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 postmortem) 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 pelves 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 (Collini, 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

We are indebted to the curators of all these collections, and others, for their cooperation, especially to Dr. Peter Wellnhofer of the Bavarian State Collections, Dr. Günter Viohl of the JuraMuseum, Eichstätt, Dr. H. Kollman of the Naturhistorisches Museum, Vienna, and Dr. John H. Ostrom of the Yale Peabody Museum.

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), Pennycuick (1988), and Rayner (1989a, b). The specimen (figs. 1, 2) was assigned to the species *Rhamphorhynchus muensteri* by Wellnhofer (1975b),

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.
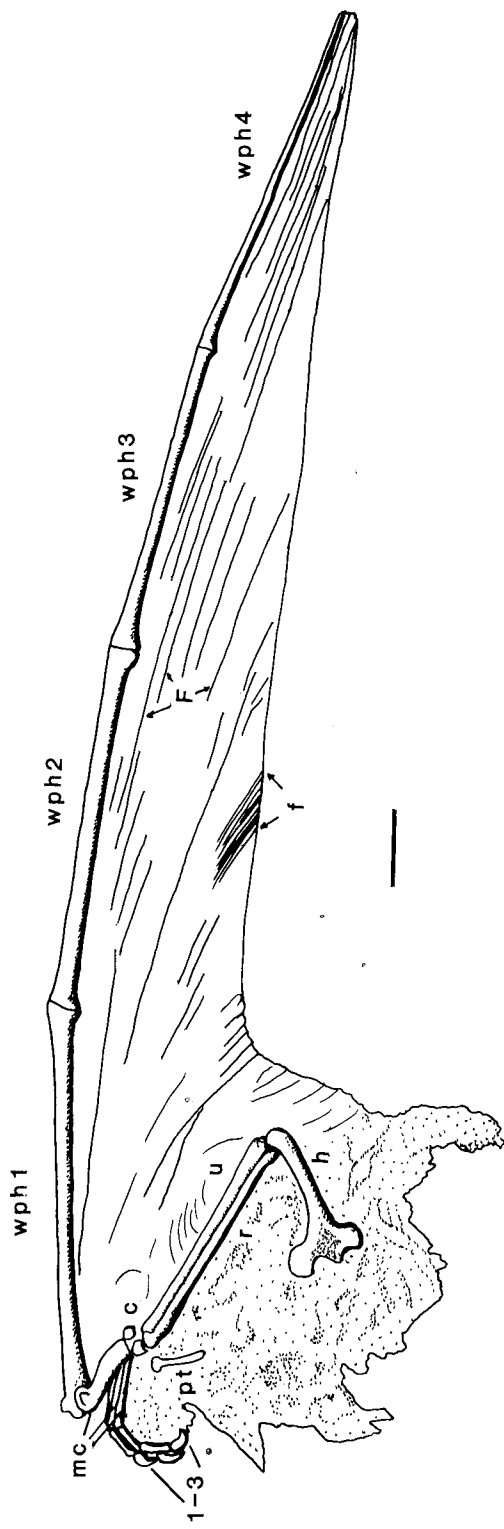
Fig. 2. Diagram of the Zittel wing (fig. 1), showing generalized features of the pterosaur wing. Abbreviations: c, carpus; F, folds; f, fibers (only some can be shown); h, humerus; mc, metacarpus; pt, pteroid; r, radius; u, ulna; 1–3, first three manual digits; wph 1–4, four phalanges of wing-finger (digit 4). The stippled area is skin surface, probably not pertaining to the wing.

although some (mainly older) workers refer it to *R. gemmingi*. This specimen preserves more fine detail of the wing more completely than any other, though others are illuminating in many respects. Other specimens of particular interest that we consider in this paper include *Rhamphorhynchus* in the Yale Peabody Museum (YPM 1178), in Munich (BSP 1938 I 503, BSP 1907 I 37, BSP AS I 772), in Zürich (PMZ A/III 107), and in several private collections; those of *Pterodactylus* in Vienna (NHMW 1975/1756) and in Munich (BSP 1937 I 18, 1924 V 1); and one fragment of the wing of a large tapejarid (Kellner, 1989, 1991), probably of the genus *Tupuxuara* (Wellnhofer, 1991a, p. 152) (table 1).

Many more pterosaur specimens preserve evidence of the wing, or of soft tissues, and we list these in table 1, based on our own observations and on reports in the literature. Soft part preservation in pterosaurs can be identified in a number of ways: most important are the clear traces of the wing and its structure and extent, but these are relatively rare. More common are impressions of the border of the wing or those left by folded or creased wings. In some cases there is evidence that the wing structures have (at least in part) undergone diagenesis and are preserved *in situ*, while in others only molds or casts of the structures are identifiable. Membranes and skin may often be seen as regions of relatively smooth surface distinct from the remainder of the matrix. These regions may include arrays of small depressions interpreted as hair follicles (Broili, 1941; Wellnhofer, 1991a, p. 163), and on rare occasions "hair" itself appears to be present (PMZ A/III 107). Less certain evidence of the wings is provided by a filmy white deposit with an indefinite boundary, in the region of the forelimbs, particularly in various *Pterodactylus:* this has been described as iron oxyhydrate (von Meyer, 1842) or iron oxide deposited in the course of diagenesis or decomposition of the dermis (Wagner, 1837; Winkler, 1874; Wiman, 1925; Klinghardt, 1944), but is more likely a remainder of a bacterial film present during diagenesis. The tentative identification with wing or soft parts is supported by the limited topographical distribution of the deposit and by its appearance on specimens with other accompanying evidence of the presence of wing membranes (Wiman, 1925; NHMW 1975/1756 [fig. 3F].

TERMINOLOGY AND DEFINITIONS

We use the term *wing* to refer to the entire structure of the forelimb, encompassing the forearm bones and associated soft tissue. The *patagium* is the part of the structure forming the aerodynamic surface of the wing, including both the membrane of skin, and the structural components within or upon it. The *membrane* is the actual skin itself, including dermal muscles, follicles, and associated tissues, and which we suppose to be homologous to the superficial structures in related animals, from which the pterosaur patagium must have evolved. Associated with the membrane are other structures of the integument, the *structural fibers*, and the fur-like covering, which will be discussed below.

The term *pterosaur* refers to members of the reptilian order Pterosauria (Kaup, 1834), the flying reptiles (Kuhn, 1967; Wellnhofer, 1970,

TABLE 1

The table lists pterosaur specimens, including published descriptions of certain specimens, which show preservation of soft parts, primarily of the wing membrane or patagium. It is unlikely that the list contains all such specimens in easily accessible collections. A question mark indicates unavailable information for specimens we have not been able to inspect. It also indicates observations that are uncertain, or uncertain taxonomy.

Species name (1)	Location	Inventory (2)	Wellnhofer (3)	Wing membrane (4)	Folds (5)	Fibers (6)	Tail sail	Description (7)	Authority (8)	Notes
undescribed new taxon (Triassic)	MSNB	S.1431	—	3	—	2	—	—	o.o.	fibers alongside wing-finger, some soft part traces
Dimorphodon macronyx	BMNH	41346	—	—	—	—	yes	Owen, 1870	Owen, 1870; o.o.	some soft parts or skin
Dorygnathus banthensis	NHMW	?	—	3	—	—	—	von Arthaber, 1921	von Arthaber, 1921; o.o.	
Dorygnathus banthensis	IGL	?	—	2	—	—	—	Salée, 1928	Salée, 1928	
Dorygnathus sp.	BSP	1938 I 49	—	3	—	3	—	Broili, 1939	Broili, 1939, 1941; o.o.	Broili refers only to hair traces
Rhamphorhynchus longicaudus	TMH	6930	1975b/3		—	—	yes	von Meyer, 1859	Wellnhofer, 1975b	
R. longicaudus	BSP	1960 I 470	1975b/9	—	—	—	yes	Wellnhofer, 1975b	Wellnhofer, 1975b; o.o.	
R. longicaudus	BSP	1938 I 503	1975b/11	yes	yes	2	yes	Wellnhofer, 1975b	Wellnhofer, 1975b; o.o.	fibers also visible on counterslab; fig. 3C (9)
R. intermedius	JM	8-1	1975b/25	yes	yes	—	—	Broili, 1927a	Broili, 1927a; o.o.	
R. intermedius	BMNH	42738	1975b/27	3	yes	—	—	von Meyer, 1859	o.o.	
R. intermedius	priv. coll.	—	1975b/28	yes	?	?	yes	Wellnhofer, 1975b	Wellnhofer, 1975b	
R. muensteri	YPM	1778	1975b/33	yes	yes	1	yes	Marsh, 1882	Marsh, 1882; Wellnhofer, 1975b; o.o.	The Marsh specimen figs 3D, 9
R. muensteri	SMD	?	1975b/36	yes	yes	1	?	Wanderer, 1908	Wanderer, 1908; o.o. Wiman, 1925	Also hair and hair follicle impressions
R. muensteri	BMNH	37003	1975b/39	yes	yes	3	—	Owen, 1870	Broili, 1927b Wellnhofer, 1975b; o.o.	
R. muensteri	BSP	AS VI 34	1975b/41	3	—	?	—	Wagner, 1858	o.o.	
R. muensteri	BMNH	37787	1975b/42	—	—	—	yes	Lydekker, 1888	Wellnhofer, 1975b; o.o.	
R. muensteri	SMF	R4128	1975b/43	3	yes	—	yes	Gross, 1937, 1938	Gross, 1937, 1938; o.o.	(10)
R. muensteri	BMM	—	1975b/44	3	yes	—	—	Wellnhofer, 1975b	o.o.	

TABLE 1
(continued)

Species name (1)	Location	Inventory (2)	Wellnhofer (3)	Wing membrane (4)	Folds (5)	Fibers (6)	Tail sail	Description (7)	Authority (8)	Notes
R. muensteri	MSA	—	1975b/45	yes	yes	—	—	Wellnhofer, 1975b	Wellnhofer, 1975b; o.o	
R. muensteri	JM (c/s)	1954 39b (c/s)	1975b/46	yes	yes	?	—	Wellnhofer, 1975b	Wellnhofer, 1975b	Skin and hair traces figs. 3G, 4G
R. muensteri	priv. coll.		1975b/47	yes	yes	?	—	Wellnhofer, 1975b	Wellnhofer, 1975b, o.o	Skin and hair traces figs. 3G, 4G
R. muensteri	PMZ	A/III 107	—	yes	yes	?	?	Koh, 1937	Wellnhofer, 1975b	
R. muensteri	GIUA (c/s)	J.9653 (c/s)	1975b/51	3	yes	?	?	von Zittel, 1882	Wellnhofer, 1975b	The Zittel wing figs. 1, 2, 4A–E, 7
R. muensteri	MNHU	114 29	1975b/53	3	yes	?	yes	von Zittel, 1882	von Zittel, 1882; Döderlein, 1923; Wellnhofer, 1987; o.o.	
R. muensteri	CM	1880 II 8 (11)	1975b/57	yes	yes	1	—	Wellnhofer, 1975b	Wellnhofer, 1973; Döderlein, 1929a; Klinghardt, 1944; o.o.	
R. muensteri	BSP	11427	1975b/59	3	yes	?	—	Wellnhofer, 1975b		The Döderlein specimen (12); figs 3A, 4F
R. muensteri	CM	1907 137	1975b/60	yes	yes	1	yes	Döderlein, 1929a	Wellnhofer, 1975b	
R. muensteri	BSP		1975b/62	yes	yes	2	—	Wellnhofer, 1975b	Wellnhofer, 1975b	
R. muensteri-	JM	?.1989 XI 1	—	1,3	yes	2	—		o.o	(14)
R. muensteri	BSP		1975b/67	yes	yes	?	yes	Wellnhofer, 1975b	o.o	(15)
R. muensteri	BMM		1975b/65	yes	—	—	yes	Wellnhofer, 1975b	Wellnhofer, 1975b	
R. gemmingi	MSA		1975b/76	1	yes	3	—	Wellnhofer, 1975b	Gilmore, 1906; o.o	hair follicles
R. gemmingi	priv. coll.	2420	1975b/77	yes	yes		yes	Gilmore, 1906	Wellnhofer, 1975b; o.o	
R. gemmingi	USNM	SoS 3358		yes	yes			Wellnhofer, 1975b		
R. gemmingi	JM		1975b/79	yes	yes	?	—	Wellnhofer, 1975b	o.o	(16)
R. gemmingi	MBH	—		yes		?	yes	Wellnhofer, 1975b	Wellnhofer, 1975b;	
Rhamphorhynchus sp.	JM	1953/28	1975b/91	yes		3	yes	Wellnhofer, 1975b	Wellnhofer, 1975b;	
R. sp.	JM	1955.135a	1975b/92	yes	yes	2	—	Wellnhofer, 1975b	o.o. Wellnhofer, 1975b	wing membrane partly disassociated from wing, but intact
R. sp.	JM	1971.27	1975b/93	—	—		yes	Wellnhofer, 1975b	o.o. Wellnhofer, 1975b;	tail sail visible in u.v. light
R. sp.	priv. coll.		1975b/94	yes	yes	?	—	Wellnhofer, 1975b	Wellnhofer, 1975b	(17)
R. sp.	priv. coll.		1975b/100	yes	yes	1	—	Leich, 1964	Leich, 1964, 1968; Wellnhofer, 1975b, 1983	
R. sp.	BMM		1975b/102	—	—		yes	Wellnhofer, 1975b	Wellnhofer, 1975b;	
* R. sp.	MSA	—	—	yes	yes	—	—	—	o.o.	(18)

Species	Institution	Specimen no.	Fig.					Reference	o.o. / other	Notes
R. sp.	MBH	—	—	3	yes	—	—	—	o.o.	complete, articulated specimen dorsally preserved (19)
R. sp.	MBH	—	—	3	yes	—	—	—	o.o.	isolated wing; untraced (20)
R. sp.	? priv. coll. untraced	—	—	yes	yes	?	yes	Wiman, 1925	Lewin, 1982	(21)
R. sp.	untraced	—	—	yes	yes	—	—	—	Wiman, 1925	
Scaphognathus crassirostris	GPIB	1304	1975b/109	3	?	2	—	Goldfuss, 1831	Goldfuss, 1831, et cetera, Wellnhofer, 1975b	(22)
S. crassirostris	MSA	1922 I 42	1975b/110	3	—	?3	?n/a	Wellnhofer, 1975b	o.o.	
Anurognathus ammoni	BSP	—	1975b/111	3	?yes	2	?	Döderlein, 1923	Döderlein, 1923, 1929b; o.o.	
Sordes pilosus	PINM	2585/3	—	yes	—	1	yes	Sharov, 1971	Sharov, 1971; D. M. Unwin, personal communication	extensive impressions of hair and skin
P. antiquus	BMM	13 105	1970/7	3	yes	—	n/a	Winkler, 1874	o.o.	
P. kochi	TMH	—	—	1	—	—	n/a	—	o.o.	
P. kochi	BMNH	42736	1970/8	1, 3	—	3	n/a	von Meyer, 1842	Winkler, 1874; Lambrecht, 1928, 1929 von Meyer, 1842; zu Münster, 1842; o.o.	
P. kochi	BSP	1924 V 1	1970/11	1, 3	—	2	n/a	Broili, 1925	Broili, 1925; o.o.	fig. 4i
P. kochi	BMM	—	1970/17	1	?	—	n/a	Wellnhofer, 1970	o.o.	
P. kochi	AMNH	1942	1970/20	3	—	3	n/a	Abel, 1925b	Abel, 1925b	
P. kochi	BSP	1937 I 18	1970/21	2	yes	2	n/a	Broili, 1938	Broili, 1938; o.o.	
P. kochi	BSP	AS XIX 3	1970/23	1	—	—	n/a	Wagner, 1837	Wagner, 1837; von Meyer, 1856; o.o.	(23) also shows throat sack and propatagium; fig. 3G, 10B
P. kochi	SMF (c/s)	R 404 (c/s)	—	1	—	—	—	—	o.o.	
P. kochi	BSP	1929 I 18	1970/25	—	—	1	n/a	Döderlein, 1929c	Stromer, 1913; Döderlein, 1929c; Klinghardt, 1944; o.o.	soft parts on body, throat sack and feet
P. kochi	NHMW	1975/1756	—	yes	yes	1	n/a	Wellnhofer, 1987	Wellnhofer, 1987; o.o.	figs. 3F, 4H, 5A, 10A
P. kochi	MSA	—	—	1	—	?2	n/a	Wiman, 1925	o.o.	
P. kochi	UUPI	1970/24	1970/24	1	?	?	—	Klinghardt, 1944	Wiman, 1925	
P. scolopaciceps = P. kochi?	MNHU	?	—	1	yes	—	n/a	—	Klinghardt, 1944; museum photograph	
P. scolopaciceps = P. kochi?	BMNH	R3949	—	3	yes	—	n/a	—	o.o.	
P. micronyx	BSP	1964 XXIII 100	1970/32	2	—	?3	n/a	Wellnhofer, 0	o.o.	
P. micronyx	BSP	1911 I 31	1970/42	3	?yes	—	n/a	Wellnhofer, 1970	o.o.	strip of membrane, skin or muscle alongside wing-finger

TABLE 1
(continued)

Species name (1)	Location	Inventory (2)	Wellnhofer (3)	Wing membrane (4)	Folds (5)	Fibers (6)	Tail sail	Description (7)	Authority (8)	Notes
P. micronyx	JM	1983/2649a	—	2, 3	yes	2	n/a	—	o.o.	(3) swimming membrane on foot
P. elegans	BSP	1875 XIV 501	1970/45	3	yes	—	n/a	von Zittel, 1882	von Zittel, 1882	
P. elegans	BSP	1867 II 1	1970/46	3	yes	?3	n/a	von Zittel, 1882	Broili, 1925, o.o.	(24)
P. elegans	MBH	—	1970/51	1	—	—	n/a	Wellnhofer, 1970	o.o.	(25)
P. elegans	JM	37-25	—	?3	—	—	n/a	—	o.o.	
Germanodactylus rhamphastinus	destroyed (was BSP)	—	1970/63	—	—	—	n/a	Münster, 1831	Goldfuss, 1831; Wagner, 1857	hair; may have been the untraced *P. medius* of Wagner, Quenstedt, 1867, et cetera
G. rhamphastinus	BSP	AS I 745b	1970/64	?3	—	?3	n/a	Wagner, 1851	o.o.	very large, isolated wing
Pterodactylus sp.	BMNH	R8573	—	3	yes	—	n/a	—	o.o.	
Pterodactylus	untraced priv. coll.	—	—	1 or 2	?	?1	n/a	Fikenscher, 1872	Fikenscher, 1872	(26)
azhdarchid		—	—	yes	yes	?1	n/a	Campos and others, 1984; Wellnhofer, 1991c	Campos and others, 1984; Campos & Kellner, 1985; Leonardi, 1984	
azhdarchid	DNPM	D6M 488-LE	—	yes	—	possible	n/a	Martill & Unwin, 1989; Martill and others, 1990	Martill & Unwin, 1989; Martill and others, 1990	skin structures identified in SEM
tapejarid (*Tupuxuara*?)	?	—	—	yes	—	1	n/a	Wellnhofer, 1991b	P. Wellnhofer, personal communication; o.o.	(27)
pterosaur	JM	SoS2441	—	2	yes	—	—	—	o.o.	distal flight-phalanges only

(1) Species name is that to which the species was assigned or to which it has been redescribed. It is not necessarily the name under which it was originally described or which it presently borne by the specimen.

(2) Inventory numbers are given where known; some, usually private, collections may not assign numbers.

(3) Number assigned to specimen if described in the monographs of Wellnhofer (1970) (*Pterodactylus* and relatives) and (1975b) (*Rhamphorhynchus* and relatives).

(4) Wing membranes or patagia. If the presence of a membrane or patagium is not immediately obvious; (1) membrane preserved as area of different coloration with no other change to matrix (although described as wing membrane by several authors (von Meyer, 1842, Winkler, 1874, Wiman, 1925), these colored regions (? of iron oxy-hydrate) lie consistently in the expected area but often have indistinct boundaries; it is not obvious in some specimens, particularly of *Pterodactylus*, that this represents wing membrane); (2) membrane preserved as impression, visible as smooth area of matrix; (3) membrane identified only by presence of other features (folds, fibers, et cetera).

(5) Folds: identified as grooves or indentations in matrix due to distortion of the sediment by the wing membrane or its trailing edge prior to decomposition or diagenesis; in some cases these are called by others folding of the membrane itself. In some specimens the membrane might be present, but unprepared. See text for further definition. Also indicates the presence of creases or wrinkles in the patagium.

(6) Fibers: (1) extensive preservationo of fibers over all or large part of the wing(s); (2) localized areas of fiber preservation; (3) small, possibly indistinct, areas of fibers reported by other workers, or tentatively identified by ourselves, which cannot be confirmed.

(7) First, or major, description of the specimen. See Wellnhofer (1970, 1975b) for further references on most specimens.

(8) Source of observation of wing or other soft part observations. o.o. refers to our own observations. See also Wellnhofer (1970, 1975b, c).

(9) Also preserves skin impression as dark ochre coloration; swimming membrane on foot.

(10) The right wing has been altered by preparators; the left wing remains with minimal preparation, showing folds.

(11) Referred to also as inventory AS 1771 by Wellnhofer (1975b) and some older sources.

(12) Fibers and folds are clearly preserved as impressions on the main slab and as casts on unmounted fragments of the counterslab; hair; food remains in throat sack.

(13) The wing membrane remains intact but has become detached from the distal end of wing-finger; no fibers are visible on the counterslab.

(14) Patches of membrane are visible as an extensive strip of brown coloration, running parallel to the wing spars, with fiber striations in places.

(15) A large *Rhamphorhynchus* specimen composed of well preserved slab and counterslab. Brown colored regions indicating the wings on this specimen are preparation artifacts, possibly varnish, and do not span the whole area of the wing as indicated by the extensive fold impressions on both wings. Small regions of fibers are visible following an S-shaped curve below the elbow joints, reminiscent of the folding behind the elbow in the Zittelwing.

(16) A complete, but badly disassociated *Rhamphorhynchus*; both wings are intact, with the right wing in dorsal view, the left (with trailing edge outline) in ventral.

(16) Specimen shows a clear wing membrane with folds and fibers, including a broken section of wing; skin, hair, hair follicles.

(18) A large *Rhamphorhynchus* specimen, composed of slab and counterslab, both broken and incomplete.

(19) Specimen consists of the skull and proximal portion of both wings, lying on its left side; membrane folds are preserved in the angle behind the sharply flexed wrist.

(20) A well preserved *Rhamphorhynchus* in dorsal view with wings partly outflexed. This specimen has not been described formally and is known only from a single illustration in the popular literature. If the apparent wing traces are genuine, it provides unequivocal evidence that in *Rhamphorhynchus* the wing membrane did not extend to the hind leg.

(21) The oldest specimen to be described with obvious soft parts, but the evidence is equivocal and has been the source of much contention. Possible hair impressions are present over much of body and wings; interpreted by some authors as wing membrane; may be fibers. Undulating surface of parts of the matrix may represent folded or wrinkled membrane.

(22) Structures around large portions of the specimen were interpreted by Döderlein as hair but are similar to fibers on other specimens. Possibly folds and wrinkles are present as the matrix surface is uneven. Possible swimming membrane on feet but maysimply be residual soft tissue from foot.

(23) Regions of fine striation were described by Abel as preserved muscle fibers; from the description and their location they are more likely to be membrane and fibers.

(24) Broili (1925) reports the presence of fibers, but we believe some of his observatins may relate to preparatin marks.

(25) Faint traces of membrane are visible; the membrane may originally have been more extensive but since been prepared away.

(26) An early report in the literature of a specimen withmembrane, which appears not to have reached a major public collection; details of preservation unknown; lines running through membrane may be fibers.

(27) A recently discovered specimen composed of most of the wing bones of both wings on a single slab, of a small azhdarchid. Membrane impressions as a colored film, with striations representing fibers, are clearly visible on both wings. We are grateful to Peter Wellnhofer for permission to inspect and report on this specimen.
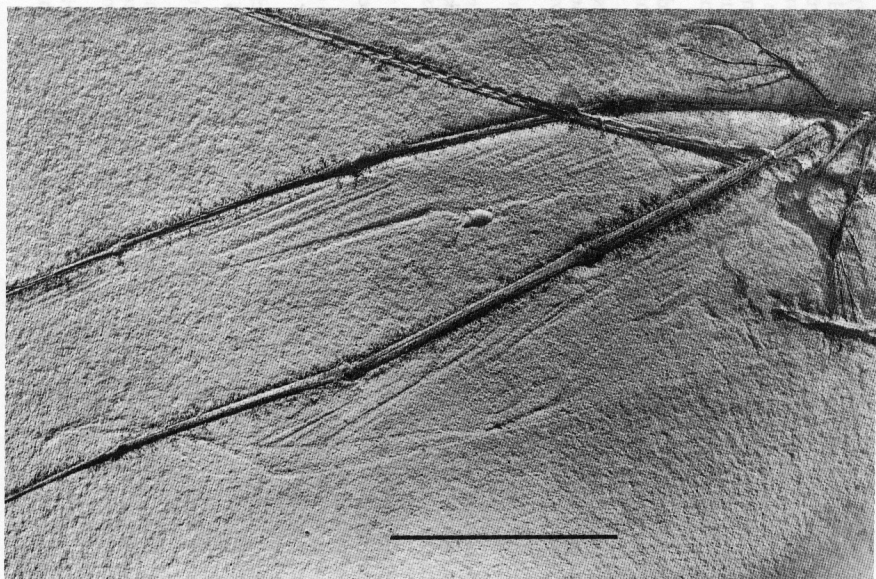
Fig. 3. A selection of pterosaur specimens showing wing and structural fiber impressions. (A) The Döderlein specimen of *Rhamphorhynchus muensteri* (BSP 1907 I 37; Döderlein, 1929a); various fragments of the counterslab of this specimen are also preserved (not illustrated here; see fig. 4F), many of which show fiber and hair impressions. The pieces of the main slab are mounted in a distorted configuration, and much of the central region of the specimen has been repaired with plaster. (B) The counter slab of the von Ammon (1908) specimen of *R. muensteri* (BSP AS I 772), in which part of the wing has detached from the distal part of the leading edge spar. (E) The Zürich specimen of *R.* muensteri (PMZ A/III 107). Portions of membrane are preserved along the right wing-phalanges, and between the right wing and the tail. The distal part of the right patagium has separated from the spar in two places, but appears to have remained attached to the spar at the third interphalangeal joint. There is extensive soft part preservation above the skull, including traces of hair and hair follicles. (F) *Pterodactylus kochi* from Vienna (NHMW 1975/1756; Wellnhofer, 1987); this specimen has the best preserved wings of any Pterodactylus specimen, and includes extensive remains of structural fibers. See also fig. 5A. (G) *P. kochi* from Munich (BSP 1937 I 18; Broili, 1938), another splendidly preserved example, similar to the Vienna specimen. Fibers are visible on both wings, particularly adjacent to the leading edge spar. Scale bars in (C), (F), (G), cm; in (B), (E) 10 cm.
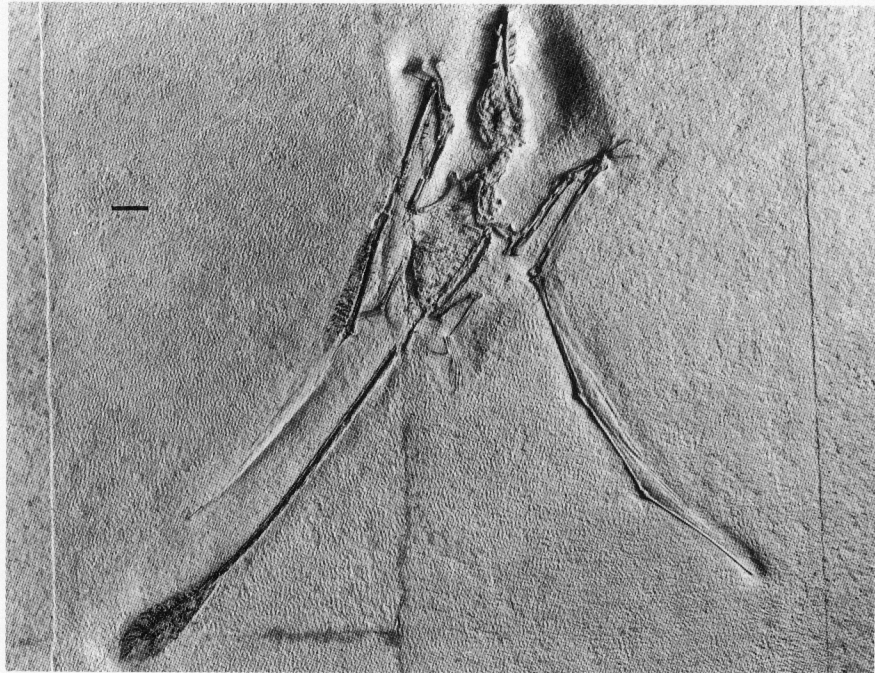
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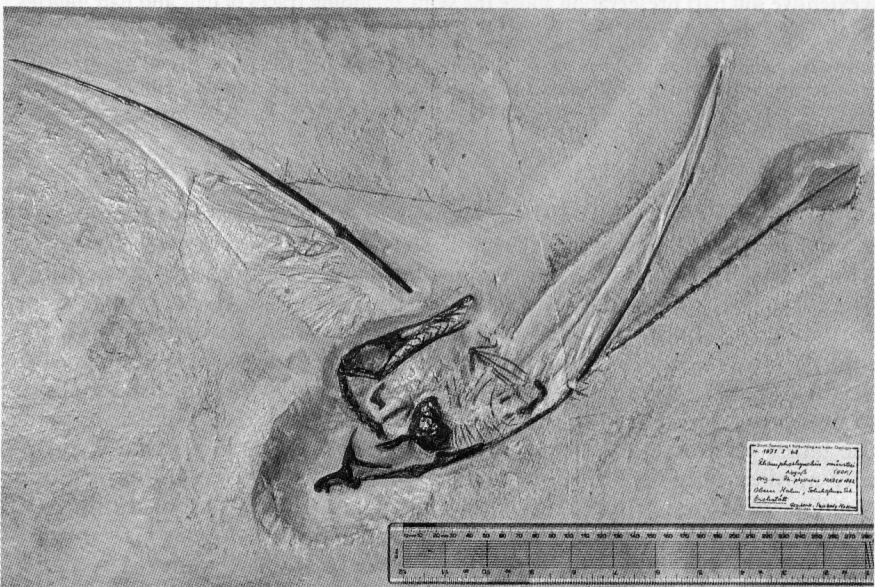
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(C) *R. longicaudus* (BSP 1938 I 503a) at Munich. This specimen (Wellnhofer, 1975b) has very narrow wing impressions, possibly because the wings were flexed and folded as at rest; fiber impressions may be discerned along large parts of the leading edge of both wings. (D) the Marsh specimen of *R. muensteri* (YPM 1778; Marsh, 1882). The distal portion of the left wing has been reconstructed in plaster. (This is a photograph of a cast of the specimen at Munich; a detail of the original is shown in fig. 9.)

Fig. 3 (continued). (E) The Zürich specimen of *R. muensteri* (PMZ A/III 107). Portions of membrane are preserved along the right wing-phalanges, and between the right wing and the tail. The distal part of the right patagium has separated from the spar in two places, but appears to have remained attached to the spar at the third interphalangeal joint. There is extensive soft part preservation above the skull, including traces of hair and hair follicles. (F) *Pterodactylus kochi* from Vienna (NHMW 1975/1756; Wellnhofer, 1987); this specimen has the best preserved wings of any *Pterodactylus* specimen, and includes extensive remains of structural fibers. See also fig. 5A. (G) *P. kochi* from Munich (BSP 1937 I 18; Broili, 1938), another splendidly preserved example, similar to the Vienna specimen. Fibers are visible on both wings, particularly adjacent to the leading edge spar. Scale bars in (C), (F), (G), 1 cm; in (B), (E) 10 cm.

1975a, b, c, 1978, 1980, 1991a), which forms the closest major sister-group to the Dinosauria (Padian, 1984a; Gauthier, 1986; Gauthier, Kluge, and Rowe 1988). The Pterosauria are traditionally divided into two suborders, the long-tailed Rhamphorhynchoidea (Late Triassic-Late Jurassic), and the short-tailed Pterodactyloidea (Late Jurassic-Late Cretaceous). However, the "Rhamphorhynchoidea" is a paraphyletic group, because some of its members (including *Rhamphorhynchus* itself) are closer to pterodactyloids than to other "rhamphorhynchoids." Hence we place the latter term in quotation marks. The informal term *pterodactyl* properly applies only to the monophyletic group Pterodactyloidea, though many authors use it incorrectly to refer to all pterosaurs, and others to members of the genus *Pterodactylus* alone. The neologism "rhamphorhynch" (Pennycuick, 1988) should be understood as a general morphologic descriptor of early (long-tailed) pterosaurs and has no phylogenetic significance.

Fig. 3 (continued)

MODELS OF THE PTEROSAUR WING

It is perhaps not surprising that most attempts to reconstruct the topography and mechanical function of the pterosaur wing have been influenced strongly by the extant flying tetrapods, the birds and the bats. As we have explained above, early representations of pterosaurs were uniformly "bat-like," even long before any reliable evidence of the structure and extent of the wings was clear (Desmond, 1975; Padian, 1987). This early assumption (Blumenbach, 1807; von Soemmerring, 1820) colored many subsequent studies of pterosaurs, and led many authors (Goldfuss, 1831; Buckland, 1836; Newman, 1843; Abel, 1912, 1919, 1922, 1925a; Wiman, 1924, 1925; Spillmann, 1925; Gaál, 1926; Bramwell and Whitfield, 1974) to consider pterosaurs as bat-like in virtually all aspects of their biology, including a hanging stance (now recognized as impossible; Padian, 1983), and even perhaps a speculative nocturnality (Oken, 1818, et cetera). However, some early reconstructions, especially in the German literature, envisaged pterosaurs as erect or semi-erect standing bipeds (Abel, 1922, 1925a; Stieler, 1922). Until very recently there have been few serious attempts to consider the pterosaur wing as anything other than a mechanically homogeneous, relatively thin membrane, comparable to the membranes of bats. Phrases like "leathery wings" are common in both popular and scientific literatures, perhaps assuming that a bat-like wing would be thick in a large pterosaur. Yet the first two specimens in which evidence of the patagium was clearly preserved—those of Marsh and von Zittel—both reveal beyond doubt that the wing was far more complex than a simple thin membrane, and bat wing membranes are anything but thick and leathery.

The problem with the "bat-like" model is more complex than anatomical and mechanical questions of the wing membrane alone. In pterosaur wings, the only bony structures are arranged along the leading edge, and a homogeneous, presumably elastic, membrane could not be stable in flapping flight with such a simple support. The bats have resolved this problem by using the third, fourth, and fifth digits to span the membrane, to stiffen the leading edge and the wingtip region (Norberg, 1969, 1970, 1972a, b; Vaughan, 1959, 1970), and to control the camber of the airfoil. Moreover, the wing attaches to the hind leg in most bats, providing an additional source of control of pitch and camber and providing a mechanism of tensing the trailing edge of the membrane. This system can only function successfully with a network of tendons within the bat membrane and along the trailing edge (Forster, 1926; Gupta, 1967; Holbrook and Odland, 1978; Kovtun, 1978; Morra, 1899; Schöbl, 1871; Schumacher, 1932), and with a considerable degree of innervation and vascularization to the tissues of the wing membranes so they may be maintained and repaired. The similarities in the diverse wing structures of megachiropteran and microchiropteran bats, and the slightly differing solutions to the mechanical and anatomical problems of constructing and controlling the wings in the two groups (Pettigrew and others, 1989; Rayner, 1991a), suggest that design constraints on a wing of this type are

strong and permit little flexibility in the gross anatomical structure that may be evolved.

Apart from the fourth digit's support of the leading edge of the patagium, and the role of the pteroid in tensing the leading edge of the propatagium (Plieninger, 1906; Hankin, 1912; Hankin and Watson, 1914; Döderlein, 1929b; Tyeryaev, 1960; Stein, 1975; Wellnhofer, 1978, 1987; Padian, 1984b), no bony elements are involved in the aerodynamic surface of the pterosaur wing. How then did the pterosaur control the pitch and camber of the wing? Proponents of the "bat-like" model generally assume (Bramwell and Whitfield, 1974) or argue (Pennycuick, 1988) that the hind leg had to be involved in the wing for this purpose, and this inevitably predicates the presence of some longitudinal stiffening structure (presumably tendon) along the trailing edge of the wing (Bramwell and Whitfield, 1974; Sneyd, Bundock, and Reid, 1982). The dilemma is that there is no fossil evidence for such a tendon (and moreover no homology within the tetrapods for it), and that evidence for any useful involvement of the hindlimb in the mechanics of the pterosaur wing is equivocal. If the pterosaur wing were a simple membrane it would be vulnerable to catastrophic damage from tears or injury; these represent a less significant risk to a bat because it can confine damage within a segment of its patagium, which is divided into panels by the digits.

If we take a step back from the inconsistencies of the "bat-like" model and accept that the pterosaur patagium must have been more than a simple membrane, then we can consider alternative models of wing anatomy and mechanics. It is essential that the patagium possess some integral form of stiffening, which should provide a means of controlling pitch and camber, should give the wing aerodynamic and mechanical integrity, and should transmit aerodynamic force generated over the wing surface to the bones of the leading edge and/or the trunk (Rayner, 1989a, b); these structures should also protect the wing from injury. With an appropriate design the hindlimb would need less involvement with the wing during flight, and the wing would not need to attach to the leg; the bulk of force generated by the wings would be transmitted to the body through the humerus, the shoulder joint, and the muscles of the pectoral girdle (Rayner, 1988a). Such a model of the pterosaur wing was advanced by Wanderer as long ago as 1908. This envisages the pterosaur wing as much more "bird-like" than "bat-like"; the shafts of the avian feathers fulfill just these functions of stiffening the wing and providing its integrity, and feathers provide control of camber and pitch by curvature of the shaft, by pre-stressing at the molecular level (Purslow and Vincent, 1978), and by the geometry of their attachment to the ulna and the hand. Moreover, the structure of the shoulder joint and the range of movements of the joint and of the pterosaur wing (Padian, 1985, 1987, 1991; Wellnhofer 1991a; Hazlehurst and Rayner, 1992a) were very similar to those in living birds.

An alternative approach to this situation is to consider the wing planform and its relation to pterosaur ecology. Most pterosaurs (at least

as preserved in the fossil record) were found in marine sediments, and many species appear to have been piscivorous. They had long, thin wings of relatively high aspect ratio (figs. 1–3), which by comparison with living birds are appropriate for large marine predators (Rayner 1988b, 1989a; Hazlehurst and Rayner 1992b). It is hard to see how the pitch and camber of a wing of these proportions could be controlled usefully by the hindlimb; by the same token, if the hindlimb were (functionally) uninvolved with the wing, we might expect the wing surface to attach only to the trunk, and not to the leg, and it would be essential for mechanical features providing the aerodynamic properties of the wing to be concentrated either at the leading edge (such as the pteroid) or within the wing itself (such as the stiffening fibers we discuss in this paper). Further, were the wing to extend to the ankle, as supposed in the "bat-like" model, the animals' aspect ratios and wing loadings would be significantly lower than those of comparable modern piscivorous birds; for such animals, a relatively thin, high aspect ratio wing is most efficient (Rayner, 1988b; Hazlehurst and Rayner, 1992b).

All of these arguments point toward a more "bird-like" than "bat-like" model for the pterosaur and its wings. However, such comparisons with extant animals must be treated with caution. They are certainly instructive, in that all three groups represent solutions to the problem of flapping flight with the foundation of the tetrapod *Bauplan* and within the mechanical and developmental constraints of the tissues available to vertebrates. But the pterosaur wing had many significant differences from the bird wing, quite apart from that of bats: the bones of the digits extended to the wingtip, and the wing surface was continuous, not formed from individual feathers as in birds. How this wing was constructed, and how it functioned, forms the subject of this paper.

CONSTRUCTION OF THE PTEROSAUR WING

The Wing Spar and the Pteroid

The spar of the wing is the part that forms the structure of the leading edge and supports the patagium. In pterosaurs the spar consists of the forelimb and particularly of the hypertrophied fourth finger, which makes up most of the leading edge (fig. 2). The wing bones and their articulations have been reviewed recently by Bramwell and Whitfield (1974), Wellnhofer (1978, 1980), and Padian (1983, 1985), and only some details are included here.

The wing is functionally divided into three parts. The humerus forms the innermost part and moves mostly up and down during flight, with a down and forward component especially in slow to medium speed flight (Padian, 1983), possibly approximating a diagonal figure of eight in some species. (In some larger pterodactyloids the dominant movement of the humerus may have been rotational [Hazlehurst and Rayner, 1992a], as in gannets and albatrosses in landing flight.) The middle part of the wing is composed of the radius and ulna, the fused rows of proximal and

distal carpals, and the elongated metacarpals. The elbow is essentially a hinge joint. The pteroid bone is possibly a neomorph of calcified tendon and is thin and hollow (at least in *Pterodactylus*), suggesting design for tension; it points medially from the carpal region and is supported by one to three medial carpals (the number depends partly on degree of fusion), which can vary according to age, size, preservation, and taxon (Wellnhofer, 1978, 1991b; Padian, 1984b). The pteroid supported the propatagium of the wing, a triangular wing segment running between the humerus and forearm, and formed much or most of the leading edge of the propatagium, which continued to the shoulder. Quenstedt (1856), Frey and Riess (1981), and Pennycuick (1988) have advanced alternative reconstructions of the pteroid involving a postulated forewing along the spar distal to the wrist, but there is no clear evidence for these, and they have not been generally accepted (see for example Padian, 1984b, p. 520; Wellnhofer, 1985, p. 174, 1987). As Wellnhofer (1987, p. 154) observed, in specimens with otherwise excellently preserved wing impressions, such skin structures would also have left their impressions behind.

The third, outermost, and longest portion of the wing spar is formed entirely by the four phalanges of the wing-finger. There are three small fingers with a typical phalangeal formula of 2–3–4; the wing-finger is generally considered the fourth, with the fifth lost. The proximal end of the first wing-phalanx has a rounded concave dorsoventral profile forming the articular surface, which rotates anteroposteriorly between the dual convex condyles of the distal end of the wing metacarpal (Wellnhofer, 1975a, 1978). These dual condyles are not quite parallel, so the wing-finger can be depressed slightly in addition to direct anteroposterior movement (Bramwell and Whitfield, 1974). There is a proximal knob on the first wing-phalanx, extending anterior to the metacarpal, which prevented hyperextension of the wing-finger and also (presumably) served as an insertion point for its extensor tendons (fig. 2). The other interphalangeal joints are simple, anteroposteriorly oriented, concave-convex articulations, with the distal bone ends convex (see also von Arthaber [1921] on *Dorygnathus*); only very limited motion was possible at each of these joints, probably only sufficient to absorb the shocks and stresses of flight. It is not unusual to find these joints intact and articulated but bent from their normal, nearly straight positions. Collateral ligament fossae near the ends of these bones are not prominent in most genera, and there is little evidence of tendinous connections between adjacent wing-phalanges in most genera (compare exceptions in newly prepared and examined specimens of *Pteranodon* and *Nyctosaurus;* S. C. Bennett, personal communication). In full, or nearly full, extension the wing-phalanges formed a slight arch, and this configuration made a major contribution to the mechanics of the composite pterosaur wing.

Shape of the Wing

The pterosaur wing has a relatively high aspect ratio, which means that its length is substantially greater than its mean chord (breadth). In

this respect pterosaur wings resemble much more the long, narrow wings of gulls and other marine birds than those of sparrows or ducks, as von Zittel (1882) first noted, or those of bats. High aspect ratio is characteristic of birds that soar in moving air associated with bodies of water, such as gulls, terns, frigate birds, and albatrosses. It is not clear that all pterosaurs had such high aspect wings, because most preserved terrestrial environments are also associated with water (lakes, streambeds, floodplains, lagoons, and so on), so there is no way to tell how much past diversity is missing from forest and upland environments (Padian and Clemens, 1985; Rayner, 1989a; Hazlehurst and Rayner, 1992b). The giant Cretaceous pterodactyloid *Quetzalcoatlus,* in fact, appears to have a relatively shorter wing-finger, given its great size, and this seems to accord with its presumed habit as a soarer over land (Lawson, 1975; Langston, 1981). Conversely, most small pterosaurs (wingspan 1.5 m or less) were almost certainly primarily flappers, not soarers.

It has not been generally appreciated that the pterosaur wing planform has a blunt tip (fig. 4A; Döderlein, 1929a). The overall impression is that the trailing and leading edges converge at a small acute angle at the wingtip, as is the case in many high aspect ratio birds; in the Zittel wing (BSP 1880 II 8), for example, this angle is approx 15°. But probably a length of about 17 mm of the apex is truncated from what would have been normally straight extensions of the leading and trailing edges. This does not seem to be an artifact because the bone of the distal wingphalanx is not broken, the wing is not torn, and there is no evidence of "missing" wing tissue on the specimen. The situation is the same in other specimens, in particular on both slab and counterslab of the Döderlein specimen of *Rhamphorhynchus muensteri* (BSP 1907 I 37; Döderlein, 1929a, Tafel I; fig. 3A), in the right wing of the Marsh specimen (YPM 1778; Marsh, 1882; Padian, 1979; fig. 3D), and in a Munich example of *R. longicaudus* (BSP 1938 I 503, fig. 3C). There are good mechanical and aerodynamic reasons why we might expect this slight rounding of the tip, though it cannot always be predicted on biological grounds. First, the wingtip is stronger if it is not excessively attenuated, for a sharp apex would concentrate mechanical stress; second, local turbulence is reduced around a blunted wingtip. A high aspect ratio planform with a narrow taper is ideal for efficient flight because of its effect on the vortex airflows generated in the wake (Rayner, 1986, 1988b, 1990, 1992), but the local geometry of the wingtip has a relatively small effect on the overall pattern of forces. The wings of birds with high aspect ratio very rarely come to a sharp point, and the tip of the longest primary is usually slightly rounded. In bats, the tip, formed in most species by the ends of the second or third digits, is pointed, but this is inevitable with an elastic membraneous wing stretched by relatively thin cylindrical bony spars. If the pterosaur patagium were a simple bat-like membrane it would not be possible to construct anything other than a sharply pointed wingtip, with the trailing edge reaching the end of the bone. The facts that in pterosaurs the tip is
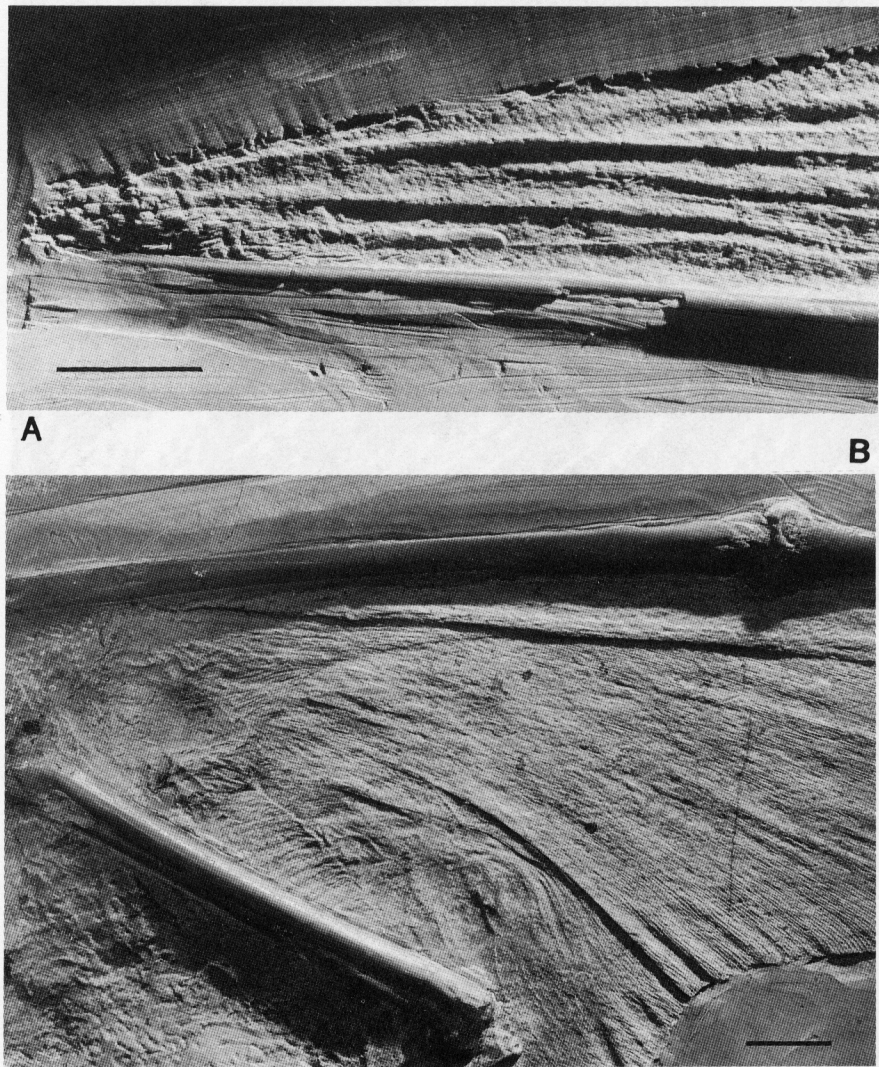
Fig. 4. Details of the Zittel wing (A-E; BSP 1880 II 8; fig. 1) and other important specimens (F-I) showing structural fibers. (A) Wingtip, showing the blunt planform of the very tip of the wing; folds and fibers run to the wingtip. (B) The region adjacent to the ulna and the wrist in the Zittel wing, showing the S-shaped curve in the fibers which represents folding of the patagium as the elbow, wrist, and metacarpo-phalangeal joints are flexed.

not sharp and that the trailing edge does not run precisely to the end of the fourth wing-phalanx are strong support for our argument that the wing was more than a simple membrane. Internal stiffness is essential if a rounded tip is to be mechanically resilient.

Fig. 4 (continued). (C) Trailing edge of the Zittel wing, showing fraying or detachment of fibers from the ventral side of the membrane. (D) The region of the Zittel wing behind the wrist joint (compare (B), where the trailing edge is sharply curved and waved; fibers curve so that they are approximately perpendicular to the trailing edge.
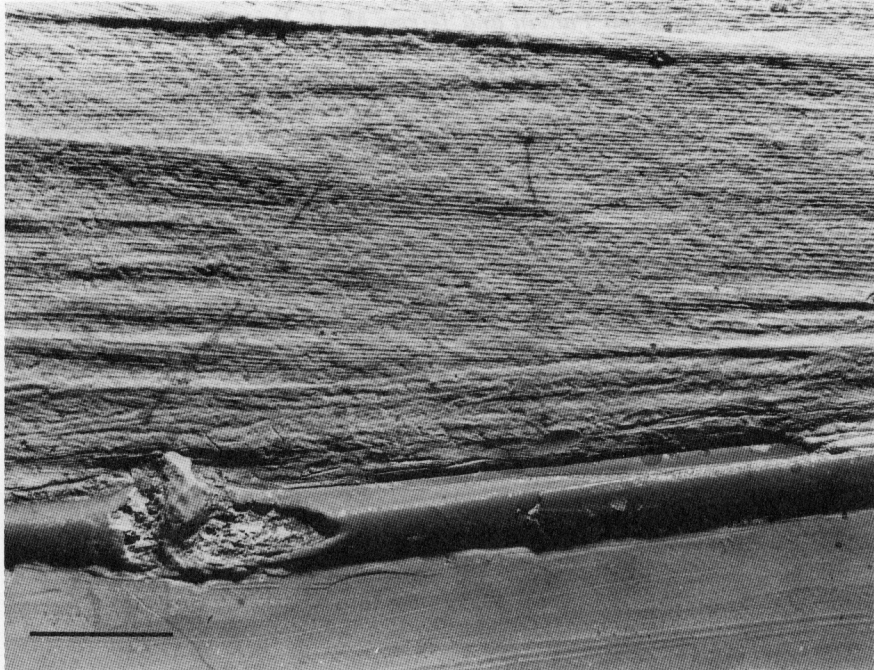
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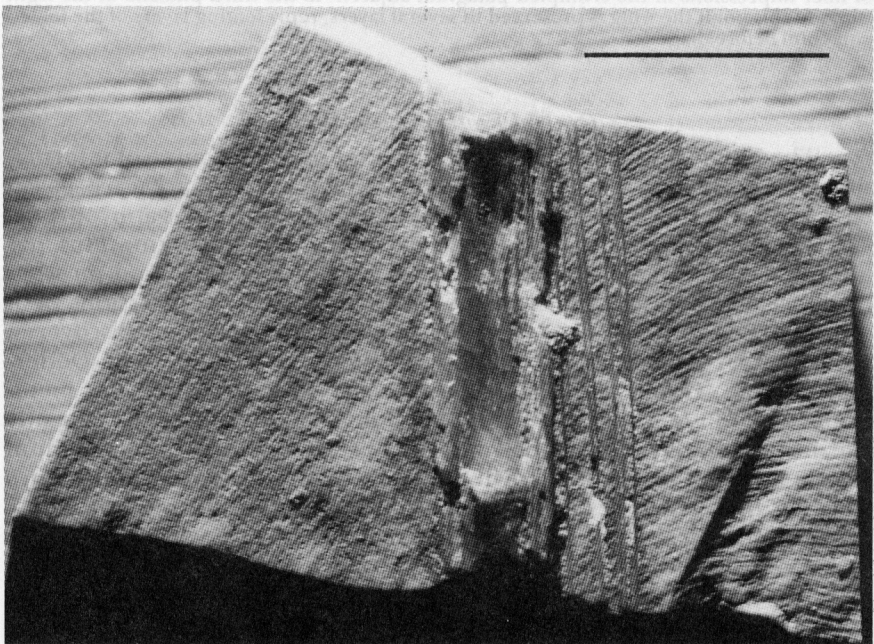
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(E) The region of the second interphalangeal joint of the Zittel wing, showing the straight course of fibers in the distal portion of the patagium, the strip of tissue behind the leading edge spar, and the groove in the phalanges of the flight-finger, which is slightly infilled with matrix to the left of the picture. (F) One of the counterslab fragments of the Döderlein specimen (BSP 1907 I 37; fig. 3A), showing fibers; the bone across the center of the fragment is a section of the tail, showing the stiffening ossified tendons.

Fig. 4 (continued). (G) The Zürich specimen (PMZ A/III 107; fig. 3E), showing detail of fiber impressions in the crumpled patagium adjacent to the third phalanx of the right wing. At this point the wing is preserved in several layers, representing layers of the folded patagium before diagenesis.

General Features of the Wing

The Zittel wing (BSP 1880 II 8) provides our best source of information about structures of the pterosaur wing; our remarks are based largely on this specimen, but we make reference to others as appropriate.

The wing membrane is manifestly constructed of skin. This has always been assumed, although it is difficult to trace how, and on what evidence, the supposition first entered the literature. Impressions of at least parts of the wings are relatively common in specimens discovered since about 1870, and many authors, including von Zittel, Abel, Döderlein, Wiman, Broili, and von Arthaber, have discussed the wing membrane as a matter of course. The patagium structure has been recently clarified by the analysis of a Brazilian Cretaceous pterosaur patagium fragment by Martill and Unwin (1989 and personal communication), showing fine structures of the dermis and epidermis, though the exact topographic position and orientation of their fragment, as well as the details of variation across the patagium, are still controversial.

Medial wing attachment.—The patagium is attached along its leading edge to the spar of the forelimb and wing-finger. Proximally it runs along the body wall caudally. Its posterior limit is not clear and has long been a matter of debate; possibly this varies among genera. Since von Soemmerring's (1820) original reconstruction based on a misidentification, the
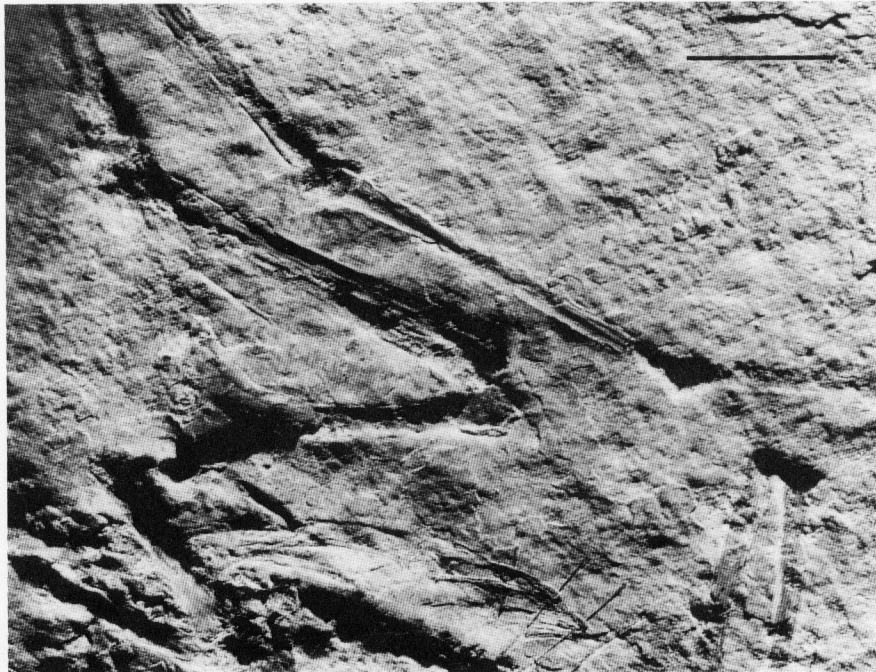
Fig. 4. (H) Detail of the right wing of the Vienna specimen of *Pterodactylus kochi*, showing fibers, the oval region bounded by the trailing edge of the wing (see also fig. 10A), and the notch-like area at the top of the oval, immediately behind the elbow, where multiple layers of the wing are overlaid; multiple layers are preserved between the ulna and the wing-phalanges, as is evidenced by the varying courses of the fiber axes. (I) Detail of small patches of well-preserved fibers on the wing of *P. kochi* (BSP 1924 V 1; Broili 1925). Fibers are identified on this specimen by small, brown patches, presumably of different chemical composition; the fiber orientations match exactly those on the two *Pterodactylus* specimens illustrated in figure 3. See figure 9 for detail of the Marsh specimen. All scale bars 1 cm.

A
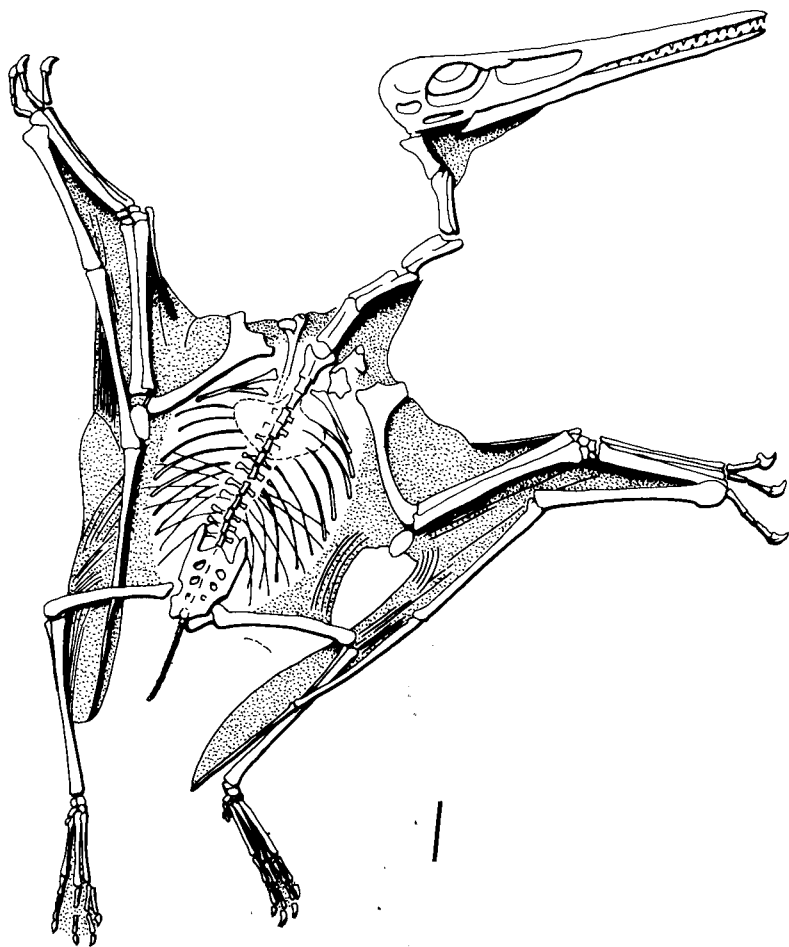
Fig. 5. Diagrams of pterosaur wing outlines according to different models. (A) Vienna *Pterodactylus kochi* (NHMW 1975/1756; after Wellnhofer, 1987, and fig. 3F); the stippled areas mark the extent of preserved or impressed soft parts. Scale bar 1 cm.

early tendency was to draw the wing extending to the ankles, as in bats, though there was—and remains—no direct evidence for this. Von Zittel (1882) noted the high aspect ratio of the wing, in contrast to Marsh's (1882) wide-winged reconstruction (strongly inspired by Owen's drawing of *Dimorphodon* [1870]), but von Zittel still sent the wing plunging to the foot in his own reconstruction, despite the fact that in Marsh's specimen—as in many others—the foot is clearly free of the wing (Padian, 1979, 1987; fig. 3D).
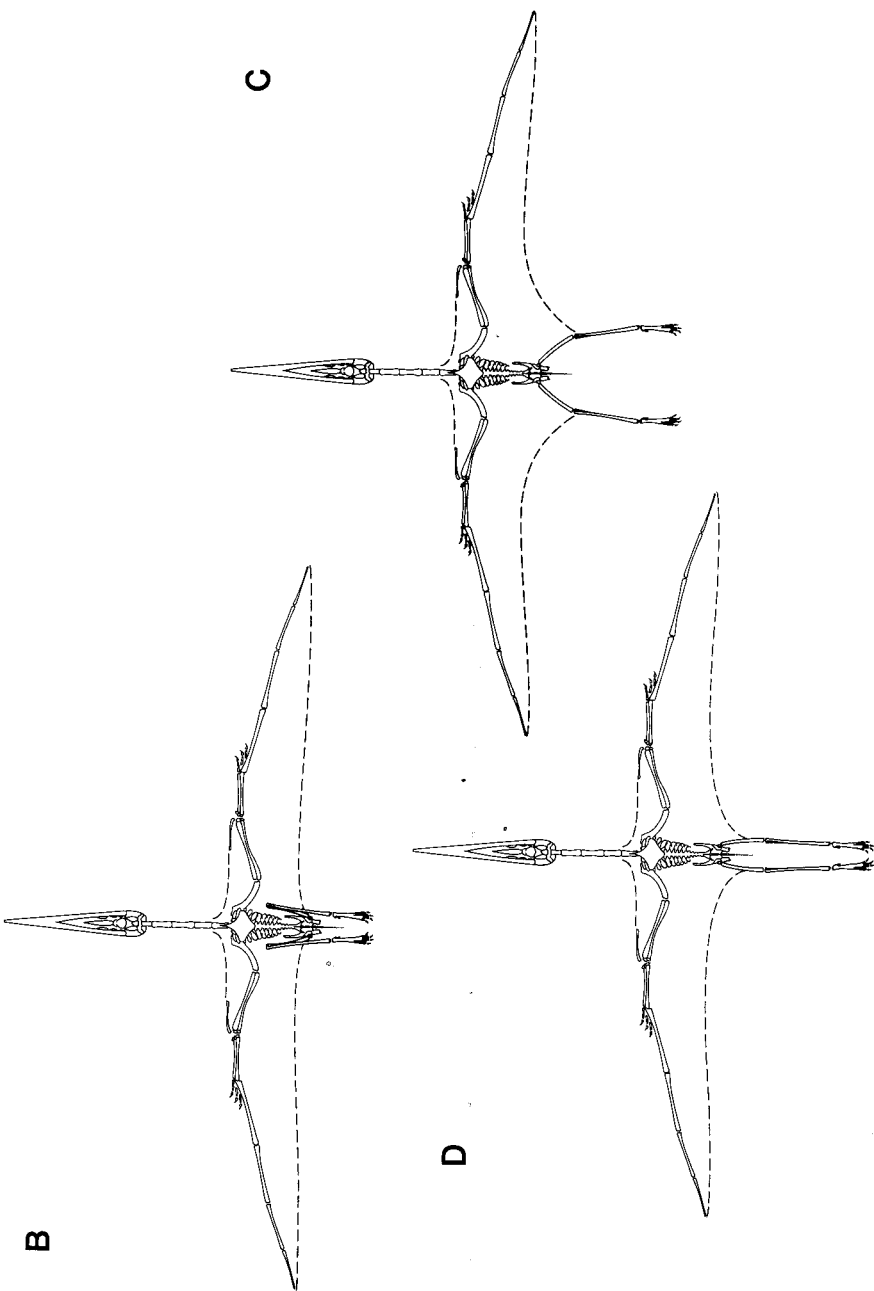
(B) Restoration of *Pterodactylus* with hindlimb free (Padian, 1983). (C) Restoration of *Pterodactylus* with patagium to knee (after Wellnhofer, 1987). (D) Restoration of *Pterodactylus*, with the femur trailing behind.

Most recent authors have connected the wing to the upper leg or knee (Wellnhofer, 1978; fig. 5A, C, D). Padian (1983) showed that the pelvis and hindlimb of pterosaurs are constructed and articulated like those of birds and other dinosaurs and concluded that the wing was probably not connected to the hindlimb (fig. 5B) because (1) the wing planform was too narrow; (2) the femora probably folded forward under or parallel to the body during flight, like those of birds; and thus (3) in this position the wing would have folded and created a pocket that greatly increased drag near the body. However, in 1987 Wellnhofer described the *Pterodactylus kochi* in Vienna (NHMW 1975/1756) in which the wings apparently connected to the thigh about two-thirds of the distance along the femur (fig. 3F, 5A, D). Wellnhofer suggested that the patagium in this specimen might have stretched alongside the lateral face of the tibia but is now hidden beneath the tibia; we see no direct evidence to support this view. Moreover, the specimen is preserved in dorsal aspect, and inasmuch as (with this model) the wing would have to attach to the *rostral* or *dorsal* side of the leg to avoid restricting terrestrial movement, it is likely that it would have been visible on this specimen. The hindlimbs of *Pterodactylus* do not differ fundamentally from those of other pterosaurs. If the Vienna specimen can be taken at face value (and we consider the complex configuration of the left wing sufficient reason to question this), then either (1) the femur extended backward, not under the body, during flight (fig. 5D); or (2) the femur rotated forward, upward, and outward at the hip joint slightly (fig. 5C). In this position the wing would have remained taut and the legs could still have accommodated bipedal terrestrial locomotion. Structural fibers are less prominent in this region of the patagium (von Zittel, 1882; Wellnhofer, 1975c), and we have looked for them on all available specimens, finding them only very rarely. This may reflect a real structural difference in the wing: if the most proximal part of the membrane lacked structural fibers, it could have been sufficiently elastic that in flight the "pocket" became stretched out. It would not matter whether the leg were stretched behind the body in flight (fig. 5D) or retracted under the body in the manner of birds (fig. 5B), because the aerodynamic loss to the airfoil would be negligible.

No specimen to our knowledge gives incontrovertible evidence that the patagium attached to the lower leg or foot *in any pterosaur*. It is at present impossible to say whether the mid-thigh configuration was common to all pterosaurs or to certain taxa only. But regardless of the reconstruction the hind leg could not have usefully influenced the wing mechanically in flight.

Uropatagium.—No incontrovertible evidence for an interfemoral membrane or a uropatagium has been advanced for any pterosaur. Sharov (1971) reconstructed one for *Sordes pilosus,* but the specimen is so distorted in preservation that the inference is tenuous at best. Bennett (1987a) argued that the morphology of the tail of *Pteranodon* suggested that a membrane was attached to it, but there was no direct evidence for such a membrane, and in any case it would not seem to have involved the

hindlimbs to any degree. There is never evidence of interfemoral membranes in *Rhamphorhynchus* or *Pterodactylus* (Wellnhofer, 1987), the two genera known from the greatest number of specimens with preserved wing remains. Pennycuick (1986, 1988) reconstructed a uropatagium (an interfemoral membrane involving the tail) for the latter genus, based on a groove present behind one knee on one specimen of *P. kochi* (BSP 1937 I 18; Broili, 1938; fig. 3G), but this reconstruction cannot be conclusive because this specimen shows many remains of soft tissue around the neck, wings, free fingers, legs, and feet, but otherwise none behind the legs. Pennycuick's supposed uropatagium would have been broadest at the knee, not at the midline of the tail region where it would have had greatest aerodynamic effect. Similar traces of a putative tail membrane are absent on all other *Pterodactylus* specimens we have examined, even where preservation is comparable to that of the Munich *P. kochi*.

The aerodynamic necessity of such a tail membrane is questionable at best, given that *Pterodactylus* was a relatively small, active flapping flier. Moreover, if pterosaurs were bipedal and erect, and their gait parasagittal, as we discuss below, an interfemoral membrane would only have interfered with terrestrial locomotion. Some specimens have suggested to various paleontologists a webbed membrane between the digits of the foot (table 1; Broili, 1927a; Döderlein, 1929c; for recent reviews see Wild, 1978; Wellnhofer, 1970, 1975c, 1978, 1987, 1991a), possibly for use in swimming, but there is as yet no way to tell traces of such a webbing from those of any soft tissues.

Trailing edge tendon?—There is no evidence for a tendon running from the wingtip toward the body along or near the trailing edge in any specimen, particularly in the best preserved such as the Zittel, Marsh, and Döderlein specimens of *Rhamphorhynchus*, or the Munich or Vienna *Pterodactylus*. Because of the internal construction of the wing, which we will explain later on, such a tendon would have been structurally and aerodynamically unnecessary. Other models of the wing do require a trailing edge tendon. Pennycuick (1988, p. 311) postulated a trailing edge tendon in *Rhamphorhynchus*, based on a single specimen (SMF R4128; Gross, 1937, 1938) in which the legs appear to be pulled forward. There are several problems with this interpretation. First, there is no direct evidence on this specimen of the preservation of any such soft tissues apart from several folds in the patagium, so the inference is purely speculative. Second, as Gross (1937) indicated in his original description of the specimen, one of the wings was removed to its present position during preparation (compare his fig. 1 and pl. 1), so the condition does not reflect the natural preservation of the fossil. Consequently, this specimen does not support Pennycuick's inference.

Wing-finger groove in Rhamphorhynchus.— As noted by Kremmling (1912), Gross (1937), and Wellnhofer (1975a), in the Zittel specimen, as well as in others of the genus *Rhamphorhynchus*, there is a groove-like indentation along the caudal edge of the wing-phalanges (which is also present in the closely related, and perhaps congeneric, form *Nesodactylus*;

Colbert, 1969). The Zittel wing and other specimens show that this groove was not the origin of the patagium; rather the patagium lay *above* this groove (not topographically *below* it as preserved in the Zittel wing, which lies on its dorsal side), at the level of the dorsal edge of the wing spar and the caudal projection of the dorsal part of the bones of the wing-phalanx (fig. 4E). The groove probably did not house a tendon attached to proximal muscles that retracted or flexed the wing, because, as we have argued above, there is no evidence for any substantial flexure of the interphalangeal joints, and we see no obvious behavioral or aerodynamic reason for them to move. Indeed, if these joints were semi-rigid they would better resist bending backward under aerodynamic drag while in flight. The C-shaped cross-section produced by such an indentation in the bone's cross-sectional profile may have given strength to the phalangeal bone wall, but the obvious question is why *Rhamphorhynchus* and *Nesodactylus* are unique among pterosaurs in possessing such a groove: in other species the bones are typically subcircular or ellipsoidal (Bramwell and Whitfield, 1974; Wellnhofer, 1970, 1978; Currey and Alexander, 1985). The groove may possibly have been the site of cells and their associated innervation giving rise to the membrane and the fibers within it, but the same question may be raised about its variable taxonomic distribution.

Tissue posterior to the spar.—Just behind the trailing edge of the wing-finger of the Zittel wing is a narrow strip of patagium in which the fibers characteristic of the rest of the membrane run in a direction more parallel to the wing spar than do those behind it (fig. 4E; also noted by Pennycuick, 1988, p. 307). This strip is 6 to 7 mm wide at its broadest part behind the joint between the first and second wing-phalanges and remains fairly uniform in breadth until halfway along the third wing-phalanx, where it abruptly disappears and regular fibers resume their course. A similar strip may also be visible in the Marsh wing (fig. 3D). We propose that this may represent the position of a strip of tissue (muscle, nerves, and connective fascia) adjacent to the leading edge spar. This tissue may have been ventral to the patagial fibers (which are themselves on the ventral surface of the patagium; see below), thereby obscuring them. We considered the alternative that this region may represent a slight separation of the patagium from the spar, caused by post-mortem rotation of the wing. But this possibility is falsified by the presence of fibers within this region and by observing the part of the wingtip distal to the third wing-phalanx. Here the fibers are clear from immediately behind the bone to the trailing edge and wingtip. Close observation of the strip behind most of the proximal wing reveals occasional evidence of fibers, presumably beneath the ventral surface of the patagium, and perhaps within the tissue; so we are led to conclude that this strip is actually tissue ventral to the wing surface and to the fibers in this area. It may however have been distorted by post-mortem rotation of the spar.

Features of the patagium.—Several other conspicuous wing structures have been noticed and described by many authors. Two of these are the folds (*Falten*) and the fibers (*Fasern*), which are the subject of the following

sections. Here it is necessary to note only that the membrane surface is invested with fine, long, parallel structures, often called fibers (fig. 2). Although the fibers may curve along their lengths, they are virtually never bent or broken (Wellnhofer, 1975c; Padian, 1983). They are often gathered into folds, parallel to the grain of the fibers, and impressions of these folds are visible in many specimens, even where no sign of the presence of fibers or any other soft tissues remain (table 1). The fibers are essential structures of the patagium, but the folds are not real structures; rather, they are symptoms of deformation of the patagium when the wing folds and flexes. We can also identify creases and wrinkles, which are generally the result of post-mortem disturbance. Our observations of these structures form the major part of this paper and are discussed in the next sections.

The Zittel Wing and its Preservation

To examine pterosaur wing structures further we must concentrate on the Zittel wing (fig. 1, 2). This wing is a disarticulated left forelimb preserved in ventral view, with no evidence of the rest of the body. We emphasize that this is a real fossilized patagium or is at least a positive replacement (cast) of it, not a mold (negative impression). It is unusual among Solnhofen fossils in that the wing appears to be preserved on the *upper* surface of the stone slab (our observations; P. Wellnhofer, personal communication) rather than on the *lower* surface, as is more usual (de Buisonjé, 1985); no counterslab is known.

Our strongest evidence for the claim that this is a real fossilized patagium comes from the area near the trailing edge directly behind the joint between the second and third wing-phalanges. *In this region several fibers, preserved in positive relief, have separated from the surface of the wing to cross other adjacent fibers that remain in place* (fig. 4C). This fact is sufficient to falsify Pennycuick's (1988) assertion that these features are merely wrinkles, not structural fibers. These fibers take the form of thin threads raised in relief above an otherwise smooth surface. There are two possibilities: either the specimen comprises the actual ventral surface of the patagium, or it is an impression (mold) of the dorsal surface, and the actual patagium has disintegrated. Let us consider the second possibility first. If the specimen were an impression of the patagium (fig. 6A), then

Fig. 6(A) If the Zittel wing were an impression (mold), we would see mostly fiber impressions (fi), with positive relief showing impressions of grooves (gi) where fibers had been displaced. The displaced fibers themselves (dfi) would appear as deeper indentations. (Most other specimens showing fibers are molds, and the fiber courses are marked by fine grooves.) (B) Instead, we see the fibers (f) as positive structures; displaced fibers (df) stand out clearly in positive relief against their former grooves (g). The Zittel wing is therefore a cast of the wing itself. Spanwise extent of membrane in each figure is 1 mm.

what appear to be fibers would have been grooves or indentations on the original, and this is inconsistent with the patterns of crossing of the fibers that can be seen. Moreover, when the fibers were displaced from their natural positions the grooves would be deeper where the fibers had originally been ("dfi," fig. 6A), because the fibers would only have been preserved as impressions to begin with; yet in these positions the surface is *lower*. Where fibers are present there is in fact increased positive relief, which is to be expected if the actual wing (or a cast of it) is preserved (fig. 6B).

These arguments demonstrate either that the actual patagium (not a mold) has been preserved or that a mold of the patagium formed during diagenesis has secondarily formed the cast of the specimen as now preserved. Other specimens are not preserved in this way; for instance, the Döderlein specimen appears to be composed largely of a mold of the ventral side of the wing, together with a cast of some of the isolated fragments of this specimen.

Structural Fibers of the Patagium

Von Zittel (1882) seems to have been the first to recognize the fine parallel structures that invest the surface of the pterosaur wing, at least the part distal to the elbow (fig. 1, 2, 4, 7), although with hindsight we can recognize that some previous authors (von Meyer, Wagner, et cetera) had probably considered similar structures to be hair. Von Zittel called these "Streifen," or *striae,* and recognized that they were integral structural elements (1882, p 53):

> They show up very distinctly, remain mostly undivided, and are never curled into undulations. In the trunk region, where the wing is broader, their course is more oblique; they press together more closely and curve downward in the region of the trailing edge. At the same time there frequently appears a bifurcation of the striae near the trailing edge. In general, however, the striae show a certain rigidity, and therefore cannot at all be compared with the highly irregularly-running and wavy, curved or undulating small folds in the patagium of a bat. (our translation)

Many subsequent authors—including ourselves—have returned to von Zittel's specimen, and subsequent descriptions of the structural fibers in this and other *Rhamphorhynchus* specimens (Wanderer, 1908; Döderlein, 1923, 1929a; Wiman, 1925, et cetera) reveal few discrepancies with the observations of von Zittel.

Topography of the fibers.—Nearly every worker who has examined von Zittel's specimen has been impressed by the fact that the striae are parallel and are never bent or folded against their longitudinal axis. Von Zittel himself noted, in addition to the striae, folds in the patagium that were "scrupulously parallel" to the striae; we describe the folds below. He also noted other parallel, rust-colored marks he thought may have been stiffened ligaments, but later workers have not sustained this view. These marks appear to be artifacts of mineral deposits running along the grooves left by the fibers; identical colored marks run along cracks in the bedding plane of the specimen and are common in the Solnhofen limestone.
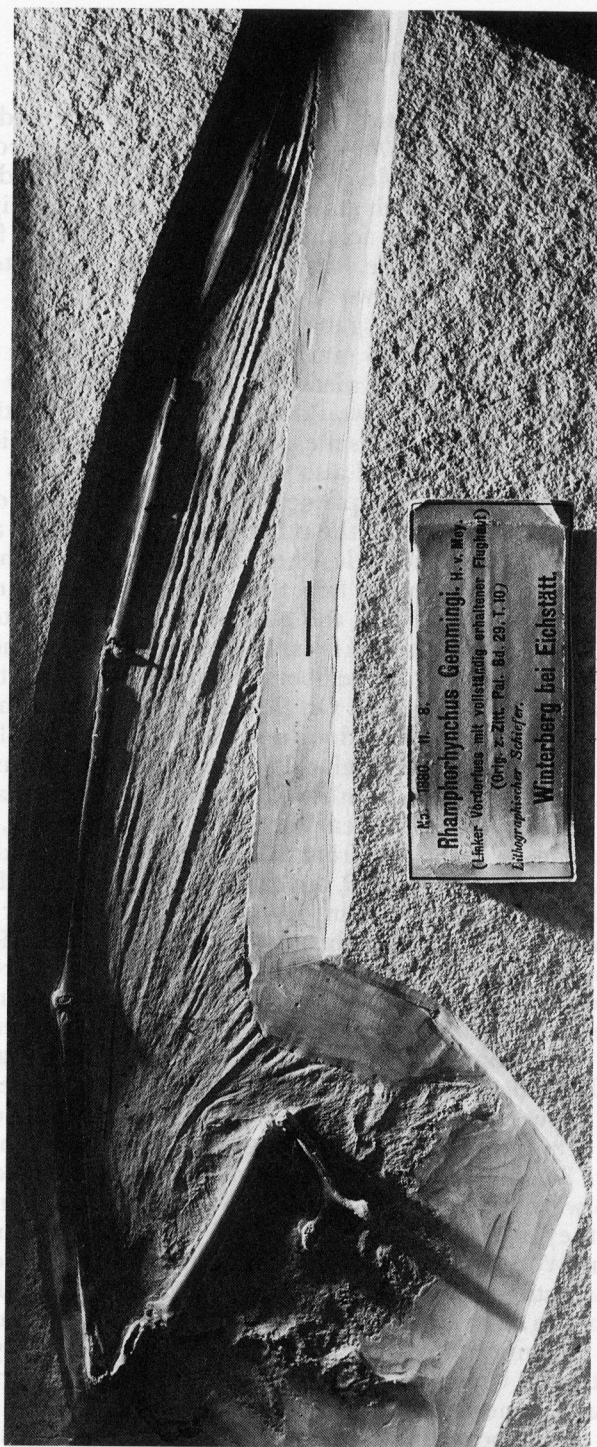
Fig. 7. The Zittel wing (BSP 1880 II 8) in shallow, oblique light, lit directly rostral to the leading edge. Folds and structural fibers stand out clearly in positive relief. (This specimen was originally referred to *Rhamphorhynchus gemmingi*; Döderlein was responsible for the old misidentification as the right wing in dorsal aspect, noted in manuscript on the label.) Scale bar 2 cm.

Wellnhofer (1975b, c) and other workers have adopted the term *Fasern,* which means *fibers* (or *threads*) for what von Zittel called *striae.* To emphasize their functional role, Wellnhofer (1987) suggested changing the term to *Aktinofibrillen,* which makes sense as a precise descriptor of the fibers of the *Aktinopatagium,* or actuating patagium. However, for want of an appropriate English cognate, it may be simpler in English to conserve the term *structural fibers,* which we do here.

Wellnhofer (1975c, 1987) gauged the thickness of the individual structural fibers at approx 0.05 mm, with a uniform distance of 0.2 mm between parallel fibers; similar measurements were given by Döderlein (1923). Four or five such fibers would be present in the breadth of 1 mm. We have confirmed Wellnhofer's measurement of the fiber thickness at a uniform 0.05 mm, but we have also observed that in places where the wing is most stretched, for example near its trailing edge, there may be as few as three fibers per mm. On the other hand, there can be as many as eight fibers per mm near the folds, where the patagium is gathered.

There is some question just how thick the actual fibers are, and the interpretation depends on how the patagium is reconstructed. Wellnhofer's (1987, fig. 2) hypothetical cross section suggests that most of what appears to the eye is skin, with the fibers occupying perhaps a third of the skin's vertical thickness (fig. 8A). On the basis of further examination of the specimen, this embedding does not seem to us plausible, because near the trailing edge of the Zittel wing, where the fibers have separated from the membrane and cross other fibers (fig. 4C), their diameters do not change. If the fibers were breaking free of the membrane, such as an electrical wire might break free from its insulation, they would appear to be thinner where they were freed, but this is not the case. Furthermore, if the fibers were embedded within the membrane, the layer of dermis overlying them would soften their image (see also Wiman, 1925); yet in the Zittel wing, Marsh specimen, and others, they are preserved in extreme sharpness, even where they are frayed near the trailing edge.

On the other hand, we have noted a marked difference in the appearance of the dorsal and ventral surfaces among individual *Rhamphorhynchus* and *Pterodactylus* wings. The ventral sides, such as one sees in the Zittel wing, show more clarity and greater relief than the dorsal sides, such as one sees in the slab and counterslab of the Döderlein specimen. As our figure 8C shows, the fibers were embedded in the skin on one side only and so were more prominent on the ventral side, whereas on the dorsal side they are distinguishable only as vague softened impressions through skin. We advance this as a possibility that must be tested through further observations; perhaps at some point a specimen of patagium (rather than of a cast) may come to light that might be sectioned, or to which SEM magnification can be applied. The specimen analyzed in this way by Martill and Unwin (1989) was reported as lacking structural fibers and may have come from the propatagium on the cranial side of the radius and ulna, between the forearm and the humerus; however, subsequent investigations have revealed relatively large circular struc-
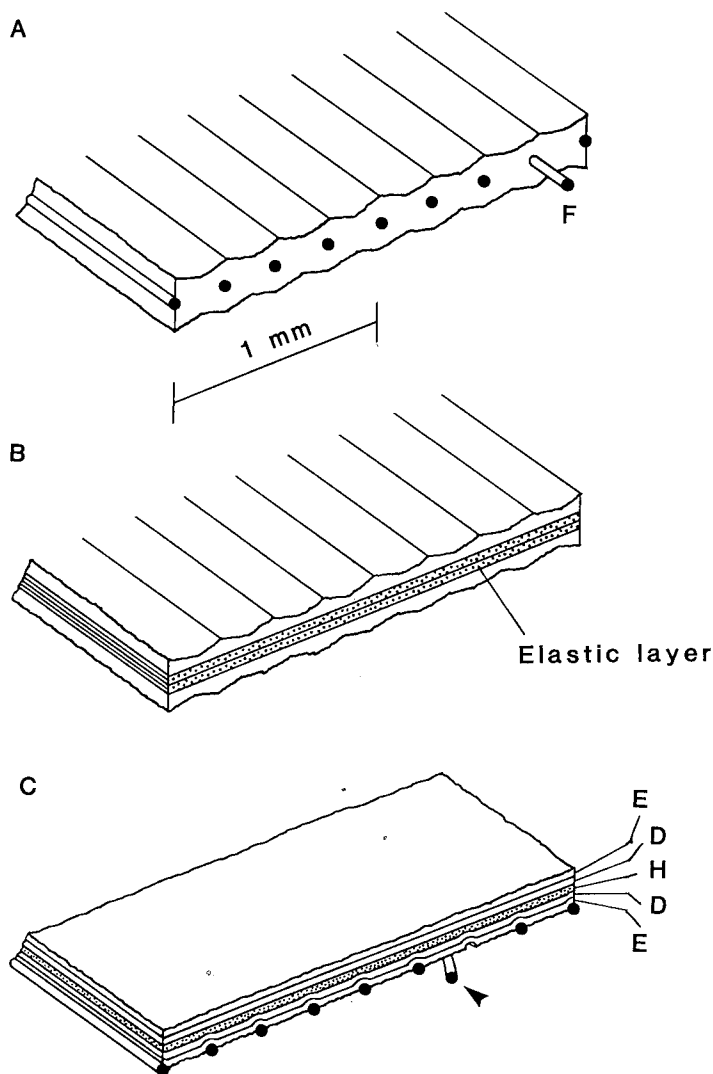
Fig. 8. Models of the pterosaur patagium. (A) Structural fibers embedded in the membrane (after Wellnhofer 1987). (B) Dermal membrane with intrinsic elastic layer (after Martill and Unwin, 1989). (C) Dermal membrane with superficial fibers on the ventral surface. Our arguments indicate that model (B) is untenable on aerodynamic and mechanical grounds and is inconsistent with the fossil record, and that model (A) is unlikely since features such as the displaced fibers imply the structural fibers were superficial on the ventral surface (or possibly covered with an extremely thin layer of epidermis). D, dermis; E, epidermis; F, fibers; H, hypodermis. Arrow in (C) indicates a displaced fiber.

tures in cross section close to one (unknown) surface of this fragment, and these may represent fibers (D. Martill, personal communication).

Continuous or discontinuous fibers?—Several further features of the distribution of fibers are of general interest here. As many authors have noted, it is difficult to trace individual fibers from the leading edge to the trailing edge of the wing and to be sure where they begin and end, because the paths of fibers may become temporarily indistinct or may run into folds and be lost from sight temporarily. So it is very difficult to judge the average length or rate of intercalation of the fibers in even the best specimens. Sometimes the fibers appear to recede anteriorly beneath the wing surface, and often they are gathered near the folds, where the distances between adjacent fibers diminish, probably as a function of contraction of elastic interfibrillar tissue. In many places where a fiber seems to disappear, it can be observed that the fibers previously on either side of the lost one now run more closely together, and frequently this is also symptomatic of the appearance of a fold. Two fibers may through their course widen the distance between them, and the intervening gap is eventually occupied by a third fiber. *However, our examination of the Zittel wing and other specimens convinces us that these intercalations are comparatively rare.*

Additionally, fibers appear to bifurcate near the trailing edge, as many authors beginning with von Zittel (1882, p. 53) have noted. We do not think these are truly bifurcations; instead, this is the region where some fibers have frayed and become loosened from their positions in the membrane, which we discussed above: one sees a fiber and the course of its former groove. We have observed, particularly along the trailing edge, directly behind the junction of the second and third wing-phalanges in the Zittel wing, that many such fibers bend and cross over other fibers that continue in their regular channels (fig. 4C). This is conclusive evidence not only that the fibers were real, but that they were important structural elements, not merely wrinkles as Pennycuick (1986, 1988) maintains. It is also strong evidence for our inference that the fibers are superficial structures on the ventral surface of the wing.

The fibers as structural elements.—The distribution of structural fibers in the wing is noteworthy. As Padian (1983, 1985) observed, the fibers are arranged in a pattern that parallels the feather shafts in birds and the third, fourth, and fifth fingers in bats, which are the main structural elements of the respective wings. In the forearm region the fibers run caudally to caudolaterally, but moving distally along the wing-phalanges, the fibers run progressively more laterally, until they nearly parallel the wing spar. Avian primary feathers run laterally out to the tip of the wing, but the secondary feathers of the arm run caudally. Wellnhofer (1987) has supported this view, but Pennycuick (1988, p. 305–6) has disagreed, viewing the fibers (which he believes are merely wrinkles) as more akin to the barbs of feathers than to their shafts. This is true as regards their fineness, but their direction is with the shafts, not with the barbs, and the fibers are not hooked and do not interlock like barbs. They are indeed

thinner than feather shafts, but there are many more of them in the pterosaur wing than there are feathers in the bird's wing, just as there are more feather shafts in the bird's wing than fingers in the bat's. Moreover, the fibers alone do not form the wing surface, any more than do bird feather shafts or bat digits; in each case these are the stiffening elements that give the wing its structural integrity, and that transmit aerodynamic force generated on the wing surface proximally to the wrist and arm bones, and ultimately to the trunk (see below). In the pterosaur the fibers were embedded onto, and connected by, a membrane formed primarily of skin. Pennycuick's analogy therefore fails on structural and functional grounds (see below).

Folds, Creases, and Wrinkles in the Wing

Folds parallel to the fibers (fig. 2) run all through the Zittel wing distal to the metacarpo-phalangeal joint, as well as behind the ulna, and are most clearly seen in very oblique light (fig. 7). They are also visible in many other *Rhamphorhynchus* specimens, and occasionally in *Pterodactylus* (figs. 1, 3; table 1). Commonly in *Rhamphorhynchus* a fold runs distally from the first interphalangeal joint, possibly representing slight chord-wise contraction of the patagium when at rest. The right wing of the Marsh specimen (figs. 3D, 9) lies alongside the tail and has a series of folds that increase in number and proximity toward the wing spar, where the wing is folded upon itself parallel to the structural fibers. The left wing of the same specimen is incomplete past the mid-point of the second wing-phalanx, but it shows similar folds in its distal region, as well as many near the trailing edge of the more proximal part. These smaller folds are parallel to the local direction of the structural fibers, which here run obliquely to the trailing edge in this region. Fibers are also clearly visible in this specimen (fig. 9), and similar folds can be seen on the Zittel wing (fig. 4D, 7). Superimposed on this structural pattern in the Marsh specimen is a series of patternless deformations of the wing (fig. 9). The latter are actual wrinkles in the wing, as can be told by examination of the matrix of the specimen, which is full of ripples and bends that give the bedding plane an irregular surface. These ripple marks and diagenetic deformations of the sediment have crumpled the wing to create true wrinkles. Similar features are reported on the Leich (1964) and Wanderer (1908) specimens and are visible on the Zürich specimen (PMZ A/III 107; figs. 3E, 4G) but the Zittel wing shows no such features distal to the metacarpo-phalangeal joint, presumably because it was preserved on a perfectly flat, uniform bedding plane. However, the bedding surface is uneven in the region of the humerus and forearm, as many authors have noted, but nowhere else on this slab. The most reasonable explanation of this, to us, is that the wing is flexed at the wrist joint, and post-mortem contraction in this area is responsible for the unevenness in the bedding plane, and hence for the crumpled condition of part of the patagium. So true wrinkles can be distinguished from the gathered, parallel structural fibers, *which are not wrinkles*. Behind the ulna the fibers
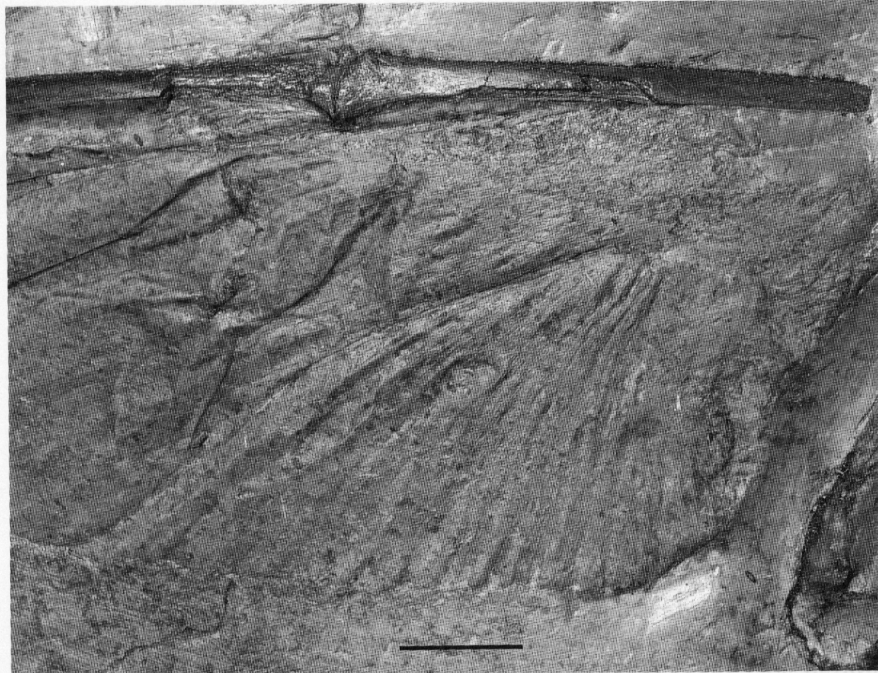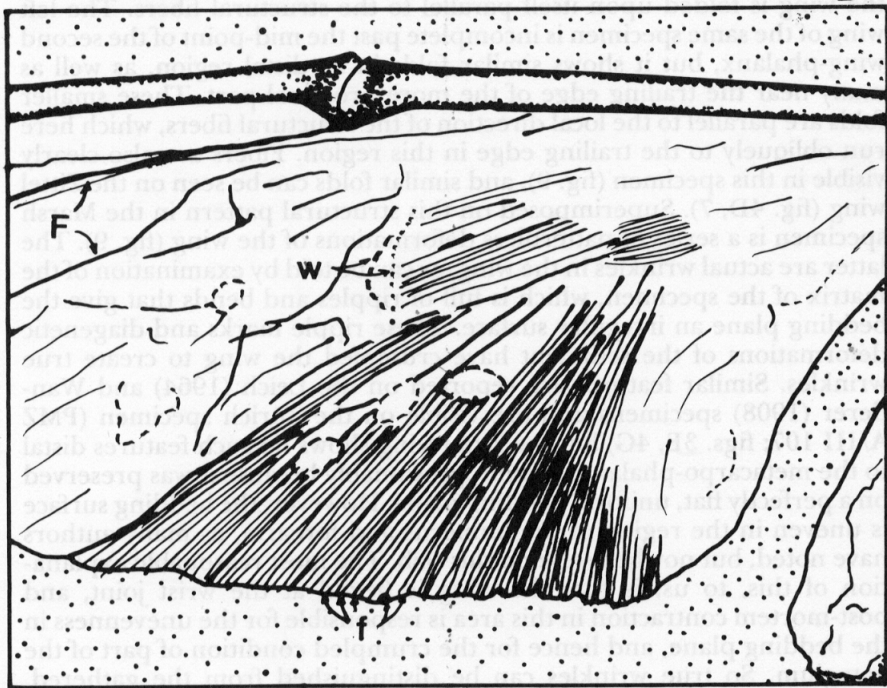
Fig. 9. Detail of the left wing of the Marsh specimen of *R. muensteri* (YPM 1778; Marsh, 1882; fig. 3D), showing folds (F), structural fibers (f), wrinkles (W) and deformations of the patagium surface (dotted lines). Scale bar 1 cm.

follow a sweeping S-shaped curve (fig. 4B) where the wing has flexed at the wrist, but the folds and wrinkles still remain broadly parallel to the local axes of the fibers. Similar patterns of fiber orientation are visible in this area in a fine, complete *Rhamphorhynchus* specimen in the Bürgermeister-Müller-Museum, Solnhofen, and in PMZ A/III 107 (fig. 4G).

Folds are also known in specimens of *Pterodactylus;* Wellnhofer (1987) described folds in the Vienna specimen of *P. kochi* (NHMW 1975/1756; fig. 3F), parallel to the direction of the structural fibers, which are clearly visible on many areas of the wing surface (Pennycuick, 1988, p. 308, demurs, interpreting them as mineral stains marking contractions in the wing). Between the right elbow and the femur in this specimen, and also in BSP 1937 I 18, there is an oval marking the posterior outline of the wing, and the oval has a pointed indentation near the elbow (Wellnhofer, 1987, p. 155; fig. 10). Wellnhofer suggests that this point marks the collection of contracted structural fibers in that area, originating from the carpal region and virtually seeming to poke through (*durchstoβen*) the posterior margin of the wing (see Pennycuick [1988] for a dissenting opinion). Fibers adjacent to this region run in two different directions, probably because multiple layers of the wing are preserved in this area. The latter specimen also shows a deep groove representing folds parallel to the fibers and phalanges of the left wing. Wellnhofer's
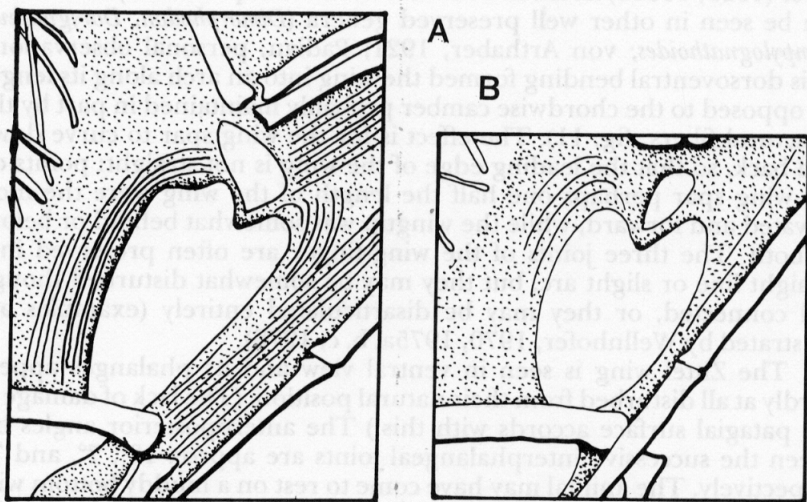
Fig. 10. Diagrams of the right wings of (A) Vienna (NHMW 1975/1756; figs. 3F, 4H, 5A), and (B) Munich (BSP 1937 I 18; fig. 3G) specimens of *Pterodactylus kochi,* showing the oval hole formed by the absence of the patagium behind the elbow and folding of the patagium adjacent to the body. In (A) it is unclear whether the patagium passes over or under the knee. The geometry of the two specimens is extremely similar; both show structural fibers, although the nature of preservation and the type of matrix differs somewhat. In (B), the most obvious regions of fibers are seen on the left wing, although a few are visible on the right wing.

observations of the rigidity of these fibers and the folds that gather them in the wing accord with our own.

A problem that has not hitherto been considered in any detail is the geometry of the pterosaur wing when at rest. Some specimens with highly flexed wings (*Rhamphorhynchus* BSP 1938 I 503 [fig. 3C]; *Pterodactylus* NHMW 1975/1756 [figs. 3F, 5A]) appear at first sight to have very narrow patagia close to the wing spar. This may represent extreme chordwise contraction of the membrane between the fibers. However, we conclude that in both these specimens, as in several others, the wing has been folded along creases parallel to the fibers and fell into multiple layers, possibly like a Roman blind. Only the more superficial of such layers would of course be impressed on the substrate. This form of folding would also give rise to marked creasing of the proximal part of the wing adjacent to the ulna when at rest (for example, the Zittel wing, where the degree of flexure is smaller; PMZ A/III 107; fig. 3E).

Post-mortem Rotation of the Wing Spar

The wing spar in pterosaurs, unlike that of most airplanes, was not held perfectly horizontal. This is partly because it had to be moved during flight and so undertook the generation of both weight support and thrust, instead of just weight support. But even the wing-finger was not horizontal: individual phalanges had a slight dorsal arc, as Wellnhofer (1985, 1991b) noted in Brazilian Cretaceous pterodactyloids and as can be seen in other well preserved genera (*Dimorphodon, Dorygnathus, Campylognathoides;* von Arthaber, 1921; Padian, personal observation). This dorsoventral bending formed the wing into an arch along its length (as opposed to the chordwise camber probably maintained in part by the structural fibers; fig. 11). The effect is for the wing spar to curve down and back, so that the leading edge of the wing is not straight: points on the wing spar perhaps one half the length of the wing were the most elevated and forward, while the wingtip was somewhat behind or below, or both. The three joints of the wing-finger are often preserved in a straight line or slight arc, but they may be somewhat disturbed though still connected, or they may be disarticulated entirely (examples are illustrated by Wellnhofer, 1970, 1975a, b, c, 1978).

The Zittel wing is seen in ventral view and its phalanges appear hardly at all disturbed from their natural position. (The lack of damage to the patagial surface accords with this.) The anteroposterior angles between the successive interphalangeal joints are approx 12°, 7°, and 7°, respectively. The animal may have come to rest on a muddy bottom with some possibility of sinking those portions of highest relief into the substrate; however, they did not sink much because the membrane has been stretched perfectly flat and in the distal portion of the wing is not dorsoventrally distorted. Because the wing has been compressed by post-mortem distortion into a dorsoventrally flat and horizontal plane, the wing-phalanges must have experienced some backward rotation or
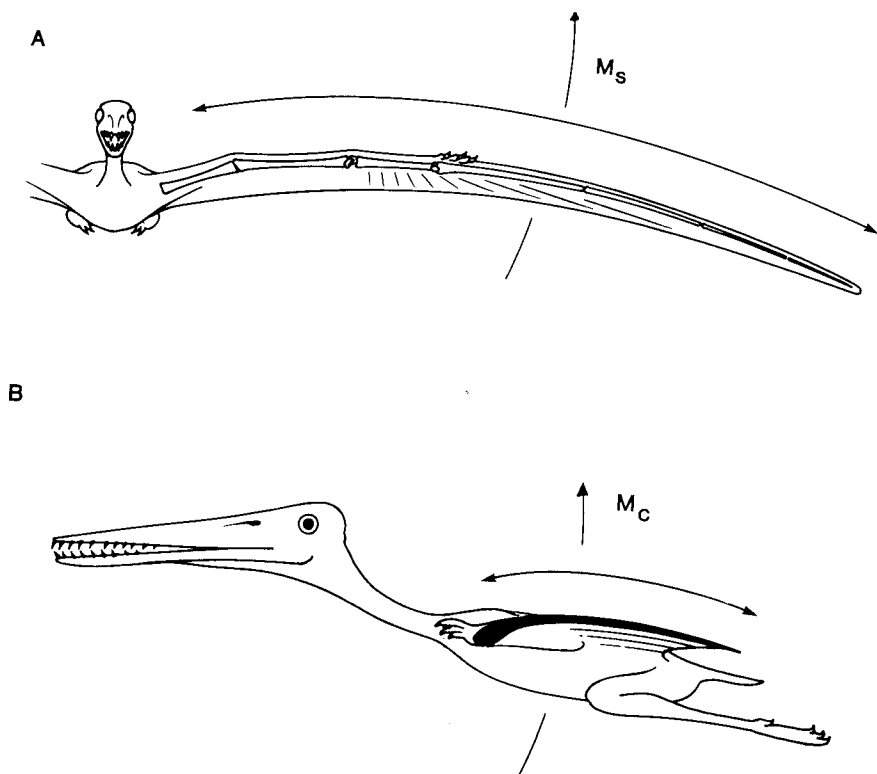
Fig. 11. The arched leading edge spar of the pterosaur, in (A) anterior and (B) lateral (sectioned) views. The cross section of the wing forms an effective airfoil. Lift distributed over the wing results in a spanwise bending moment M_s distorting the wing out of its plane and a chordwise bending moment M_c relative to the leading edge tending to pronate the wing. Combined with the straight orientation of the fibers, the arched shape of the leading edge spar maintains the shape of the wing under these loads.

supination of the wing spar with respect to the patagium. The bone shafts have cracked but have not been shattered; therefore any dorsoventral stress could only have been released at the joints, which would have been translated anteriorly as the ventral edge of the wing spar rotated backward. This explains in part the slight angle between successive interphalangeal joints, which we suggest may be flexed slightly more than in life. This post-mortem rotation would also have had an effect on the tissue adjacent to the wing spar, which would have been stretched perpendicular to the spar as the spar rotated. This explains the greater width of the tissue strip behind the second and third interphalangeal joints, where vertical movement of the wing under compression would have been greatest.

Attachment of the Patagium to the Spar

This topic is one of the most important aspects of the mechanical problem of reconstructing the pterosaur wing, yet as far as we can tell no previous author has described or attempted to reconstruct the attachment of the patagium onto the bones of the wing skeleton.

To understand the attachment to the wing-finger, we must bear in mind that we are speaking of living tissue: the membrane cannot have been a dead (or metabolically passive) organ, like a hair or feather, because the animal was growing through life, and the membrane had to be repairable. (We will deal further with these considerations later on.) The wing membrane seems to have been very close to the surface of the wing spar, separated from the bone perhaps only by the periosteal membrane and a thin layer of muscle and tendon, as in birds and bats. From the Zittel wing it is apparent that the patagium originated from the dorsal side of the spar and not from the groove that runs along the posterior side in this genus (figs. 4E, 12), as noted earlier. The patagium is clearly not torn away from the groove; rather, it lies in a plane that conforms to the continuation of the dorsal edge of the wing-finger and more proximal bones. The cross section of the wing, in marked contrast to typical airplane wings, but not unlike those of most birds and bats, shows a pronounced wing spar profile and a thin airfoil behind it (Bramwell and Whitfield, 1974; Wellnhofer, 1978). Tissue directly behind the spar and below the membrane could have lessened turbulence and could have included the tisuses and cells, blood vessels, and nerves that produced and supplied the membrane, as just noted; it would also be important to sustain a tension under the patagium and the spar, because lift acts to rotate the patagium relative to the spar (fig. 12).
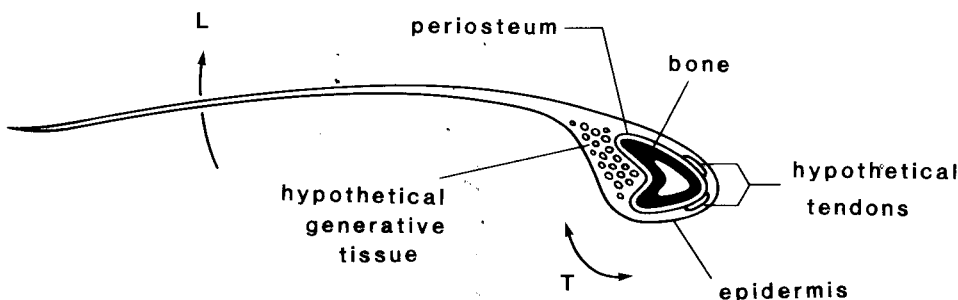
Fig. 12. Hypothetical cross section of the wing of a typical rhamphorhynchid pterosaur, showing location of patagium in relation to the groove in the leading edge spar. Lift L is generated across the chord and is greatest behind the leading edge. Deformation of the patagium when the wing is outstretched is prevented by the arched leading edge spar and the structural fibers. Pronation of the patagium relative to the leading edge spar is prevented by tension T in the tissues beneath the spar. Lift would impose only a small transverse tension attempting to detach the membrane from the spar.

It is noteworthy that patagium attachment scars have never been reported on the wing-phalanges. We consider it possible that the patagium attached more to a sheath of fascial tissue surrounding the bone, than directly to the bone itself. Tension along this spanwise axis in flight would have been relatively small, and presumably could be accommodated by the tissues around the bone. In a few specimens of *Rhamphorhynchus* (BSP AS I 772; von Ammon, 1908 [fig. 3B]; PMZ A/III 107 [figs. 3E, 4G]; JM 1955.135a) the distal patagium of one wing has been separated from the spar (whether before or after death is not possible to tell) and creased or folded on itself, parallel to the fibers. But the patagium, although folded, does not appear to be otherwise damaged. It appears that the spar attachment is the weakest part of the wing, being more susceptible to injury than the wing membrane itself with its structural components. Thus we would not expect to see obvious evidence in the bones of the wing of a mechanical attachment of the patagium to the wing digit and ulna (or for that matter to the femur, if such was the case) comparable to the quill nodes on the ulna in living birds.

Pterosaur Wing Construction—a Summary

To summarize our findings about the construction of the pterosaur wing, our primary conclusion is that the structures of the wing traditionally called "striae," "fibers," or "Aktinofibrillen" are in fact structural fibers, not wrinkles or other artifacts. They appear as features of positive relief on the ventral surface of the wing but not on the dorsal surface. Hence they are not embedded within the wing but were superficial on the ventral side; at times they separate from the wing surface, crossing other fibers. These fibers are often gathered into parallel folds, but not anastomosing networks such as one sees in wrinkled membranes. Real wrinkles and creases can be identified on some specimens and are very different from the structural fibers; they may represent the geometry of the flexed, resting wing, or post-mortem disturbance.

The fibers have a uniform thickness of 50 microns in a typical wing of about 1 m wingspan, but the distance between fiber axes can vary, depending on the stretching of the membrane. Aspect ratios of the fibers are at least 2000:1 or higher; the exact value is difficult to determine because individual fibers cannot be followed continuously from leading to trailing edge. It is possible that some fibers were continuous, but others might have been intercalated toward the trailing edge, because along the leading edge spar the fibers change their angle from nearly perpendicular to nearly parallel to the spar as they radiate distally along the wing.

MECHANICS AND AERODYNAMICS OF THE PTEROSAUR WING

Thus far we have reviewed the structure of the pterosaur wing and introduced new observations and inferences. Now we proceed to ask how the wing should be reconstructed, based on these considerations, to accomplish the performance that was necessary on aerodynamic grounds.

To do this, we first consider what the wing needs to do and then suggest the most likely way or ways in which this was achieved.

Functions of the Wing

The characteristic mode of aerial locomotion in pterosaurs was flapping flight, similar in most mechanical respects to that of living birds and bats. All three groups of animals had to survive in essentially the same fluid environment (Mesozoic air presumably had much the same characteristics as today's air) and were built from tissues with effectively similar mechanical properties. Patterns of wing shape variation in pterosaurs are directly comparable to those of birds and bats (Rayner, 1989a; Hazlehurst and Rayner, 1992b). Because mechanical factors shape wing design and its relation to ecology, we infer that broadly the same mechanical factors influenced pterosaurs and extant flying vertebrates. This does not mean that the wing functioned in precisely the same way in all three groups—we have already identified fundamental differences in structure and anatomy—but it does mean that the aerodynamic mechanisms by which forces are generated are the same, as are the constraints these forces impose on wing design to ensure transmission of aerodynamic forces to the body, adequate safety factors, and sufficient behavioral flexibility or plasticity in flight.

Our reasons for expecting predominantly flapping flight in pterosaurs are based on comparison with birds and bats. The majority of pterosaurs were small and of a size at which gliding and soaring are generally inefficient and ecologically unhelpful. Even though an animal may glide for much of the time, it must be able to flap to take off, to escape predators, and to cope with unpredictable events such as strong winds. Although the long, high aspect ratio wing of most species is indicative of soaring, we cannot expect this mode of locomotion to be prevalent in the smaller Jurassic species. Soaring was beyond doubt dominant for the giant Cretaceous pterodactyloids, but these represent a derived group whose (smaller) "rhamphorhynchoid" ancestors would have relied primarily on flapping flight, as undoubtedly did the small Jurassic pterodactyloids. The basic structure of the wing and pectoral girdle of those pterosaurs preserved clearly show adaptations for flapping (Padian, 1983), although these structures may be modified in larger pterodactyloids in accord with specialization for soaring (Hazlehurst and Rayner, 1992b), just as the larger albatrosses have features for sustained wind gradient soaring that are absent in other birds. However, most previous studies of pterosaur biomechanics and aerodynamics have been concerned with the larger species such as *Pteranodon, Nyctosaurus,* and *Quetzalcoatlus* and have concentrated on gliding and soaring flight (Hankin and Watson, 1914; Short, 1914; Hoepke and Kramer, 1936; von Kripp, 1943; Bramwell, 1971; Heptonstall, 1971; Bramwell and Whitfield, 1974; Stein, 1975; Brower, 1983; McMasters, 1984; Alexander, 1989a, b). Von Holst (1957a, b) constructed flapping models of *Rhamphorhynchus,* but he knew that some features of his construction were anatomically or mechan-

ically incorrect. In this paper we do not attempt to estimate mathematical parameters of pterosaur flight such as glide angles, flight speeds, or power output. Rather, we describe qualitatively the mechanical requirements of flapping flight and show how these accord with what is known of the pterosaur wing; the approach is similar to that employed by Rayner (1991b) in reconstructing the flight of *Archaeopteryx*, and further details of flapping flight aerodynamics can be found in that paper. For background information on flight aerodynamics see Norberg (1990).

The wings of pterosaurs were primarily flight organs. But because pterosaurs were not always in the air, their wings probably had to accommodate other functions and behaviors. Little is known of these matters. By comparison to birds, they might have assisted with directional changes during running (as in *Geococcyx*, the roadrunner); in signalling or display functions related to aggression or intraspecific competition, or to mating; in behavioral thermoregulation; in nest protection; and so on. Apart from the wings themselves, the three small fingers, which bear large trenchant claws both larger and more curved than those of the feet, may have served many different roles, including capture and manipulation of food items, grasping objects, climbing, fighting, and so on. There is no direct evidence for any of these functions, but we feel it important to note that the wing cannot be regarded simply as an organ shaped adaptively for flight. It must serve other uses, and it must be constructed from materials that are available in the animal's skeleton (Seilacher, 1973). Moreover, it must evolve in accordance with the maintenance and further evolution of the behavior of the group.

Aerodynamics and Mechanics

Given the above considerations, we can set limits to what the pterosaur wing had to achieve. In all flapping animals (as opposed to airplanes) the wing is the organ that produces both thrust and weight support. In level flapping flight, aerodynamic lift from airfoil action on the surface of the wing must on average act both upward, supporting the weight, and forward, providing a thrust to overcome the drag generated as air flows past the body and wings. In climbing flight or take-off additional vertical force and thrust are needed, while in landing the horizontal component of lift may act backward, retarding the animal. In gliding or soaring flight, by contrast, lift acts perpendicular to the flight path, and the animal can obtain a force to overcome drag only by descending relative to the surrounding air (Rayner, 1988a, 1990, 1991c). The purpose of flapping the wings is to generate thrust in the form of a mean forward and horizontal component of lift sufficient to balance drag.

Airfoil action.—A wing generates lift by airfoil action (fig. 13A): air flowing over the top surface of the wing travels further, and faster, than air travelling underneath, and the resulting pressure differential is experienced as a lift force normal to the local airflow. To generate a difference in air flows over the two surfaces, the wing must either be set at an angle to the airflow or must be asymmetric. A rigid, thin flat plate can
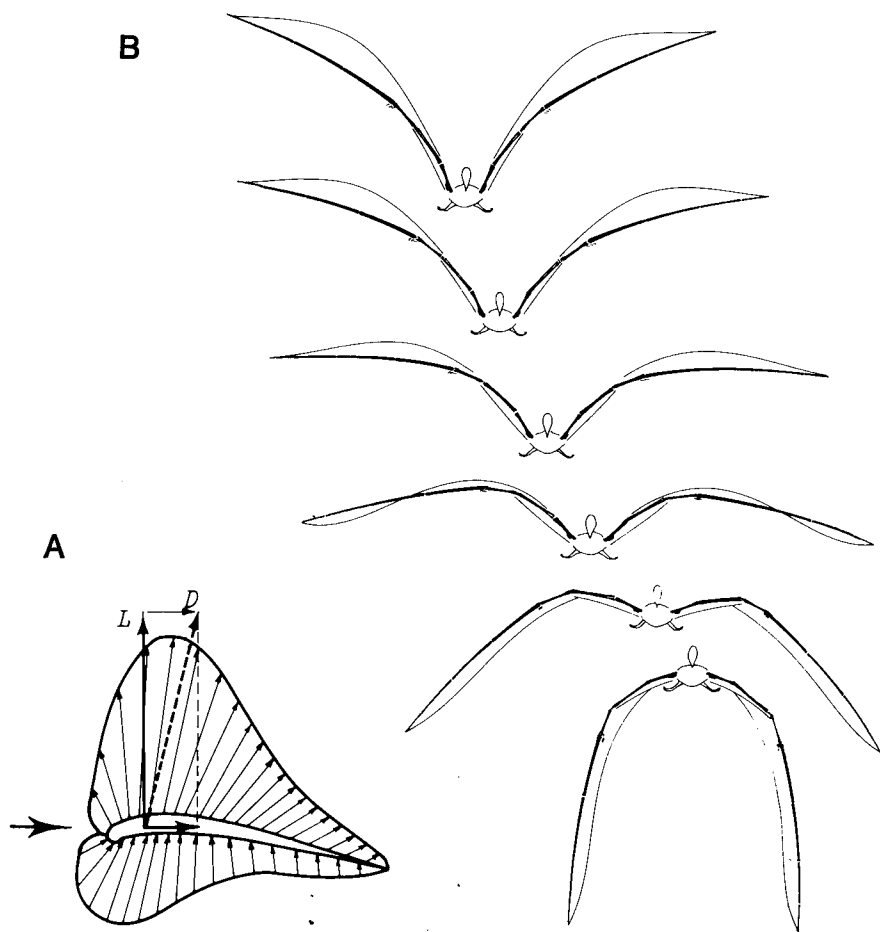
Fig. 13(A) The cross section of an airfoil and the pressure distribution it generates over its surface as it moves steadily through the air. These pressures are conventionally resolved into lift and drag forces, where lift acts normal to the flight path, and drag parallel to it. Lift is the greater of these forces and is distributed over the wing chord; the center of lift is invariably behind the leading edge of the airfoil and therefore in pterosaurs forms a bending moment tending to rotate the patagium around the leading edge, pronating the wing. The structural fibers prevent this rotation. (From Rayner, 1986.) (B) The downstroke of a pterodactyloid pterosaur in steady cruising flight, as reconstructed by Wellnhofer (1991a: 153). The apparent change in shape of the wing is caused by a pitching of the wing during the stroke, which results from the geometry of the shoulder joint (compare Padian, 1983) and not by significant flexure of the elbow, wrist, or metacarpo-phalangeal joints. During the upstroke the wing would flex at the metacarpo-phalangeal joint, so that the effective wingspan is shorter, and this mechanism ensures that a mean positive thrust is generated. The wingbeat would look very similar to that of many long-winged birds, typified by the black-browed albatross *Diomedea melanophris*. (C) from Rayner, 1988b, after Scholey, 1983.
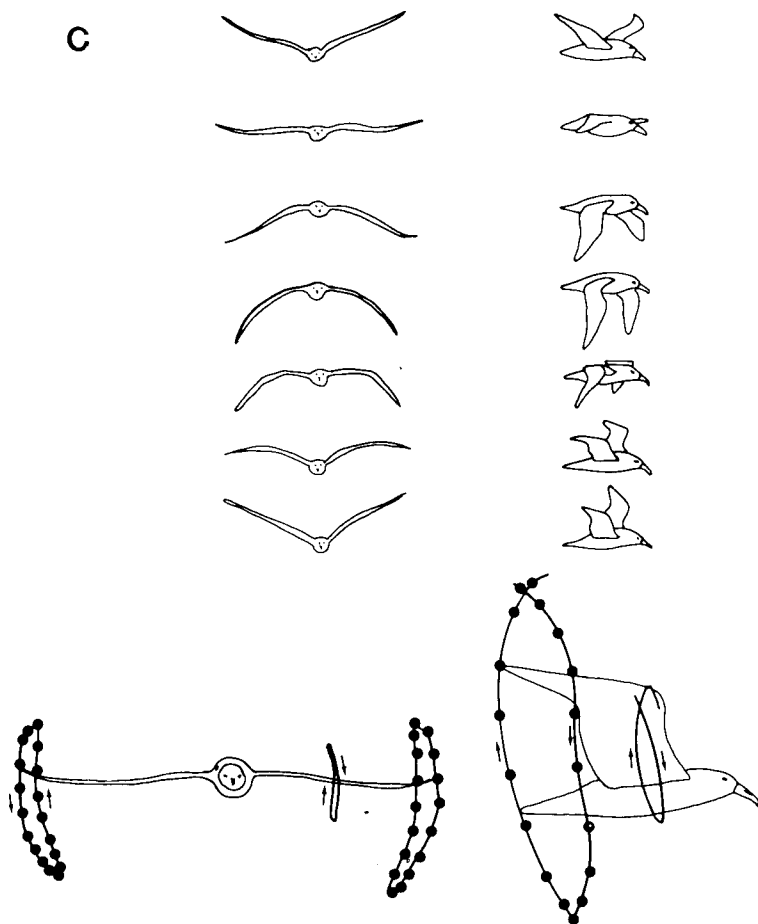
Fig. 13 (continued)

generate lift (inefficiently) when set at a small angle, but efficient airfoils have a cambered profile, with a rounded leading edge, a sharp trailing edge, and moderate thickness at least in the forward part of the section; this profile generates maximum lift with minimum drag. The magnitude of lift is determined by the speed of the airflow, the degree of camber, the breadth of the chord, and the angle of incidence between the chord of the airfoil and the local airflow.

When the wing is flapped, the direction and magnitudes of the airflows approaching each section of the wing vary, and therefore lift also varies through the wingstroke. On a fixed airfoil, the center of lift (the point on the chord of any wing section where lift is concentrated) lies

approx 1/4–1/3 along the chord behind the leading edge (fig. 13A). In flapping flight the center of lift on any chord will move during the wingbeat, so torsion relative to the leading edge spar will not be constant and must be compensated for throughout the wingbeat. But the center of lift will always remain behind the leading edge spar.

During the stroke the animal must control the geometry of the wing so that the mean lift and drag are such that it can fly in equilibrium, so that the peak forces on any section of the wing are within safety limits set by the properties of the wing structure, and also so that force generation is accomplished with minimum energetic investment. This factor constrains the wingbeat significantly and is the main reason why the wing-beats of birds and bats are similar in the temporal patterns of force generation (Rayner, 1986, 1987, 1988b). Because the drag to weight ratio varies with flight speed and other conditions, the solutions to this optimization problem may vary widely with speed.

Chordwise torsion of the wing.—Development of an airfoil section able to generate appropriate (varying) lift forces is only part of the problem of achieving successful flapping flight. The wing must act effectively through the wing stroke, and forces generated on the distal portion of the wing must be transmitted to the body, where they support the weight of the body and overcome the body's drag. The wing section must have chord-wise integrity, in that the cross section of the wing, from front to back, must be more or less maintained under a variety of conditions and must tolerate the torsion (relative to the leading edge) arising from the distribution of lift across the chord (fig. 11B, 12).

If the pterosaur wing were a membrane of skin, otherwise unsupported, it would too easily be deformed under this torsion, which would cause the membrane to pronate relative to the leading edge; when a high aspect ratio flaps, wing torsion is probably the dominant force distorting the membrane at some phases of the wingbeat (Rayner, 1991c, 1992). Without some means of preventing torsion, the wing would be unstable: the trailing edge wing would rise uncontrollably above the leading edge, and the wing would stall like a flapping flag. This is a common phenomenon with the sail of a yacht, and to prevent it high performance sails (and also many hang-glider wings, occasionally cited as possible analogues to the pterosaur wing) contain stiffening battens that reduce the risk of this form of stall. Insect wings contain various patterns of struts that prevent the airfoil collapsing under torsion (Ennos, 1988; Wootton, 1992); bird wings resist torsion primarily through the curved, pre-stressed, and arched shafts of the flight feathers (Purslow and Vincent, 1978); in bats the second and third digits are linked so that the leading edge cannot twist (Norberg, 1969), and the fifth digit and the femur hold the mid-point of the trailing edge in position. .

This problem of stall under torsion is most significant with a long, high aspect ratio wing, and several authors (Bramwell and Whitfield, 1974; Sneyd, Bundock, and Reid, 1982; Pennycuick 1986, 1988) have tried to resolve it in pterosaurs by claiming that the hind leg controls

spanwise tension, and/or that the trailing edge of the membrane is formed by a stiff tendon to transmit this tension. We have already shown that this model of the wing is not supported by the fossil evidence. In addition, it is mechanically inconsistent: Bramwell and Whitfield (1974) have shown that an elastic membrane under high spanwise tension exerts too great a load on the leading edge spar (also Sneyd, Bundock, and Reid, 1982). And with a long, thin wing the tension along the trailing edge would have to be considerable if that edge were to be prevented from bending upward under aerodynamic lift. For these reasons we dismiss the hypothesized trailing edge tendon. The pterosaur wing must incorporate stiffening structures, particularly to counter tension; we shall demonstrate below how these are provided by the curved leading edge spar and the stiffening fibers associated with the membrane.

Chordwise torsion is not uniform, either through the wingstroke or across the wingspan. Spanwise bending (discussed in the next section) is more important in the wingtip and distal wing, because the wing is thinner there and is moving faster, generating more lift. On the inner portion of the wing the center of lift is farther behind the leading edge spar, because the wing is broader, and the flapping velocity is lower; in this region chordwise torsion dominates. For this mechanical reason bats have a fifth digit located where it is, and bird secondary feathers run caudally. For the same reason, pterosaur structural fibers run caudally or caudo-laterally in the region behind the ulna and the metacarpus.

Spanwise bending and force transmission to the body.—Lift generated over the surface of the wing must be used both to support the weight and to provide thrust. Weight support is usually the greater component, because mean thrust equals drag, and total drag is on the order of one-tenth of weight for a well designed animal or man-made aircraft, particularly when aspect ratio is high.

In flapping flight, weight support is generated over the entire wing and is the dominant force over the whole wing surface. Because it is determined both by forward air speed and the local flapping velocity, it is greatest on the middle and outer thirds of the wing. In pterosaurs this is the region distal to the wrist, adjacent to the proximal phalanges of the wing-finger (fig. 12A). Aerodynamic force generated over this region is ultimately transmitted to the body through the humerus and the pectoral muscles (Gray, 1968) but must pass first from the wing surface to the bones of the arm and hand. The vertical component of this lift has the effect of an upward spanwise bending moment that tends to raise the distal part of the wing relative to the bones of the arm. We see no evidence in the shape of the bones or the interphalangeal joints (see above) that the phalanges of the wing-finger are designed to accommodate this force. The spar is curved downward to resist such upward bending, but the interphalangeal joints are too simple and unable to articulate, and there are no scars for the substantial tendon on the ventral side of the spar that would be necessary to prevent it distorting upward if it were subject to the aerodynamic loads generated on the wing. And a

trailing edge tendon could have had no real effect in preventing the wingtip of a long, thin wing from bending upward under aerodynamic loads. We hypothesize that these bending loads are transmitted from the distal part of the patagium to the metacarpals and the ulna by the stiffening fibers. Again we see a close parallel with the function of the bird and bat wings; this is why the axes of the fibers are very similar to those of bird feather shafts or of the digits of the bat wing. This implies that the wing-finger of pterosaurs had relatively little mechanical involvement in wing function, in that it was not subject to mechanical loads resulting from aerodynamic lift on the wing surface: rather, it served as the origin of the patagium and—by curving backward and downward—ensured that the patagium had the integrity to resist chordwise torsion under aerodynamic lift.

Mechanical strength of the fibers.—Partly because he thought that the structural fibers were discontinuous (that is, a single fiber does not appear to traverse the entire width of the wing between the spar and the trailing edge), Pennycuick (1988, p. 307) stated that their arrangement "clearly is not adapted to collect bending loads and transfer them to the wing skeleton, as a bird's flight feathers do." We do not accept this view for two reasons: first, the patagium was not flat and worked in a very different way from a plane, stiffened wing; and second, there may be little difference in effectiveness between fibers that run continuously from the leading to the trailing edge and those that are discontinuous, of somewhat shorter length, but nonetheless closely intercalated (fig. 14). The bending moment that lift causes would tend to distort the fibers out of the plane defined by a group of adjacent and parallel fibers (fig. 12A). Bending within the plane of the wing (in response to drag) is small (Rayner, 1986). Chordwise variation in lift does produce a significant torsion across the wing chord and therefore along the length of the fibers, but this would be resisted by the surrounding membrane material; above all it would be countered by the effect of the arched leading edge spar to impose a chordwise camber on the wing surface.

Compared with other animal structures, the pterosaur wing is unusual in being a uniaxial, thin laminate subjected to substantial bending loads perpendicular to its local surface. Unless the stiffening fibers were *very* stiff this would be a poor design for a *planar* wing. But the wing was not planar, particularly in the distal region, and like the wings of other fliers its shape must have varied during flight. The combination of a membrane with a curved leading edge, straight stiffening fibers, and a nearly straight trailing edge ensures that when outstretched the patagium must have been curved both chordwise and spanwise and would resist forces attempting to deform it far more effectively than if the wing were flat (fig. 12). A useful analogy for the interaction of the leading edge spar and the fibers with the wing membrane is the umbrella: the curved spars (here the structural fibers radiating from the leading edge) together with tension between those spars stiffens an otherwise unstruc-
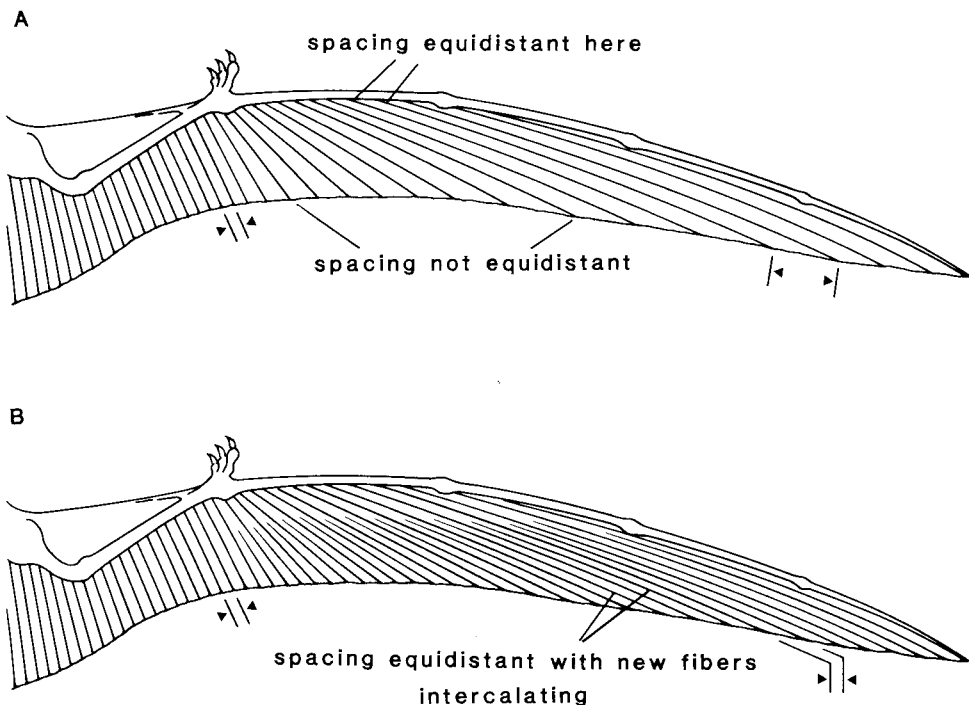
A

B

Fig. 14(A) If all pterosaur wing fibers were continuous from leading to trailing edge, then their axes could not have been equidistantly spaced throughout, because the angle between fibers and wing spar changes spanwise (see fig. 17). (B) Because the fiber axes are in fact equidistantly spaced, there must be some intercalation of new fibers chordwise. Note in this sketch that (1) only about 2 to 3 percent of the actual fiber density is represented, and (2) though for simplicity the new fibers are drawn as if their longitudinal joints co-occurred, this would not be likely on mechanical grounds (see text).

tured membrane. Wootton (1981, 1990, 1992) and Ennos (1988, 1989) discuss similar mechanisms in insect wings.

Although the plane laminar wing is a somewhat different structure than normally adopted by animals, and we know no obvious modern, natural analogy for it, the arguments above give every reason to think it formed an effective flapping wing. Conventional composite building materials indicate the importance of the length of the structural fibers, since the aspect ratio—defined as the ratio between the length and breadth of the individual fiber (wood cells, fiberglass strands, et cetera)—is a major determinant of the strength of the composite material (Gordon, 1968; Hull, 1981). In materials such as wood or in fiberglass or other artificial laminates, aspect ratios of the range of 50:1 and above are considered high, and with these proportions the strength of the material is largely independent of aspect ratio. Ratios substantially lower than 50:1

are considered low and usually result in reduced stiffness to loading in some axes. The fibers of particle board, for example, have a lower aspect ratio than the cells of natural wood and also less organized orientation. Unreinforced particle board does not have the same strength as does wood planking. The fibers in the pterosaur patagium of 0.5 m span have a length of 50 to 100 mm or perhaps much more and a breadth of 0.05 mm, giving an extremely high aspect ratio of at least 1000–2000:1. In these circumstances the main sites of structural weakness are the longitudinal joints between contiguous fibers, so a pattern of many short fibers has the potential for many more lines of weakness. On the other hand, if the aspect ratio of fibers is high enough, *and if they are intercalated such that their longitudinal ends do not co-occur,* strength in resistance to bending loads out of the plane of the fibers does not significantly depreciate even if the fibers are not continuous across the entire surface. Moreover, flexibility and resilience to deformation transverse to the fibers may improve, depending on the material between the fibers. Hence, whether or not the fibers were continuous along the wing chord, if there were a sufficient number of them and their intercalations staggered, it may have made no real difference to the mechanical integrity of the wing. Furthermore, this structure has good resistance to bending out of its plane even if the Young's Modulus (the extent to which the material resists deformation under an applied stress) of the material comprising the fibers is only slightly different from that of the material comprising the remainder of the wing (Gordon, 1968), largely because of the difference in shape of the cross section of the fibers compared to that of the membrane itself.

In a uniaxial laminate of the form we envisage, the greatest stresses arise within 5 to 10 diameters of the ends of the individual fibers. The stress would be concentrated where the transverse tension across the fibers is greatest, and the fiber ends are close together, as happens at the trailing edge of the wing, *and there only.* Resistance to distortion and dislocation would be minimized if the terminal portions of the fibers run perpendicular to the trailing edge, and this explains why the fibers bend as they approach the posterior edge of the membrane. This concentration of stress could explain in part why the trailing edge of the Zittel wing became frayed and tattered; further, this region might be more vulnerable to damage from contact with obstacles.

Deformation during the upstroke.—The final constraint on the geometry of the wing is imposed by the need to obtain a net thrust to balance drag. Thrust is the horizontal component of lift and is produced by flapping the wing relative to the body at the shoulder joint. When the wing moves downward relative to the body, the horizontal component of lift is positive and propels the animal. However, when the wing moves upward, lift acts backward and retards the animal (Rayner, 1986, 1991c, 1992). If up– and downstrokes were symmetrical, positive and negative components of lift would cancel, and there would be no net thrust. Yet thrust generation is the major purpose of flapping the wings. There are two ways of responding to this problem, both of which involve the

introduction of asymmetry between down– and upstrokes, so that lift during the upstroke and hence the negative thrust are reduced. The downstroke is in all circumstances responsible for the bulk of thrust and weight support.

One solution is to reduce the angle of incidence during the upstroke by controlling the wing pitch. The upstroke generates some aerodynamic force, but the force is reduced owing to the smaller incidence and hence the lower strength of the vortex bound on the wing. However, this strategy is not appropriate for bird and bat wings, because it can introduce large short–term aerodynamic drag forces (Rayner, 1986, 1991c). As a result, in slow flight, all vertebrates feather the wing during the upstroke and generate no lift during this phase: *all* weight support and thrust are provided by the downstroke, and the wing is often flexed close to the body in the upstroke to reduce drag and inertial forces. Limits to the ability of the downstroke to produce sufficient force may constrain slow flight and hovering performance (Rayner, 1991c).

The second solution is to deform the wing so that the effective wingspan is shortened during the upstroke. This is the typical wingbeat used by birds and bats in cruising flight (fig. 13B, C), and the only species in which it has not been observed are small and have very short, rounded wings (for example, passerine birds, some vespertilionid bats). This gait is particularly efficient because the vortex on the wing that gives rise to lift can be maintained constant throughout the wingbeat, and the sense and magnitude of the lift forces on the wing sections are controlled geometrically rather than aerodynamically. In bats, the wing is shortened during the upstroke by retracting the humerus and flexing the elbow; in this way the hand wing remains under chordwise tension (Rayner, 1986, 1987). In birds, it is more usual for the wing to flex at the wrist, with the hand wing and primary feathers sweeping back relative to the shoulder joint; there may also be some flexure of the elbow (Rayner, 1988a,b, 1991b).

Pterosaurs had the same flexibility in their major wing joints as birds or bats (Bramwell and Whitfield, 1974; Padian, 1983), and the hinge joint of the metacarpo–phalangeal joint is ideally adapted for sweeping the wingtip during the upstroke in a movement analogous to that in birds. With their long, thin wings the pterosaur wingbeat would have appeared very similar to that of long–winged birds such as gulls or albatrosses (Wellnhofer, 1991a; fig. 13B, C), and it can be presumed that they generated aerodynamic force in a similar way. Given the difference in course of the structural fibers between proximal and distal portions of the wing, flexure of the metacarpo–phalangeal joint would not affect the mechanical properties of the distal part of the wing; during the upstroke the patagium may have needed to contract or deform slightly in the region behind the carpus.

Aerodynamic plasticity.—The wing of any flying animal must be able to adapt to varying conditions and flight patterns. Although this fact is self–evident, it is seldom considered in discussions of pterosaur flight capability. Bramwell and Whitfield (1974), for example, suggested that

pterosaurs became extinct because of a postulated change in the average wind speed at the end of the Cretaceous. This inference allows for very little aerodynamic plasticity in the wings and is likely to be even less relevant to smaller species which would inherently have enjoyed greater aerodynamic and behavioral flexibility. The conclusions of Bramwell and Whitfield depend on their model in which the wings of pterosaurs were wide and connected to the ankles, with spanwise tension as the principal means of providing integrity to the airfoil. This model requires pterosaurs to have held their wings fully outstretched at all times during flight, making them defenseless against changes in winds or even sharp gusts. A wing formed of a thin elastic membrane would need to be held outstretched; indeed, the presence of the digits cannot prevent this from being a significant constraint on bat flight ability (Rayner, 1986, 1987).

We cannot accept that such restrictions on flight ability applied throughout the Pterosauria. A gliding bird changes speed and/or glide angle by flexing the wingtip, and one of the mechanisms by which flight speed is varied is controlling the degree of flexure of the wings during the upstroke (Rayner, 1992). To have been effective flying animals, able to adjust to a range of conditions, pterosaurs would need to control wing planform and profile. Our arguments suggest that the movements they made were very similar to those of birds, despite the anatomical differences in the wing. And we argue that the structural fibers played a very similar role to bird feather shafts in transmitting aerodynamic force from the wing to the bones of the arm, while resisting deformation of the wing surface under chordwise and spanwise tension.

The Pterosaur Patagium and the Bat Wing Membrane

Despite rotation of the wing spar in the Zittel specimen, the fibers behave as if no distortion were present, even though the patagium is clearly stretched unequally. This speaks for their structural integrity, certainly, but raises the question of how their composition could achieve this. We have followed such other authors as von Zittel, Döderlein, and Wellnhofer in inferring that the structural fibers must be stiff enough to provide overall structure and aerodynamic integrity to the wing membrane, yet be elastic enough to absorb without damage the strains and shocks of flying. Hence the fibers must have had a (perhaps only slightly) higher elastic stiffness than the surrounding skin of the membrane; they could not have been like the collagen and elastic fiber network of bats (Holbrook and Odland, 1978; see also Schumacher, 1932), which run *transverse* to the structural elements of the patagium (fig. 15; *pace* Döderlein, 1923; Spillmann, 1925; Pennycuick, 1988).

Pterosaur wings are often compared to bat wings, so it is important to establish some differences. The wing of bats varies greatly in thickness from 0.02 to 0.06 mm in mid–patagium, depending on the species (Studier, 1972). The tissue layer consists of dorsal and ventral epidermis and dermis surrounding a central hypodermis, so that there are five main tissue layers. These may be thicker near the wing bones and body,
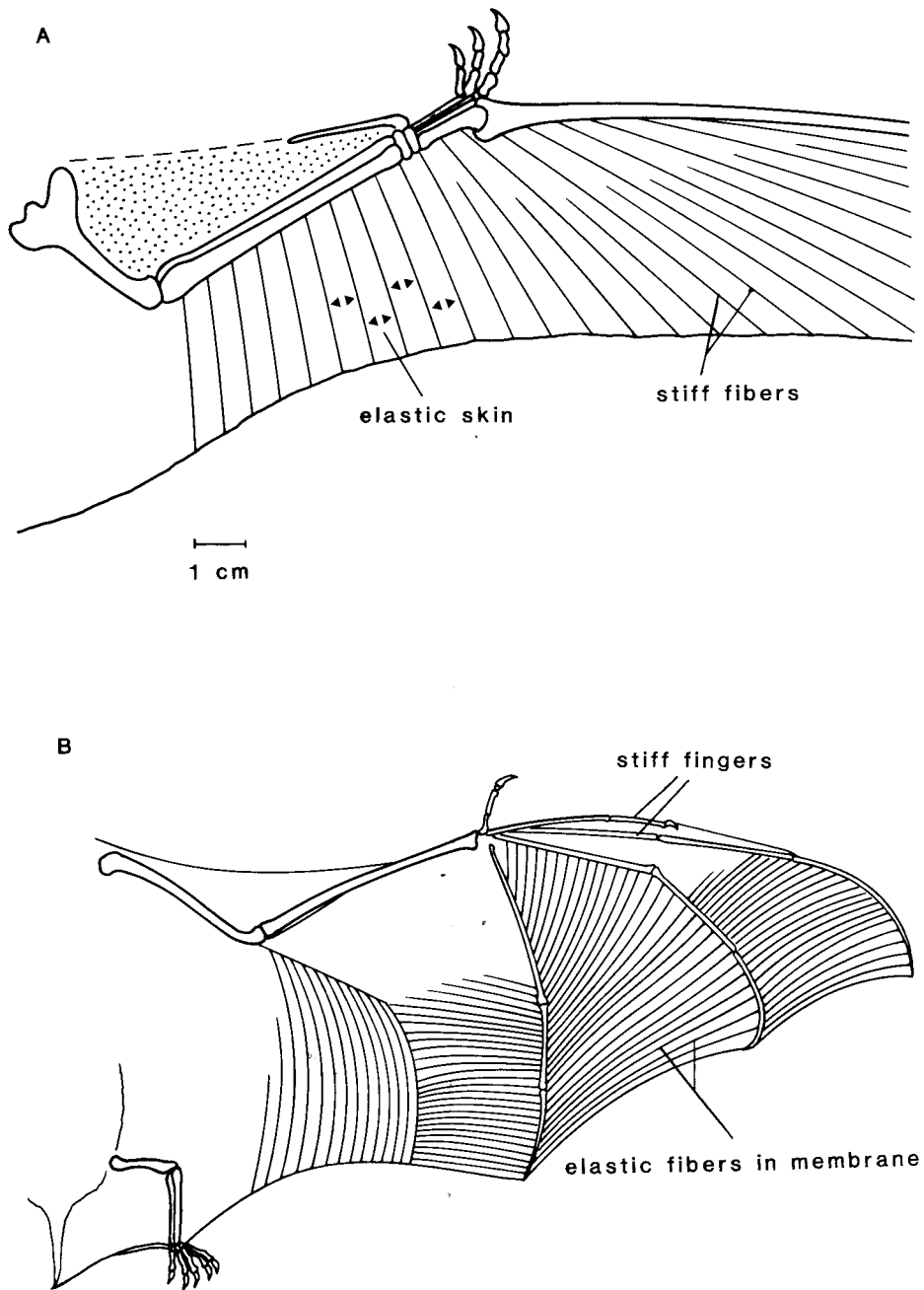
Fig. 15. Schematic of the wings of (A) pterosaur and (B) megabat (after Vaughan, 1970) to show the orientation of various fibers and structural elements. For clarity, only a few fiber axes are represented. In the bat wing the elastic fibers run perpendicular to the fingers, keeping the membrane taut as the digits are spread. In the pterosaur wing, the structural fibers run where they support aerodynamic loads, that is perpendicular to the bones of the arm and hand (and to the proximal trailing edge), but acutely to the bones of the wing-finger (and to the distal trailing edge).

especially the hypodermis, which contains the muscles and fibrous bundles (Schumacher, 1932; Gupta, 1967; Holbrook and Odland, 1978).

Elastic fibers have been well known in bat wings for a century (Schöbl, 1871; Allen, 1889); in much of the wing they are attached to muscles that change the tension of the membrane (Schumacher, 1932). It is now known that elastin and collagen combine into fibrous networks that "should permit flexibility yet provide tensile strength and limit extensibility of the wing membrane, all properties which are clearly significant for flight" (Holbrook and Odland, 1978: 21). This example also shows the value of the properties of composite biological materials, which we suggest were very important in the performance of the pterosaur wing.

The configuration and therefore the structure of fibrous tissue seem to have been quite different in bats and pterosaurs. Schumacher (1932), studying the megabat *Pteropus*, and Holbrook and Odland (1978), studying the microbat *Tadarida*, both found networks of fibrous tissue, resembling a tennis net, in the plagiopatagium. In the dactylopatagium the fibrous bundles took a more lateral and diagonal direction, frequently arising from ligamentous arcades. As Vaughan (1970) showed, these elastic fibers run parallel to the wing's trailing edge in the posterior region and are used to tense the wing. Hence their direction and function are precisely *opposite* to the structural fibers in the pterosaur wing (Padian, 1983). The pterosaur's structural fibers may have had both tensile strength and elasticity, but we consider them to have been relatively stiff. There is no evidence that they extended in flight, like the fibers of bat wings, and it is difficult to see how this could have been done, or how it could have been advantageous. It is possible that between (or dorsal to) these structural fibers a system of elastic fibers may have run transversely, to support the membrane spanwise as it deformed, but to date there is no evidence for such a system in pterosaurs.

The composition of the pterosaur structural fibers is not known; von Zittel (1882) thought they were stiffened tendons, but this is unlikely because tendons are usually muscular extensions, and it is improbable that the patagium or its homologue would have had so many individual muscles. Wellnhofer (1975c, 1978) also suggested that the fibers were collagenous and thus homologous to either tendon or bone. The most likely alternative composition is keratin (Padian, 1983), which would be consistent with development from scales or scale analogs (see below), would provide both strength and flexibility, and is also consistent with the superficial distribution of the fibers on the ventral side of the membrane; this seems to us the most probable material. McGowan (1991) suggested that these fibers could only have been effective in stiffening the wing if they were tubular. He would be correct if the wing were supposed to be held rigid, with *all* bending loads being taken by the fibers alone, as in the avian feather shaft. As we have discussed, the pterosaur wing was a composite formed by the wing membrane and the fibers and would have had greater relative stiffness than either material by itself.

The elongated structure and uniform cross section of the fibers give longitudinal stiffness and resistance to bending perpendicular to the fibers' axes. The fibers do not prevent folding parallel to their axis as noted above (see also von Zittel, 1882; Wellnhofer, 1975c, p. 17). But we argue that stiffness in this direction—that is, chordwise—is less important, because the small amount of chordwise tension required in flight can be maintained by the wing spar. The thin strips of membrane between the structural fibers will have the capacity for only slight transverse stretching. No transverse stretching is possible at the proximal ends of the fibers, where they approach the wing bones. Transverse stretching may appear at the trailing edge, where the mechanical composite of the wing is at its weakest; the effects of this stretching are seen in the fraying of the fibers near the trailing edge, notably in the region behind the joint between the second and third wing–phalanges, as noted earlier (fig. 4C). Thus the combination of the structural fibers and the more elastic membrane enhances the mechanical properties of each individual element.

We have argued that the patagium must be stiff to spanwise and chordwise bending, so that aerodynamic force is transmitted from the wing surface to the hand and arm, and so that the wing resists unstable pronation and stall during flapping flight. We have demonstrated that a thin, homogeneous elastic membrane attached to the leading edge spar cannot fulfill this role, even with a putative trailing edge tendon. We could postulate a stiff, homogeneous structure that acted as a rigid wing, but this model cannot be sensibly pursued because it is impossible to imagine how such a wing could be developed and maintained, and it would have none of the flexibility or deformability required in flapping flight. We therefore find no adequate alternative reconstruction of the pterosaur wing to that proposed by Wellnhofer (1978, 1987) and Padian (1983, 1985), in which the stiffening fibers play a central structural role.

We see a further argument against the model of the wing as a simple membrane extending unbroken from body to wingtip: such a wing would be extremely vulnerable to tearing or puncture. This is of course also a problem for bats, but damage to a segment of the bat wing is confined to the panel between adjacent digits, and there is at least a chance that flight performance need not be significantly impaired and that the damage may be repaired. A tear or puncture in a pterosaur membrane of the form envisioned by Pennycuick (1988) would be much more likely to be catastrophic. The reconstruction we propose with an extensive distribution of stiffening fibers would resist damage and would confine tears to an axis parallel to the fibers and—in the distal portion of the wing—to the leading edge.

Pterosaur Wing Mechanics—a Summary

To summarize our findings about the relationship between wing structure and aerodynamics in pterosaurs, it is first important to consider the advantage of the wing as a mechanical composite of skin and struc-

tural fibers. This composite allowed greater strength, flexibility, and plasticity than either material could do alone. The fibers, as their orientation in the wing showed, translated loads from the patagium to the bones of the hand and forearm, whence they passed to the wing root and the body. Aerodynamic loads were probably concentrated a third to a quarter along the chord behind the leading edge and about two-thirds of the way out along the wing toward the tip; in these places the lift on a flapping wing is greatest. The fibers therefore had to resist bending both spanwise and chordwise, perpendicular to the leading edge spar. Pterosaurs had no trailing edge tendons; the fibers bore the mechanical loads of flight and prevented the wing from billowing like a flag, or pitching unstably and stalling.

GROWTH AND DEVELOPMENT OF THE PTEROSAUR WING

Although many authors have studied the shape and composition of the pterosaur wing, there has been almost no discussion of how the patagium grew. Consideration of this question is not limited to speculation; some possibilities can be eliminated and others strengthened on the basis of indirect evidence. The question is intimately connected to questions about the structure, function, and mechanics of the wing. But no consideration of these questions can make sense without some presumptions about how the patagium developed. Several points are relevant here.

Ontogeny of the Wing

First, despite the absence of direct evidence, it has been presumed that pterosaurs hatched from eggs. Bennett (1987b) discussed the configuration of the pelvic canal in *Pteranodon*. As flying animals, female pterosaurs (like birds and bats) would probably have benefited from minimizing the additional weight of developing embryos, and so it is reasonable to suppose that they were limited to carrying one or a few embryos at a time, or that the eggs were laid at a relatively early stage and incubated for a substantial time, or both.

The previous inference implies that pterosaurs hatched in an altricial state, and therefore, because of their dependence on flight, some parental care and feeding until fledging is equally implied. We do not wish to become overly speculative on these points, because there is no direct evidence; but the alternative is that upon hatching pterosaurs immediately ran away—and perhaps even flew off—to forage on their own, and this hardly seems likely. One reason is that the size and geometry of the egg would have constrained the length of the wing, which in most pterosaurs is several times greater than that of the body. (Individual wing-phalanges are often longer than the torso itself.) Therefore the development of the wing must have been mostly outside the egg, and it may well have been rapid (Padian, in preparation; Hazlehurst and Rayner, 1992a). Before becoming airworthy, the wing bones would have had to become sufficiently elongated, calcified, and articulated, the

muscles large enough to provide aerodynamic forces, and the structural fibers sufficient to form with the wing membrane a patagium large enough and strong enough to support flight. No information is available about the rate or schedule of this growth, but it must have involved the wing membrane, the structural fibers, and the bones of the wing-finger. Small Jurassic pterosaurs apparently did not have determinate growth (Wellnhofer, 1970, 1975c; Mateer, 1976), although *Pteranodon* seems to have grown to a limiting size (Bennett, 1988, 1991). The wing continued to grow with age, and because most fibers run along the chord from wing spar to trailing edge, the fibers also must have grown. The fiber axis is only slightly acute to the leading edge of the wing, and so the relative change in length of the fibers from hatching to first flight must have been considerable.

Non-pterodactyloid pterosaurs ("rhamphorhynchoids") also had a long tail stiffened by elongated zygapophyses and ossified tendons (Döderlein, 1929a; Wellnhofer, 1975a; Ostrom, 1969a), much as in the theropod dinosaur *Deinonychus* (Ostrom, 1969b). The tail could not have been stiff at birth and quite possibly was not fully stiffened at the time of fledging if the animal continued to grow.

Development of the Fibers

Perhaps the central question is *how* the fibers grew: were they formed uniformly along their length, or at definite sites along their axes, or did they grow only at one end? Although we do not think there is yet enough evidence to decide this question, we formulate three hypotheses. (1) The fibers grew posteriorly only from cells near the wing spar, and the distal part of each fiber was "dead" tissue, like scales, hair, feathers, and similar integumentary structures (fig. 16A). (2) The fibers were formed in place, embedded in, and potentially sustained by, the wing membrane; in this case they may have been composed of active tissue, perhaps more like dermal scutes in many physiological respects (fig. 16B). (3) The fibers were formed by follicle cells at various sites on the membrane; this would account for their regular spacing along the patagium through ontogeny, although well preserved specimens such as the Zittel wing show no evidence of such follicles adjacent to the fibers (fig. 16C). Whichever of these alternatives proves to be the case, the surrounding membrane would have had to be physiologically active epidermal tissue, for two
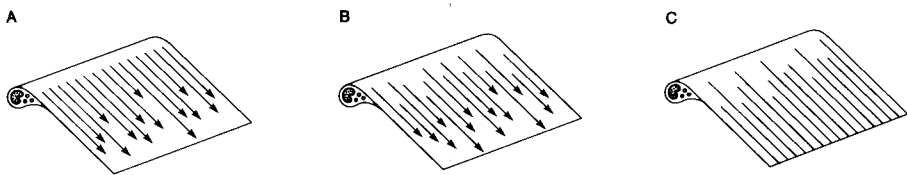

Fig. 16. Three possible models of wing fiber growth. For explanation see text.

reasons: first, it needed to be activated and adjusted by nerves and muscles; and, second, it would have had to be able to repair itself in case of damage (tears in bat wings heal within hours). Our second and third possibilities would also require extensive vascularization within the wing membrane to support the fibers; the first possibility would confine the generation of tissue for the fibers to the band of tissue posterior to the spar.

It is remarkable that the spaces between the long axes of the fibers are consistent throughout the whole of the Zittel wing (apart from slight local stretching and bunching of the membrane), regardless of their distance from the leading or trailing edges. The fibers lie at different angles to the leading and trailing edges along the length of the wing, so if the fibers were always continuous, they could not be equidistantly spaced along their lengths (figs. 14, 17). Discontinuities between adjacent fibers may indicate formation of fibers *in situ;* it is however hard to imagine the physiological mechanisms that could support such an extensive distribution of fibers without adding excessive bulk and weight to the wing. Fibers could be formed from cells or follicles spaced along the leading edge spar and would grow back on the lower surface of the membrane at a shallow angle to the spar (figs. 12, 17). At the same time membrane could also be formed from the leading edge, growing backward as the wing increases in size during ontogeny. A mechanism of timed cell death theoretically could be responsible for the discontinuous fibers within the membrane, and this might have been essential to ensure even inter-fiber spacing in the region of the trailing edge of the distal part of the wing, where otherwise the fibers would be too widely spread. On the other hand, an intra-membraneal system capable of forming fibers in place might not have been too unwieldy, inasmuch as some system had to be capable of repairing axial tears in the membrane, much as in bats.

This brings us to the trailing edge: how did the wing end posteriorly where it did? In one sense the answer to this question is linked to the points between which the wing was stretched, namely the wingtip distally, and either the body or part of the thigh proximally. But along its length,
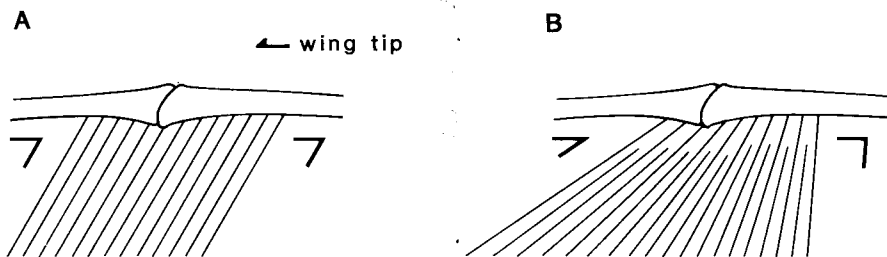

Fig. 17. The angle between fiber axes and the wing spar changes spanwise, becoming more acute distally (to the left). Thus, to preserve a uniform distance between fiber axes, new fibers must be intercalated chordwise, away from the leading edge spar.

the wing membrane and fibers grew perpendicular to the trailing edge, or at an oblique or acute angle to it. How did these fibers, and the membrane, "know" where to stop growing?

One answer could be that abrasion of the patagium, against air and solid substances, could have maintained the shape of the trailing edge. And, indeed, abrasion may have removed some of the fibers from their grooves in the wing membrane near the trailing edge (fig. 4C, discussed above). But this is unlikely as a general mechanism, for several reasons. The trailing edge is uniformly straight or very smoothly curved in all specimens of *Rhamphorhynchus* and *Pterodactylus* with patagia; it is unlikely that abrasion would have been so consistent along the entire length of the trailing edge. Also, other evidence of abrasion, such as a tattered or uneven edge, would be expected, but this has not been observed. (Apparent unevenness along the trailing edge of the Zittel wing, for example, is an artifact of preparation marks on the matrix next to the specimen, an optical illusion that disappears on close examination.)

A second answer is that the ends of the fibers were molted, like feathers or snake skin. Speaking against this possibility as a means of maintaining the shape of the patagium is the fact that, because the fibers were unequal in their lengths, they could not be expected to molt at their ends at precisely the same time to produce a straight trailing edge.

The third, and perhaps most satisfactory, answer is a complex of epigenetic mechanisms involving timed fiber and membrane growth. Hairs, whiskers, antennae, limbs, and other animal organs, while showing variety and variability, are remarkably consistent in form and length within taxa. It seems reasonable to suppose that the epigenetic controls on growth usual in these organisms would have similarly been present in pterosaurs. Similarly, synchronized molting of portions of the wing membrane's epidermis might have played an important role. Molting of scales, skin, feathers, and hair is almost universal in birds, other reptiles, and mammals, so we might expect it to have occurred in pterosaurs. We can envisage mechanisms with comparable sophistication—and variety—to the molt habits of birds, but the pterosaur fossil record provides no information to direct our speculation.

INTERSPECIFIC VARIATION

Our evidence for the presence of fibers in the pterosaur wing is drawn from a wide range of species, from the Triassic of southern Europe to the Cretaceous of South America. Although the nature and quality of preservation vary through this range, effectively the same structures can be identified throughout the history of the group. This implies that the stiffening structures of the wing appeared at an early stage in pterosaur evolution and subsequently remained a conservative feature. The completely unrelated gliding (?) reptile (possibly archosauromorph) *Sharovipteryx* shows remarkably similar features in the uropatagium spanning the hindlimb (the forelimb is absent) (Sharov, 1966, 1971; Gans, Darevski, and Tatarinov, 1987). We would not in any way argue for

either any homology or any direct apomorphy between these structures and the pterosaur wing, but they may indicate the evolution of stiffening fibers in the reptilian dermis to be a relatively straightforward process.

We cannot however rule out the possibility that the anatomy and gross structure of the wing varied within the Pterosauria. For instance, *Rhamphorhynchus muensteri* and *Pterodactylus kochi* are far more common in our list in table 1 than their relative abundance would suggest, but we are unable to suggest whether this arises from chance, from some preservational bias, or from a real difference in the features of the wings. As we have noted, *Rhamphorhynchus* is the only genus with a groove in the wing-finger spar, and if this had a role in wing mechanics, it may indicate a fundamental difference in wing structure. At present the available record is too incomplete for us to identify any pattern in this respect.

The presence of some variation in attachment of the wings to body and thigh, and perhaps also in stance and gait, cannot be eliminated, although the latter seems unlikely owing to the conservative design of the pelvis and hindlimbs within the Pterosauria. In bats the posterior attachment of the membrane to the leg is very variable, with no obvious effect on aerodynamic performance; in most species the membrane reaches to the tibia close to the foot; in some the tibia is free, while in others (*Dobsonia* [Pteropodidae]) the wing membranes meet along the dorsal midline, and the whole hindlimb may be free; in *Dobsonia,* this design facilitates vertical climbing flight (Wilson, 1985; Richards, 1986). In *Pterodactylus kochi* the wing seems to have attached to the mid-thigh, while the leg appears to have been completely free in *Rhamphorhynchus,* and *Sordes pilosus* gives the impression (perhaps misleadingly owing to postmortem disturbance) that the membrane reached the ankle. Nonetheless, we conclude that in all pterosaurs, whatever the gross anatomy of the wing, the mechanical integrity of the wing, enabling it to function effectively in flapping flight, was provided by stiffening fibers, and the hindlimbs played only a minimal role in flight.

STANCE AND GAIT

The implication of our understanding of the structure and growth of pterosaur wings for the structure and function of the hindlimbs and their use in terrestrial locomotion is that they are two very highly adapted—*yet essentially independent*—functional systems. The forelimbs propelled the animal through the air, and the hindlimbs supported it on land. The form of the wing seems to have been controlled completely by muscular movements of the forelimb and the pectoral girdle; the wing's aerodynamic integrity was maintained by the system of structural fibers that permeated its surface, and the hindlimb had no significant mechanical role in the function of the wing. How then did the hindlimbs function?

Pterosaur hindlimbs resemble in great detail those of dinosaurs and other ornithodiran archosaurs, to whom they are most closely related (Padian, 1984a; Gauthier, 1986), and are convergent in some fine details to those of birds (Padian, 1980, 1983; fig. 18). They are different from
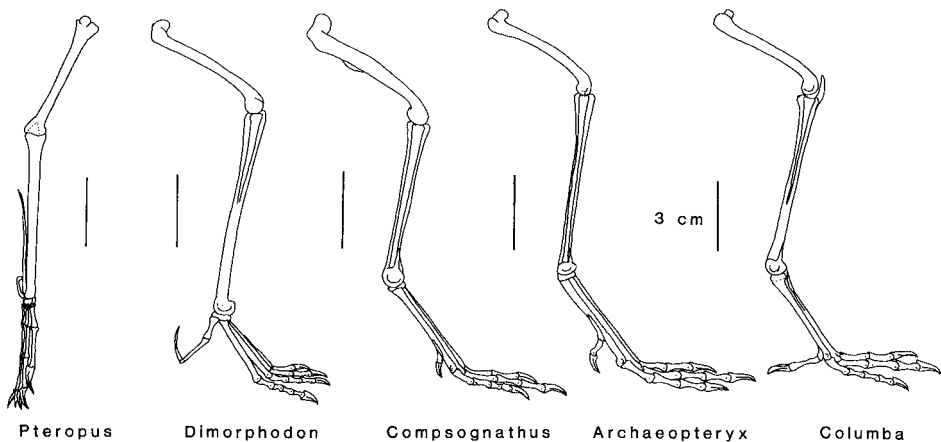
Fig. 18. Right hindlimbs, seen in natural articulation in lateral view, of the megabat *Pteropus*, the pterosaur *Dimorphodon*, the small carnivorous dinosaur *Compsognathus*, the earliest known bird *Archaeopteryx*, the living pigeon *Columba*.

those of bats in all structural and functional details (except one: the knee is a hinge joint, as it is in nearly all other amniotes). Consequently it seems far more probable that pterosaurs were bipedal, with an erect stance and parasagittal gait (Stieler, 1922; Padian, 1983, 1985; Wild, 1984; Bennett, 1990; Gauthier, 1986; for contrast see Unwin, 1987; Wellnhofer, 1988, 1991b; Pennycuick, 1988); unfortunately no footprints have been discovered to settle the matter (Padian and Olsen, 1984; Unwin, 1989). No one has doubted these observations in the literature, so they need not be repeated and argued here. Workers who have not accepted a bipedal posture and a parasagittal gait (Wellnhofer, Pennycuick, Unwin) have instead rejected this evidence as circumstantial or irrelevant, in favor of other considerations.

Wellnhofer (1975a,c, 1985; 1988; Wellnhofer and Vahldiek, 1986) has argued that the ventral symphyses between the ischia were unfused in pterosaurs, and that in fact there was a wide gap between them that prevented the limbs from being brought under the body. Padian (1983) illustrated a variety of pterosaurs, all of whose pelvic symphyses fit perfectly together, and many of which were preserved that way. The pterosaur specimens that Wellnhofer considered were nearly all of *Rhamphorhynchus,* and these pelves seemed to be irregularly disarticulated and incomplete. Revised interpretations of complete pelves supported the view that the ventral symphysis is in fact fused in all adult pterosaurs for which adequate information is available. Bennett (1990), for example, showed that the ventral pelvic symphysis of the Brazilian Cretaceous pterodactyloid *Anhanguera* described by Wellnhofer (1988) is unfused because it is a juvenile; the symphysis is fused in a larger specimen

described by Bennett (see also Wellnhofer, 1991b). Padian (1983) reconstructed the fused pelvis in several different specimens of *Campylognathoides* (*pace* Wellnhofer and Vahldiek, 1986).

Whether the pelvis was fused or unfused, however, makes little difference to the question of posture and gait. Neither does the question of the direction in which the acetabulum, or hip socket, faced (Molnar, 1987; Wellnhofer, 1988; Unwin, 1978; Bennett, 1990). In the first place, the pterosaur femur did not extend vertically down from the pelvis but was oriented more or less horizontally and extended forward as in birds (Padian, 1983). Its dorsoventral excursion was probably considerably less than the anteroposterior excursion of the tibia, as in birds. And, as McGowan (1991, p. 265) notes, many birds have hip sockets that face outward and upward (a fact easily confirmed by spending a few minutes in an osteological collection), but they are nevertheless bipedal. To date, no one who objects to the idea that pterosaurs were bipedal with a parasagittal gait has offered any alternative explanation for the morphology of their bird-like hindlimbs. Pennycuick (1988), for example, has dismissed the similarities between dinosaur and pterosaur hindlimbs as simply being due to inheritance, as if natural selection could not have shaped pterosaur hindlimbs over 160 my to make them better suited for whatever kind of locomotion is proposed as an alternative to the parasagittal gait.

Pennycuick (1986, 1988) objects to the idea of bipedal pterosaurs because he thinks the pelvis was too small. His reasoning implies that the size of muscle attachment area is the arbiter of function. If that were so, it would be easy to postulate from their skeletons that bats cannot fly, because the area for the insertion of the thoracic muscles on the deltopectoral crest of the humerus is so small, compared to those of birds and pterosaurs; and of course bats have no expanded, sheet-like, calcified sternal area for the origin of the flight muscles, as do birds and pterosaurs. Pennycuick's reasoning would further imply that *Archaeopteryx* could not have flown at all, because it lacks a bony sternum and has a small delto-pectoral crest, but this is not the general view (Olson and Feduccia, 1979; Hecht and others, 1985; Rayner, 1988a, 1991b). Pennycuick also objects that the short-tailed pterodactyloids could not possibly have stood on their hind legs because they had lost the tail for counterbalance. This assumes incorrectly that the tail was a static mass stabilizer, instead of a muscular, dynamic stabilizer (see Ostrom's, 1969b, argument on this point for the bipedal theropod dinosaur *Deinonychus,* and Rayner, 1991b on *Archaeopteryx;* also Alexander, 1989a). But, as McGowan (1991, p. 266) points out, birds have lost their bony tails and yet walk bipedally, and they can do this in part because their internal organs are balanced over their hindlimbs (see also Gatesy, 1990).

More importantly, however, one must consider the role of tendons, muscles, joints, cartilage, and physiology in the reconstruction of extinct animals, even though direct evidence of these factors is more often than not wanting and is usually absent altogether. The functions of animals must be studied as more than the sum of their mechanical parts. The

carcass of a dead bird cannot support itself to stand bipedally. The normal human posture is inherently unstable: it is maintained by muscle tone, physiology, and a sense of balance, and if any of these are lost even temporarily, a person falls over. Nor could one expect that kangaroos could continue their hopping gait without an adaptive system involving factors ranging from muscle tone and physiology to the incorporation of elastic tendons, ligaments, and springy cartilage that stores energy (Alexander, 1988, 1989a). Ignoring the likelihood of such adaptive factors in extinct animals, given structural components that otherwise suggest such a picture, one runs the classic risk of postulating that bumblebees are incapable of flight on engineering grounds (McMasters, 1989). Even if bumblebees were wholly extinct and their flight incapable of observation, one would have to wonder from preserved fossils what their wings could have been used for if not for flight, inasmuch as their wings are similar in all other respects to other insect wings.

Beyond the question of the apparent area of muscle attachment surfaces is the question of how the joints operate. The femur moves mostly above and below the horizontal in pterosaurs, and the tibia mostly swings back and forth (Padian, 1983), as in birds (Cracraft, 1971; Gatesy, 1990). The ankles of pterosaurs (like those of other archosaurs) are hinge joints, not as unrestricted as the multi-boned ankles of bats or lizards; their metatarsals and toes are long and of differing lengths, not short and equal like those of bats; and their foot claws are small and only slightly curved, not enlarged and hooked like bat claws (fig. 18). These are adaptations for long stride and rapid progression on the ground (Coombs, 1978) and are in all respects consistent with the same features and functions seen in birds and other dinosaurs (figs. 18, 19).

This also raises the question of how phylogenetic considerations should be used in reconstructing the functional morphology of extinct animals. The closest outgroup to pterosaurs is the small bipedal ornithosuchian *Scleromochlus* (Padian, 1980, 1984a), and the next closest relatives of pterosaurs are *Lagosuchus* (and its allies) and the first dinosaurs, all of which were small, bipedal forms (Padian, 1984a; Gauthier, 1986). It has yet to be shown that pterosaurs changed this basic architecture substantially as they evolved hypertrophied forelimbs for wings. The same is true for the fused pelvis, a primitive character in all these groups, and in archosaurian outgroups (Gauthier, 1986). Therefore the burden of argument is on the opponents of pterosaur bipedality to show the evolutionary steps in an independently documented phylogenetic analysis of pterosaurs that demonstrate any such change. It is not sufficient simply to point to the size of the forelimbs, because these are constructed with extremely thin walls (Wellnhofer, 1991a) like fluorescent light tubes and weigh very little.

CONCLUSIONS

Judging from available specimens of several genera of Jurassic and Cretaceous pterosaurs, this group of animals possessed a unique morpho-
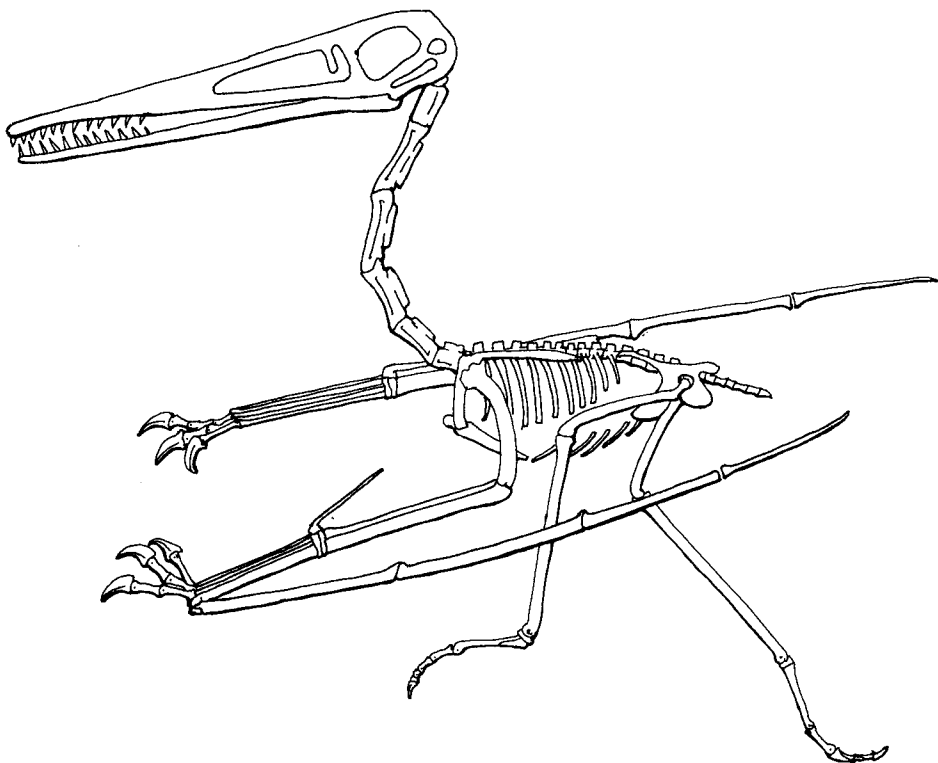
Fig. 19. Reconstruction of a bipedal *Pterodactylus* in terrestrial progression. The left forelimb is extended slightly forward, the right forelimb is retracted.

logical system of soft and structural tissues composing the patagia of their wings. The wing spar, the bones of the forelimb (particularly the elongated wing-finger), formed the leading edge and was probably sheathed in tissues that protected the bone and its associated nerves and tendons, plus the tissue probably immediately behind the spar from which the rest of the patagium arose. The membrane and associated tissues of the patagium probably originated from dermal muscle and skin. The membrane itself must have been able to repair any tears or injuries quickly, as do the wings of bats.

We have discussed a number of features by which the evidence of patagia may be diagnosed in a pterosaur fossil (table 1). It is important to distinguish real anatomical structures from the effects of natural deformation of those structures or the effects of peri- or post-mortem damage and disturbance. Fibers may be preserved in several ways: in rare exceptionally preserved specimens they are present in natural relief, sometimes extending over large parts of the wing (fig. 1), sometimes localized

according to the topography of the underlying substrate. In other cases the patagium is visible as areas (sometimes very small) of staining, usually a dull brown color, in which the striations of the fibers are visible (fig. 4I). Some specimens (*Pterodactylus kochi*, NHMW 1975/1756, *Tupuxuara*) show both forms of preservation. In several *Pterodactylus* and *Rhamphorhynchus* specimens from Solnhofen the stone in which the fibers may be distinguished is a thin, friable layer, often a dull gray in color, that separates easily; this may represent fragments of a real fossilized patagium. In many specimens (most regions of BSP 1937 I 18; fig. 3G) the patagium is preserved as a smooth surface, with no apparent fibers; in these cases the dorsal side of the patagium (or a mold of it) has been fossilized, and fibers, which lie on the ventral side only, are not visible. In the Vienna *Pterodactylus kochi* (NHMW 1975/1756), impressions of both ventral (with fibers) and dorsal (as smooth matrix) surfaces of the wing are present, in places adjacent to where the wing has creased and folded upon itself (fig. 4H).

Folds of the wing are natural features associated with the resting position of the flexed wing or of its position during diagenesis. Folds generally run for considerable distances parallel to the leading edge spar, and to the structural fibers (figs. 1, 2), and may represent a gathered patagium containing as many as ten, or even more, fibers; shorter folds are visible at the trailing edge, particularly in regions where the trailing edge is curved, and often the patagium surface in this area is slightly waved (fig. 4D); these again run parallel to the local fiber axes. To our knowledge, all specimens with extensive distributions of fibers show such folds, often with considerable relief, and always parallel to the fiber axes, while in addition many specimens show folds—often from the wing's dorsal surface—although no fibers can be seen. We have explained how deformation of the patagium when the wing is flexed, or when the patagium contracts unevenly after death, will result in folds parallel to the fiber axis, and this is strong evidence that the fibers stiffen the patagium. Some specimens of *Rhamphorhynchus* and *Pterodactylus* preserve only a narrow, sharply pointed wing shape, which results from contraction and folding of the patagium parallel to the fibers, as a series of overlapping folds. Some specimens in which the metacarpo-phalangeal joint is strongly flexed (fig. 4B) show a pattern of S-shaped folds behind the wrist and ulna, with the fibers locally distorted to lie parallel to these folds. This presumably reflects the natural configuration of the folded wing, and we suppose that during flight the orientation of the fibers changed, and the folds in this region were stretched out.

Other structures preserved occasionally include creases or large scale wrinkles in the wing (fig. 9). These may be regions where the wing folded upon itself when at rest, in which case they are creases parallel to the local fiber axis. They may also be sharp edges where the patagium (or its fossil) have fractured after death or after diagenesis or may be damage to the patagium which was sufficient to be the cause of death. These creases are not natural features of the wing, and may rarely show

evidence of trauma sufficient to snap or distort the structural fibers and the bones of the wing spar (in the Leich specimen of *Rhamphorhynchus;* Leich, 1964, 1968; Wellnhofer, 1991a). A common form of damage is separation of part of the patagium from the leading edge spar, and the patagium apparently remains intact, albeit folded and creased.

The composition of the fibers is uncertain, but they may have been homologous to the keratinous scales and feathers of other archosaurs. The patagium as a composite structure of skin (membrane) and fibers was, like other composite materials such as fiberglass, much stronger than either component alone to at least some forms of deformation. The wing spar had a natural medio-lateral arch, and the wing had an anteroposterior camber similar to those of other airfoils. Microscopic analysis reveals the presence of much finer hair-like structures, with a diameter of 0.01 mm, on the wings of some specimens, while other specimens possess patterns of dimples that are interpreted as hair follicles (Wanderer, 1908; Döderlein, 1923, 1929b; Wiman, 1928; Leich, 1964; Wellnhofer, 1991a; PMZ A/III 107; fig. 3E); these are presumed to have been part of the integumental covering.

The wings of pterosaurs were attached along the body and perhaps posteriorly along the thigh in at least one genus (*Pterodactylus*), but the extent of this attachment is not known for certain in other genera. The planform of the wing is narrow, however, like that of a gull, in all available specimens. There was no trailing edge tendon or chord, contrary to Pennycuick's (1986, 1988) assumption, and the wing was not principally structured in such a way to counter either spanwise or chordwise tension (Pennycuick, 1986, 1988) as was shown by Bramwell and Whitfield (1974).

In all pterosaurs for which adequate evidence exists, the pelvic plates were fused along their ventromedial symphyses, at least as adults. The orientation of the acetabulum varied, as it does in birds, but the hindlimbs were without exception organized along the plan seen in birds and other dinosaurs. This evidence indicates that pterosaurs had an erect posture and parasagittal gait (Padian, 1983). The assumption that their pelves were too weak to support muscles for bipedal locomotion, as Pennycuick (1986, 1988) maintains, is falsified by the principles of comparative anatomy that demonstrate the frequent absence of hard part structures with comparable muscle attachment areas in animals with known locomotory abilities.

In this paper we also acknowledge our long-standing appreciation to Dr. John H. Ostrom, who—long before either of us entered graduate school—carried out extensive but unpublished studies of pterosaurs and came to many keen insights about their paleobiology. With this paper we celebrate his many contributions to the field of vertebrate paleontology, which he has revolutionized through his systematic observations and explorations of reptilian evolution, function, and paleoecology, and we equally celebrate his influence on a generation of paleobiologists and other scientists, in part through his long service as an Editor of this Journal.

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