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BOOK REVIEW

ARCHAEOPTERYX. DER URVOGEL VON SOLNHOFEN, by Peter Wellnhofer, 2008. Munich, Germany: Verlag Dr. Friedrich Pfeil, 256 pp., €78.00, ISBN 978-3-89937-076-8.

With the possible exception of *Tyrannosaurus rex*, *Archaeopteryx* is arguably the most widely known extinct animal. Due to exceptional preservation in the fine-grained limestones of the Upper Jurassic Solnhofen Formation of Bavaria (Germany), most of the available skeletons of this taxon retain distinct impressions of feathers. Consequently, despite the many "reptilian" features of its skeleton, the avian affinities of *Archaeopteryx* were at once apparent. The first reported specimen, a single feather, was discovered in 1861 — little more than a year after the publication of Darwin's *On the Origin of Species* in November 1859. A second specimen, an almost complete skeleton now housed in the Natural History Museum in London, was also found in 1861. With subsequent discoveries and studies, *Archaeopteryx* became firmly established as the classic example of an evolutionary "missing link" — a veritable "icon of evolution."

Peter Wellnhofer's new book is a treasure trove of information on *Archaeopteryx*, the history of its study, and its provenance. Although it is ostensibly aimed at an educated general readership, the specialist will gain a tremendous amount of information from this volume. Along with the late John H. Ostrom (to whose memory the book is dedicated), Peter Wellnhofer has long been the leader in the study of *Archaeopteryx*, and he has authored the first anatomical descriptions of several of the more recent finds. Thus, Wellnhofer brings unrivalled expertise to an account of this fascinating, complex subject.

Following a brief general introduction, the second chapter of the book provides detailed accounts of the history of the small town of Solnhofen and its environs as well as the history of quarrying operations in the eponymous Solnhofen Formation. The limestones of this stratigraphic unit have been popular as high-quality building material since Roman times. A dramatic increase in the demand for these rocks came as the result of the invention of lithography by Alois Senefelder in 1798. This printing technique utilizes the fact that water and oil do not mix. Lithography originally involved drawing an image with an oil-based medium on a smooth limestone surface, which readily absorbs both oil and water. After the oil had penetrated the porous surface of the stone a water-based solution of gum arabic was applied to seal non-oily surface areas. The stone was then inked with a roller; the oil-impregnated areas accepted the ink whereas the adjoining sealed areas rejected it and became the background. In this manner, hundreds of copies could be printed from a single slab. The Solnhofen limestones proved uniquely suited for Senefelder's printing technique. Following Senefelder's pioneering efforts, lithography in its original form remained in wide use for almost a century until its replacement by simpler and cheaper processes. Today, lithography is only used by a few skilled artisans for the reproduction of high-quality artwork.

The third chapter of Wellnhofer's book discusses the geology of the Solnhofen Formation. During the Late Jurassic, specifically the early Tithonian, the finely laminated limestones of this unit were laid down in basins or lagoons between reefs formed mainly by sponges and associated microorganisms on a shallow marine platform along the northern edge of the Tethys.

The fossils from the Solnhofen Formation represent death assemblages. At the bottom of the depositional basins, stagnant, hypersaline, and oxygen-poor water created conditions hostile to benthic life. A warm, subtropical climate prevailed during the deposition of the Solnhofen limestones and, through substantial evaporation, would have contributed to an increase in water salinity. Occasional, possibly seasonal mixing of this toxic bottom layer with the less saline, better oxygenated surface waters through storms led to the demise of countless nektonic and planktonic animals, which sank to the bottom and were quickly covered by fine calcareous mud. Heavy seasonal rainfall would have washed animal cadavers and plant debris from adjoining land into the basins. Powerful storms may have blown flying animals out to sea where they eventually drowned. The terrestrial plant fossils from the Solnhofen Formation mostly comprise dry-adapted conifers, along with a few benettitaleans and cycads, and are consistent with warm, semi-arid climatic conditions. Ferns and other plants requiring more humid conditions are absent.

Chapter 4 presents a comprehensive synopsis of the great diversity of animals and plants from the Solnhofen Formation along with extensive discussion of the history of their exploration. In 1616, the first identifiable illustrations of Solnhofen fossils appeared in a catalogue of curiosities belonging to a Nuremberg collector named Basilius Besler. The Solnhofen limestones achieved international recognition when Georges Cuvier identified the first pterosaur (*Pterodactylus*) in 1801, and the subsequent discovery of *Archaeopteryx* consolidated that reputation. Today, the Solnhofen Formation is renowned as one of the richest fossil *Lagerstätten* in the world and provides a unique window into the diversity of Late Jurassic life. Wellnhofer cites 262 currently recorded genera of marine animals and algae, but this number does not include the diverse microfossils, most of which remain undescribed. Although less common, terrestrial animals comprise over 150 described species of insects and a variety of reptiles including pterosaurs, the small nonavian theropod *Compsognathus*, and *Archaeopteryx*. (An alleged record of a temnospondyl amphibian proved to be based on the tail of a turtle.)

Chapters 5–7 provide a detailed review of the history of discovery, anatomy, paleobiology, phylogenetic position, taxonomy, and taphonomy of *Archaeopteryx*. In addition to the single feather, on which Meyer (1861) based the binomen *Archaeopteryx lithographica*, nine skeletons or parts of skeletons have been identified to date. An additional specimen, disarticulated remains of a skeleton referred to *Archaeopteryx* sp., was collected from the stratigraphically slightly younger Mörnsheimer Beds at Daiting. Unfortunately, this important fossil has disappeared into unidentified private hands and only a single colored cast remains available for scientific examination.

Chapter 5 discusses the history of discovery and presents information concerning the structure of each individual specimen. The former often involves fascinating stories replete with the kind of skulduggery more commonly associated with archaeological treasures. Unlike other German states, Bavaria never passed legislation to protect its paleontological resources and thus a thriving worldwide trade in Solnhofen fossils has established itself over the years. Any newly discovered skeletons of *Archaeopteryx* would now command millions of euros, making them unaffordable for even the largest natural history museums.

Wellnhofer distinguishes two valid species of *Archaeopteryx*, *A. lithographica* Meyer, 1861 and *A. bavarica* Wellnhofer, 1993. Like many early type specimens, the holotype of *A. lithographica* — the isolated feather — is now inadequate for taxonomic purposes, and the first reported skeleton (the London specimen) should be officially designated as the neotype. Except for the holotype of *A. bavarica*, Wellnhofer regards all other named genera and species of *Urvögel* from the Solnhofen Formation as representing various ontogenetic stages of *A. lithographica*. He differentiates *A. bavarica* primarily on the basis of its limb proportions and the proportionately greater length of its primary and tail feathers.

Chapter 6 presents a detailed, well-illustrated account of the skeleton and plumage of *Archaeopteryx* and examines various aspects of its paleobiology. Wellnhofer reconstructs *Archaeopteryx* as primarily terrestrial and insectivorous in its habits, but considers it capable of moving up into the branches of bushes and trees where its feet would have allowed it to gain a perch. He also regards *Archaeopteryx* as an active flyer although as less capable in this respect than later, more derived birds.

Chapter 7 provides an overview of the phylogenetic significance of *Archaeopteryx*. Although Wellnhofer clearly favors the almost

universally accepted hypothesis of a theropod origin for birds he briefly reviews the various alternatives advanced and dismissed over the years.

Chapters 8–10 explore broader issues of the origin and early evolutionary history of birds with emphasis on information provided by *Archaeopteryx*. Chapter 8 explores the origin of avian flight based on the longstanding debate revolving around the "from the trees down" vs. the "from the ground up" scenario. While generally presenting a comprehensive discussion, Wellnhofer does not mention the recent work by Kenneth P. Dial and his students at Montana State University, which, at least in this reviewer's opinion, should finally settle the controversy. Chapter 9 reviews the origin of feathers. Wellnhofer notes the presence of filamentous body covering or feathers in various taxa of non-avian theropod dinosaurs from the Lower Cretaceous of Liaoning (China). Based on his own observations of the Chinese fossils, he explicitly rejects recent claims that these structures merely represent degraded collagen fibers that were removed from their original context by postmortem maceration. Finally, Chapter 10 provides a concise overview of the Mesozoic fossil record of birds and early avian evolution. Although Wellnhofer includes an illustration featuring a cladogram of Mesozoic birds he only briefly notes some of the associated character transformations.

Somewhat unexpectedly, the text ends with a short poem on *Archaeopteryx* by the contemporary German poet Elke Langstein-Jäger. The extensive bibliography provides a helpful introduction to the substantial body of literature on *Archaeopteryx* and the origin of birds.

The book is richly illustrated with drawings and photographs. Particularly noteworthy are a series of specimen photographs taken by Helmut Tischlinger under long-wave UV light; by greatly enhancing the contrast between the bones and the limestone matrix, this mode of illumination reveals much otherwise invisible detail.

Peter Wellnhofer's new book represents the most detailed, authoritative account on *Archaeopteryx* published to date and belongs on the bookshelf of every serious student of vertebrate evolution. It is to be hoped that an English translation will soon give it the wide international readership it so richly deserves.

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LITERATURE CITED

Meyer, H. von. 1861. [*Archaeopteryx lithographica* (Vogel-Feder) und *Pterodactylus* von Solenhofen.] Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde 1861:678–679.

Wellnhofer, P. 1993. Das siebte Exemplar von *Archaeopteryx* aus den Solnhofener Schichten. Archaeopteryx 11:1–48.