

## THE WINGS OF PTEROSAURS

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**ABSTRACT.** The wings of pterosaurs were supported by a stiffened leading edge formed by the bones of the forelimb and notably by the hypertrophied wing-finger. The patagium was narrow in planform and was composed of a membrane of skin, structural fibers, and soft tissues that nourished and innervated the membrane. The membrane—which formed the aerodynamic surface of the wing—was invested with a series of closely spaced, parallel structural fibers on its ventral surface. These fibers are 0.05 mm thick, and 3 to 8 of them typically span 1 mm, depending on the extent of stretching of the patagium. The length of individual fibers is difficult to trace: they were at least 5 to 10 mm in length but may have been very much longer. Some of the fibers may have been discontinuous along the wing chord. Fraying of the structural fibers near the trailing edge of the wing of one specimen indicates that they were real structures, not wrinkles, that they were quite strongly attached to the ventral side of the patagium, but may have been detached under substantial aerodynamic or mechanical (possibly post-mortem) forces. The fibers may have been homologous to the keratinous scales and feathers of other archosaurs. The patagium, as a composite structure, had mechanical advantages over other non-composite biological materials and was flexible yet much stronger than any of its components alone. The arched leading edge spar spread the patagium, which formed the aerodynamic surface. The curved, cambered spar, and the structural fibers, which ran largely parallel to the leading edge, maintained stiffness of the patagium to longitudinal (spanwise) and chordwise bending. The structural fibers were responsible for transmitting aerodynamic force generated over the wing surface to the bones of the hand and the upper arm. Microscopic analysis reveals ultrafine hair-like structures, with a diameter of 0.01 mm on the wings and on other parts of some specimens; these are presumed to have been part of the integumental covering and are distinct from the structural fibers.

The wings of pterosaurs seem to have been attached along the body to the thigh in at least one specimen of the genus *Pterodactylus*, but the extent of the posterior attachment of the wings is not definitely known in other genera. There is no evidence for a tendon or other stiffening structure along the trailing edge of the wing, and the wing was not principally structured in such a way to counter chordwise tension perpendicular to the leading edge. The pelvic girdles of pterosaurs were fused along their ventromedial symphyses, at least in adults. The orientation of the acetabulum varied, as it does in birds, but the hindlimbs were organized along the plan seen in birds and other dinosaurs. This evidence indicates that pterosaurs had an erect posture and parasagittal gait. The assumption that their pelvis were too weak to support muscles for bipedal locomotion is incorrect: many animals with known bipedal locomotory abilities lack hard part structures with comparable muscle attachment areas.

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## INTRODUCTION

Pterosaurs were first described scientifically in the late 1700s (Colli- ni, 1784; Cuvier, 1801, 1809; von Soemmerring, 1812; for reviews, see Desmond, 1975; Wellnhofer, 1980, 1984, 1991a; Padian, 1987; Wenzel, 1990), but, despite two centuries of study of several hundred available specimens (mostly of the genera *Rhamphorhynchus* and *Pterodactylus*, from the Late Jurassic of southern Germany), there remain major controversies about many aspects of their biology and their flight. At the center of many of these controversies is a lack of consensus on the structure of the wings, and the structure must be understood if we are to answer questions of function, aerodynamics, and paleobiology.

From their first discovery, pterosaurs have almost universally been recognized as flying animals, and nearly all workers have acknowledged the ability to flap actively and vigorously in all but the largest species (von Meyer, 1855; Desmond, 1975; see also Winkler, 1874, on earlier claims). The first specimens with apparent evidence of the wing membranes were reported in the mid-19th Century (Goldfuss, 1831; Oken, 1831; von Meyer, 1832, p. 239–240; 1842; Münster, 1842; Quenstedt, 1852; Fikenscher, 1872; Winkler, 1874), but in each case preservation was incomplete or equivocal, and the structure and extent of the wing could not be deduced. Surprisingly little was known about the wings until O. C. Marsh (1882) and Karl von Zittel (1882) independently published papers on two exceptional specimens of the Late Jurassic genus *Rhamphorhynchus*, both of which showed evidence of preserved wings or wing impressions. By this time, however, artists had already established a number of fanciful—and largely inaccurate—reconstructions of winged pterosaurs, and these reconstructions distorted and biased many subsequent interpretations of pterosaurs and their gross anatomy. This tradition can be traced back to von Soemmerring's (1820) misidentification of a juvenile *Pterodactylus* (preserved without wing traces) as an aberrant bat (Padian, 1987). Later bat-like restorations, Padian argued, were entirely in keeping with typological expectations of the structure and biology of an oxymoronic “winged reptile.”

To date, nearly eighty specimens of pterosaurs with traces of wings, tails, and/or integumental coverings have been discovered and reported (Wellnhofer, 1970, 1975c, 1978, 1980, 1987, 1991a; Broili, 1925, 1927a, b, 1938, 1939, 1941; Döderlein, 1923, 1929a, b, c; Sharov, 1971; Padian, 1979, 1980, 1983, 1985; this paper); indeed, our observations have identified wing traces—especially of structural fibers—on a number of older specimens where they had not previously been noted. Some of these specimens bear only impressions of skin, often indistinguishable from similar impressions of other soft tissues of the body, with which they have sometimes been confused. Some show indentations and grooves impressed by structures of the creased and crumpled patagium. A surprising number of specimens show the actual structures of the patagium, though none so clearly or to the same extent as the wing of *Rhamphorhynchus* described by von Zittel. Recently Martill and Unwin

(1989) have examined under the scanning electron microscope a section of what they identified as preserved wing membrane from a Cretaceous pterodactyloid from South America, with intriguing—if somewhat ambiguous—results (Pennycuick, 1990; Martill, Wiley, and Unwin, 1990). Wellnhofer (1991a, p. 152) illustrates a fragment of wing from a similar individual.

Central to the debate on the structure and function of the pterosaur wing are the interlinked problems of the respects in which the wing was similar to and different from those of birds and bats and of how the wing obtained the stiffness or *integrity* required for effective flapping flight. Marsh (1882, p. 252) regarded the wing as a “thin smooth membrane, very similar to that of modern bats,” echoing the entrenched view common at that time (and still repeated today). But at the same time von Zittel (1882) realized that some form of stiffening was essential, and that his *Rhamphorhynchus* wing provided evidence for a widespread pattern of strong, flexible fibers. Further support for the presence of such fibers has since been given on both paleontological and mechanical grounds by a number of authors (Wanderer, 1908; Wiman, 1925; Lambrecht, 1928, 1929; Abel, 1925a, b, 1929; Broili, 1925, 1938; Döderlein, 1923, 1929a; Klinghardt, 1944; Wellnhofer, 1975c, 1987; Padian, 1983), but it has not hitherto been appreciated how widespread and overwhelming is the evidence for these fibers. Unfortunately Lambrecht’s pioneering fluorographic studies were conducted on *Pterodactylus crassipes* at Haarlem, a specimen now recognized as being *Archaeopteryx* (Ostrom, 1970, 1972); it is not surprising that he saw a similarity between what he thought were pterosaur fibers and bird feathers! Subsequent ultraviolet examinations (von Koenigswald, 1931) have been uninformative.

In this paper we examine the structure of the pterosaur wing: the components, the architecture, the materials, the growth and development, and the function of the reconstructed wing. We begin with the direct evidence of the wing’s gross structure, the composition and structure of the patagium, and the role of both the wing spar and the patagium in providing the mechanical integrity of the airfoil. We examine alternative reconstructions of the pterosaur wing, none of which has been based on unambiguous evidence, and we discuss the implications of our findings for alternative reconstructions of the wing, as well as for the stance, gait, and locomotion of pterosaurs.

#### INSTITUTIONS

We use the following abbreviations to identify institutions:

- AMNH: American Museum of Natural History, New York, United States  
 BMM: Bürgermeister-Müller-Museum, Solnhofen, Germany  
 BMNH: Natural History Museum, London, United Kingdom  
 BSP: Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany

CM:	Carnegie Museum, Pittsburgh, United States
DNPM:	Department Nacional Produccion Mines, Rio de Janeiro, Brasil
GIUA:	Geological Institute of the University of Amsterdam, Holland
IGL:	Institut Géologique de Louvain, Belgium
JM:	JuraMuseum, Eichstätt, Germany
MBH:	Museum Berger, Harthof bei Eichstätt, Germany
MNHU:	Museum für Naturkunde an der Humboldt-Universität, Berlin, Germany
MSA:	Museum am Solenhofer Aktienverein, Maxberg bei Solnhofen, Germany
MSNB:	Museo di Scienze Naturali, Bergamo, Italy
NHMW:	Naturhistorisches Museum, Wien, Austria
PINM:	Paleontological Institute, Russian Academy of Sciences, Moscow, Russia
PMZ:	Paläontologisches Institut und Museum der Universität Zürich, Switzerland
SMD:	Staatliches Museum für Mineralogie und Geologie, Dresden, Germany
SMF:	Natur-Museum Senckenberg, Frankfurt-am-Main, Germany
SMNS:	Staatliches Museum für Naturkunde, Stuttgart, Germany
TMH:	Teylers Museum, Haarlem, Holland
USNM:	United States National Museum of Natural History (Smithsonian Institution), Washington, United States
UUPI:	Paleontological Institute of the University, Uppsala, Sweden
YPM:	Yale Peabody Museum, New Haven, Connecticut, United States

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#### SPECIMENS AND PRESERVATION

The best preserved pterosaur wing (BSP 1880 II 8) was described by von Zittel (1882) and has since been discussed by many authors, including Stromer (1910, 1913), Wiman (1925), Döderlein (1923), Wellnhofer (1975b, c, 1987, 1991a), Padian (1983), Schaller (1985, 1986), Pennycook (1988), and Rayner (1989a, b). The specimen (figs. 1, 2) was assigned to the species *Rhamphorhynchus muensteri* by Wellnhofer (1975b),

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Fig. 1. The Zittel wing. This isolated left wing in ventral aspect of *Rhamphorhynchus muensteri* is preserved in the Bavarian State Collection (BSP 1880 II 8) and is one of the finest pterosaur specimens in existence, with exceptionally fine detail of the bones of the wing and the surface of the patagium. Scale bar 2 cm.

