrestrial bipedal origin of flight in pterosaurs. He also apparently does not accept cladistic methodology and questions whether the antorbital fenestra that diagnoses the Archosauria is a useful character because modern crocodylians lack one. He suggests that some eosuchians had an antorbital fenestra (although there is no evidence of that) and concludes that pterosaurs are not archosaurs, but rather form a separate group of diapsids descended directly from eosuchians.

The book continues with a review of the osteology of pterosaurs, and three chapters that, like Norman's dinosaur book, review the various taxa. Each genus is illustrated in magnificent color reconstructions by John Sibbick, with temporal range shown on a Mesozoic time scale, distributional maps, and silhouettes comparing the size of the animals to humans.

One significant improvement over Norman's book is that there are numerous footnotes so that the reader who wishes to know more is directed to the pertinent technical literature. This feature makes the book much more useful as a reference. Because there are many fewer pterosaurs than dinosaurs Wellnhofer is able to go into greater detail about individual taxa and related topics. Unfortunately, this additional detail tends to be given to discussion of the history of the specimens, rather than the anatomy or ecology of the animals. In addition, although these chapters are superficially similar to those in Norman's book, they are differently organized. The dinosaurs were reviewed in chapters dealing with different clades or groups of dinosaurs and included cladograms representing the relationships of genera, families, and higher taxa. The pterosaurs are reviewed by Mesozoic period, and there are no cladograms at all. In the chapter on Jurassic pterosaurs, he alternates discussions of rhamphorhynchoid and pterodactyloid genera, which may blur the distinction between the two. Wellnhofer rarely discusses the characters that diagnose genera and largely ignores higher categories. Readers will not know that *Pterodactylus* and a number of other genera are each isolated in a family unless they consult a summary table, and the reason for isolation in monogeneric families is not explained.

A "Lifestyle" chapter thoroughly reviews the reconstructions of the wing membranes, functional morphology, flight, ecology, and physiology of pterosaurs. Wellnhofer includes broad, if not unbiased, coverage of opposing views of osteology and functional morphology. Thus alternative reconstructions of the position and function of the pteroid bone are discussed, as are various interpretations of the flight and terrestrial locomotion. On each of these topics Wellnhofer sides with the traditional view: the pteroid extends toward the body along the wing front; the hindlimb extends out in the plane of the wing; pterosaurs were quadrupedal. There is a short section reviewing three-dimensional reconstructions of pterosaurs, both static museum displays and flying models. Lastly, there is a short section on other flying vertebrates, the variety of gliding reptiles from the Permian to the present, as well as birds and bats. We have become accustomed, even inured, to the practice of including pterosaurs, ichthyosaurs, plesiosaurs, and even pelycosaurs in books about dinosaurs, and although the inclusion of a section on birds and bats in this volume is no more inappropriate, it is more surprising.

Almost anyone who reads this book will learn a great deal about the pterosaurs and should have an enjoyable time doing it. The book has achieved its goal of being a popular reference on pterosaurs and a companion to Norman's dinosaur book, and if you or anyone else has an interest in pterosaurs, it is well worth buying for yourself or recom-

mending to them. However, the book is not without its faults. There are some minor problems that will probably only be apparent to the specialist; for example, "*Pteranodon*" *oregonensis* is listed as a pteranodontid even though Padian (1984b) and subsequent authors have noted that it is not a pteranodontid and may be an azhdarchid. A more disturbing problem is that virtually all life reconstructions of pterosaurs have the external auditory opening in the lower temporal fenestra, rather than behind the quadrate and squamosal. (In *Pteranodon* the position of the opening is indicated by a process on the squamosal that supports and partially encircles the auditory opening.)

The biggest problem with the book is that it almost completely ignores the subject of the relationships of pterosaurs. Admittedly, the phylogenetic relationships of the pterosaurs are not well understood but there has been some recent work on this subject. Wellnhofer does not comment on these studies or even suggest that our knowledge of relationships is insufficient. Similarly, although Wellnhofer does present a classification, he does not comment on other classifications such as those of Young (1964) or Kuhn (1967). In short, the book surveys the diversity of pterosaurs, while ignoring the evolution of pterosaurs, which may lead the non-paleontologist reader to conclude that phylogeny is unimportant. The book would be greatly improved if Wellnhofer, with his many years of work on the group, had addressed the question of the relationships of pterosaurs.

Despite the shortcomings, there is no other book that can compare to this volume in the depth and breadth of coverage and fine illustration of pterosaurs. This is not only because there are no other pterosaur books on the market; I suspect

that even if there were a dozen other popular, illustrated books available, this would still be the best, and I heartily recommend it to all who are interested in the pterosaurs.

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LITERATURE CITED

- Gauthier, J., and K. Padian. 1985. Phylogenetic, functional and aerodynamic analyses of the origin of birds; pp. 185–197 in M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer (eds.), *The Beginnings of Birds*, Proceedings of the International Archaeopteryx Conference Eichstätt 1984. Freunde des Jura-Museums Eichstätt, Eichstätt.
- Kuhn, O. 1967. *Die fossile Wirbeltierklasse Pterosauria*. Oeben-Verlag, Krailling, 52 pp.
- Padian, K. 1984a. The origin of pterosaurs; pp. 163–168 in W.-E. Reif and F. Westphal (eds.), *Third Symposium on Mesozoic Terrestrial Ecosystems Short Papers*. Attempto Verlag, Tübingen.
- . 1984b. A large pterodactyloid pterosaur from the Two Medicine Formation (Campanian) of Montana. *Journal of Vertebrate Paleontology* 4:516–524.
- Wild, R. 1983. Über den Ursprung der Flugsaurier; pp. 231–238 in Erwin Rutte-Festschrift. Weltenburger Akademie, Kelheim/Weltenburg.
- Young, C. C. 1964. On a new pterosaurian from Sinkiang, China. *Vertebrata Palasiatica* 8:221–255.