



6

THE MEMBRANE WINGS OF BATS AND PTEROSAURS

Unlike a wing made of feathers, one that evolved by extending a lateral patagium, like that of flying squirrels, has to be tensioned between two or more skeletal members. The diversity of bats is much less than that of birds, because of their less versatile wings, whose structure also constrains the evolution of the legs. The wings of pterosaurs also involved the legs, but may have had an elastic membrane that allowed control of span and area, with a degree of versatility nearer to birds than to bats.

This book is primarily about birds, but any animal that flies has to overcome the same mechanical problems, in the process of transforming its ancestral limb structure into a pair of wings. The other two groups of flying vertebrates, bats and pterosaurs, started from the same basic tetrapod limb structure as birds, but evolved wings in which the surface area is provided by a *patagium*. This is essentially a double layer of skin, which has no bending stiffness in itself, and has to be stretched out like a hang glider's sail by a skeletal frame, rather than being supported at one end only, as sailplane wings and flight feathers are. The diversity of both groups has been restricted in comparison

with that of birds, as a direct result of the mechanical basis of the pterygium, in ways that can be observed in bats, and inferred in pterosaurs. Beyond the limitations inherent in patagial wings, the two groups are very different.

6.1 — BATS

Bats (Chiroptera) are a widespread and highly successful order of mammals, with more living species (over 1000) than any other order. The earliest known bat fossils are from the Eocene period, some millions of years after the last pterosaur died at the end of the Cretaceous. The few survivors of the catastrophe that ended the Mesozoic Era included the ancestors of modern birds and mammals, and most of the modern orders of both groups are first known from Eocene fossils. Bats are similar in size and mass to small and medium-sized birds, but there are no goose-sized or larger bats. Like birds, they originated from ancestors that did not fly, and modified their original anatomy so as to fulfil the requirements for flight. They have wing spans and aspect ratios in the same range as birds of similar size, and the *Flight* programme, which only requires that information, will calculate their flight performance without distinguishing between them and birds.

The physical problems of evolving wings are the same for birds and bats (Chapter 3) but the solutions that the two groups have evolved are different in almost every respect. Bats are excluded from a vast range of ecological niches in which birds use their legs for walking, perching, running, swimming and catching prey, because the leg is a primary element of the wing structure in bats, whereas in birds it is not. Most bats find their way around and locate their prey by echolocation rather than vision, which makes them pre-eminent as nocturnal aerial insectivores, but not so good at other forms of predation. There are bats that eat other bats, and one bat species (*Nyctalus lasiopterus*) is believed to prey on nocturnally migrating songbirds, on the basis of feathers in its droppings at migration time. On the other hand two entire orders of birds (raptors and owls) are specialised as predators, including many raptor species which catch birds and bats in flight. Likewise, whole orders of birds are specialised for living and hunting in the water (Chapter 12), whereas there are no true water bats. Caribbean fishing bats can detect ripples on the water surface caused by a fish swimming just below, and catch the fish by dipping their hooked hind claws in the water, but no bat can swim around under water like a cormorant in pursuit of fish, or plunge-dive like a kingfisher. The mammalian method of reproduction requires bat mothers to carry



FIGURE 6.1 A female *Rousettus aegyptiacus* carrying a baby in flight. This is a small fruit bat (Megachiroptera) with a mass of about 120 g and a wing span of about 0.5 m. The plagiopatagial muscles can be seen on the left wing. The soles of the feet point forwards because of rotation of the leg at the hip joint. The ankle joints are deflected downwards to produce a downward curl at the trailing edge of the plagiopatagium. Unusually for a fruit bat, this species uses a primitive form of echolocation for obstacle avoidance. The lips are drawn back to emit clicks that are audible to the human ear. Photo by C.J. Pennycuik.

embryos and babies in flight (Figure 6.1), rather than laying eggs in a nest, and the limitations of mammalian lungs exclude bats from high-altitude flight (Chapter 7, Box 7.7). Birds are seen over the polar ice fields, but bats are not. Some bats migrate over land in short stages of a few tens or hundreds of kilometres, but no bat flies non-stop for thousands of kilometres over ocean or desert, as many bird species do. The abilities and limitations of bats begin with the mechanical principles of their wings.

6.1.1 MECHANICS OF THE BAT WING

Whereas birds have a pure cantilever wing, in which a stiff structure delivers all the bending and torsional loads to the shoulder joint, the wing membrane of a bat is flexible, with no resistance to bending or torsion. The only type of stress that the membrane can resist is tension. It has to be stretched between two stiff bony supports, which pull outwards at opposite edges. If the membrane were flat, it would only pull on the bony framework in the plane of the membrane, and would not

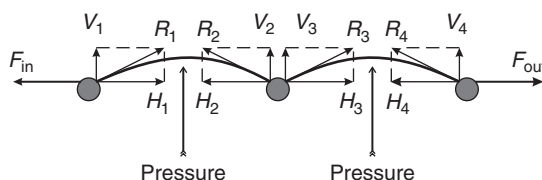


FIGURE 6.2 A bat's wing membrane can only resist tension, not bending or torsion. It has to be stretched between two or more skeletal supports (grey). The membrane bulges towards the low-pressure side of the wing, so that it pulls on the supports at an angle to the plane of the wing. The middle support is pulled by a force R_2 by the membrane on its left, and by a force R_3 by the membrane on its right. The horizontal components of these two forces (H_2 and H_3) cancel, while the vertical components (V_2 and V_3) add together, and contribute to the aerodynamic force on the wing. The vertical components on the outer supports (V_1 and V_4) also add to the aerodynamic force, while the horizontal components H_1 and H_4 have to be balanced by forces F_{in} and F_{out} , applied by the supports. These outward forces are necessary to "tension" the wing.

exert any force perpendicular to that plane (lift). It works as a wing because the membrane bulges when excess air pressure is applied to one side of it (Figure 6.2). At every point around the edges of the membrane, where it attaches to the skeleton, it exerts a large component of force pulling inwards, which is balanced by an opposing force at the opposite edge, and a smaller component, which is unbalanced, perpendicular to the wing surface. The sum of these unbalanced components makes the aerodynamic force on the wing, which is then resolved into drag (parallel to the incident air flow) and lift (perpendicular to the incident air flow). As always, the measure of the wing's efficiency is the ratio of lift to drag. The skeletal supports have to resist the unbalanced forces that translate into the aerodynamic force on the wing, as they do in a bird's wing, and in addition, they have to provide the tension in the membrane by pulling against one another.

Figure 6.3 shows the main structural components of a bat's skeleton, and the nomenclature of different parts of the wing membrane from Norberg's (1972a) account of *Rousettus aegyptiacus*. This is a small member of the suborder Megachiroptera (fruit bats), but the same description of the main wing components also applies to the other suborder (Microchiroptera, insectivorous bats), which includes the majority of bat species. From the shoulder to the wrist, a bat's wing skeleton is similar to that of a bird, except that, as usual in mammals, the radius rather than the ulna is the main structural element of the forearm.

The way in which aerodynamic forces are developed by the different panels of a bat's wing, and transferred to the skeleton, was analysed by

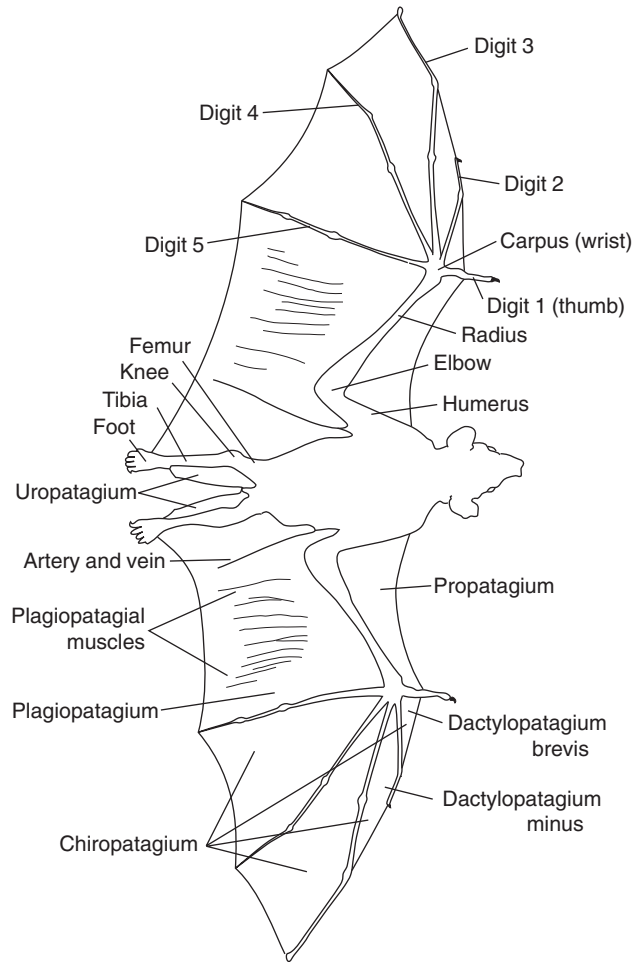


FIGURE 6.3 Nomenclature of the parts of a fruit-bat's wings, according to Norberg (1972a).

Norberg (1972b). Outboard of the wrist, where the bones of a bird's hand skeleton are reduced and thickened, those of a bat are hugely elongated and slender. The five elongated metacarpals radiate from the wrist joint, and each digit continues with three or four similarly elongated phalanges. Digit 1 (the thumb) points forwards and supports a drooped leading edge in flight, as well as being used for clambering, while Digits 2–5 support the wing surface. Digit 3 runs to the wing tip, and is augmented by the shorter Digit 2, ahead of it, to make the rhomboidal “Norberg panel”, described by Norberg (1969) and shown in Figure 6.4. This is a characteristic feature of the wings of all bats, that

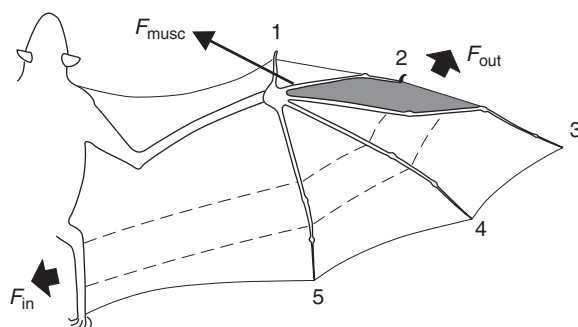


FIGURE 6.4 A bat's wing is tensioned by the *musculus extensor carpi radialis longus*, which exerts a force (F_{musc}) on the anterior side of the base of the second metacarpal. The Norberg panel (grey) is the rhomboid-shaped unit formed by the second and third digits, and the dactylopatagium minus between them. This is stiff in the plane of the wing, and transmits the pull to the membrane between Digits 3 and 4. Norberg (1969) explains in detail how this works. The forward pull due to the muscle rotating Digits 2 and 3 is eventually balanced by an inward pull exerted by the leg. The short arrows correspond to the forces F_{in} and F_{out} in Figure 6.2 The tension path between them (dashed lines) changes direction as it pass through Digits 4 and 5, which are held in compression by the pull of the membrane.

is light but stiff in the plane of the wing. It allows the hand-wing to be pulled forwards against a strong drag moment, but does not require the phalanges to be thick and heavy, as they are in a pterosaur's wing-finger (below). A hypothetical Norberg panel probably also formed an essential part of the wing of the ancestors of birds, up to and including *Archaeopteryx*, although its function has been taken over in modern birds by the fused metacarpals (Chapter 16).

The last two fingers (Digits 4 and 5) run through the membrane from the wrist to the trailing edge, and perform two distinct functions. The first is to resist the bending moment caused by the pull of the membrane as it bulges towards the low-pressure side on both sides of the finger. The bending moment in the finger is much the same as that in a flight feather shaft, but it originates differently, from the upward component of tension in the membranes attached to each side of the finger skeleton, rather than from the attachment of the cantilever bases of the stiff barbs to the sides of the feather rachis. Besides tending to bend the finger, the tension in the membrane also tends to compress the finger towards the wrist. In resisting this compression, each finger allows the tension path in the membrane to turn. Working outwards from the body, the tension paths turn a corner as they pass Digit 5, and another at Digit 4. As a result, Digit 3 can pull forwards

on the outer edge of the wing, directly opposing the leg, while pulling in an almost perpendicular direction. This allows the wings of some bats, especially Molossids, to be tensioned straight out from the body, in a rather narrow, pointed shape. Because pterosaurs lacked fingers through the membrane, they would not have been able to bend the tension path in this way, and must have depended instead on backward curvature of the wing finger to tension the membrane (below).

6.1.2 THE LEG AS WING SUPPORT IN BATS

Besides tensioning the patagium at the inner edge, the leg also controls its camber. The knees of non-flying mammals, such as ourselves, bend the wrong way for this. Flexing knees like ours would camber the trailing edge of the wing upwards instead of downwards. The two stereoscopic pairs of photographs in Figure 6.5 show a *Rousettus* fruit bat gliding in a wind tunnel, seen from above. Both pictures show that the hip joints allow the femurs to rotate outwards to such an extreme degree that the knees project outwards and *upwards* in flight, a position which is not ideal for walking on the ground. The feet are rotated around so that the toes curl downwards, with Digit 1 (the big toe) on the outside and Digit 5 towards the centreline. The ankle joint can flex so as to curl the trailing edge of the plagiopatagium sharply downwards, as seen in Figure 6.1 in the downstroke of flapping flight. Most bats have a limited ability to walk quadrupedally on their wrists and feet, with the thighs splayed wide apart. Some (especially vampires) are surprisingly agile on the ground, and can even jump, but they cannot stand or walk upright on their hind legs, because the hip joint has to be very far back, in order for the leg to support the posterior part of the wing membrane. Bats' toes are armed with sharp, hooked claws, and they typically roost hanging head downwards from their feet, with the wing membranes wrapped around the body. Unlike the versatile feet of birds, this simple bat foot is not readily adaptable to functions other than hanging up, or clambering about in branches (Figure 6.6).

6.1.3 CONTROL OF PLANFORM AND PROFILE SHAPE IN BATS

Like a hang-glider's sail, a bat's wing has to be tensioned, meaning that a steady tension force has to be applied to the outer part of the membrane, and balanced by an inward pull, where the membrane attaches to the leg skeleton, and to the side of the body. This means that if a bat reduces its wing span by sweeping back the hand wing, in the way that birds do, the membrane has to contract, which reduces the tension in its internal elastic fibres, so that the sail billows upwards (Figure 6.7).

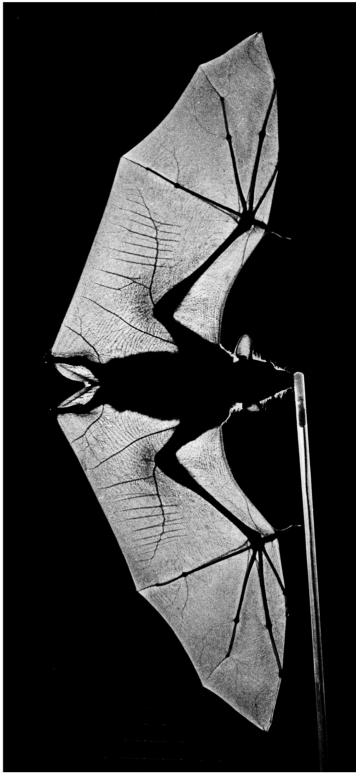
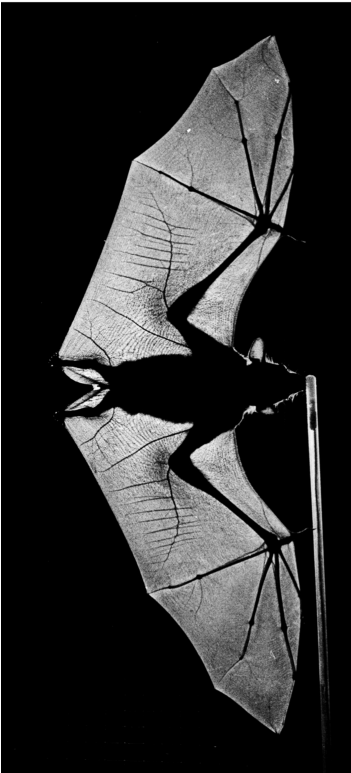
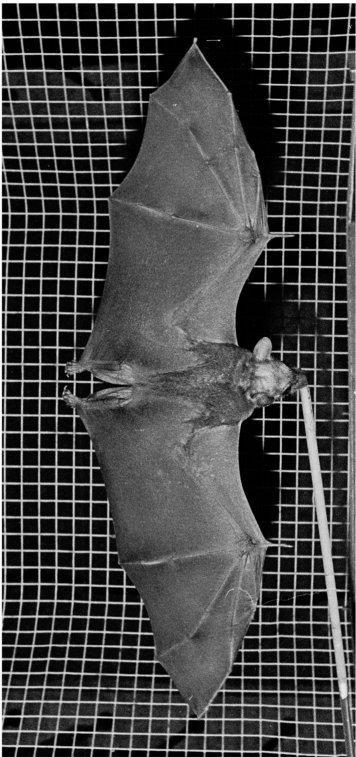
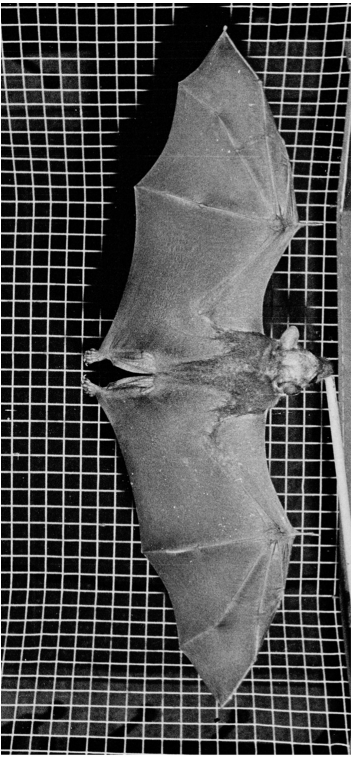




FIGURE 6.6 A typical bat foot, belonging to the fruit bat *Rousettus aegyptiacus*. All five toes are similar, with hooked claws, used for hanging inverted while roosting. Fishing bats hook fish by trailing the claws in the water. Photo by C.J. Pennycuick.

While birds drastically reduce both the span and area of their wings at every upstroke of flapping flight, without impairing the wing's ability to resist bending and twisting moments (Chapter 5), bats can only do this to a minor extent, and not without affecting the strength of the wing.

FIGURE 6.5 Stereoscopic photographs of a small fruit bat (*Rousettus aegyptiacus*) flying in a wind tunnel (from Pennycuick 1971). The air stream was inclined upwards by tilting the wind tunnel, so that the bat was able to glide. It was trained to maintain a constant position by feeding it with banana pulp, supplied through the tube on the right. The camera was aligned perpendicular to the air flow, and the upper stereo pair was taken by reflected light, from a flashgun mounted above the tunnel. The lower pair was taken by transmitted light, by mounting the flashgun below the bat, so that the light shone directly towards the camera, through the wing membranes. The stereoscopic effect can be seen by diverging the eyes, so that the left eye looks at the left picture, and the right eye at the right picture. The viewer will then see three images, the centre one being three-dimensional, formed by fusing the two pictures. This is easiest to achieve by holding the page in bright light, perpendicular to the line of sight, and starting with the upper (reflected light) image. When fusion is achieved, the wire netting will recede below the bat, and the central image will become solid. Viewers who are new to this may find it helpful to start by looking over the top of the page, and fixating on an object a few metres away, and then transferring attention to the bat images and fusing them. Photos by C.J. Pennycuick.

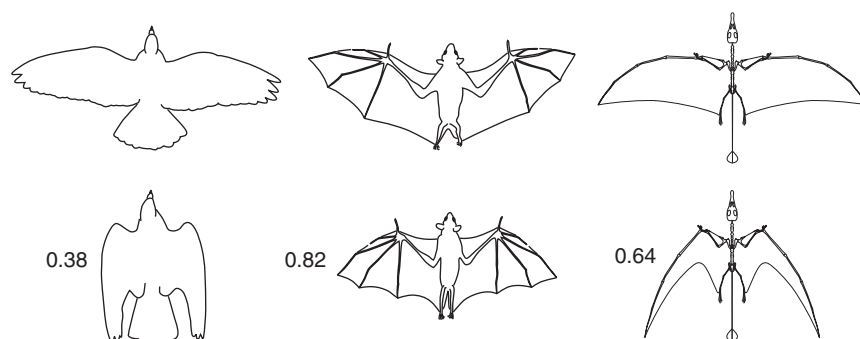


FIGURE 6.7 A pigeon (left) trained to glide in a tilting wind tunnel could reduce its wing span by a factor of 0.38 when the wind speed was increased from 8.6 ms^{-1} to 22 ms^{-1} (Pennycuik 1968a) while a fruit bat (centre) trained to glide in the same wind tunnel had a narrower speed range from 5.5 ms^{-1} to 10 ms^{-1} , and could only reduce its wing span by a factor of 0.82 (Pennycuik 1971). If pterosaurs' wings (right) worked as postulated in Figure 6.10, with an elastic membrane, they would have been better able than bats to vary their wing span and area, and perhaps comparable with birds in this respect. These planform changes also occur between the downstroke and upstroke of every wingbeat, and may be responsible for the superiority of birds over bats in long-distance migration, in which case pterosaurs' flight performance may have been more comparable to that of birds than to that of bats.

If the conjecture in Chapter 4 is correct, that birds use this planform variation to obtain an energetically efficient vortex wake, then the inability of bats to do the same thing might be one reason why their migrations seem to be confined to much shorter distances than those of birds. On the other hand, Digits 4 and 5 give a bat a much greater degree of control of the cross-sectional shape of the hand-wing than is possible in a bird (Norberg 1972b), and this is the basis of the incredible agility at low speeds for which bats are famous, for instance when catching flying insects. Bats can also control the camber of the plagiopatagium to a limited extent, by shortening a set of plagiopatagial muscles that run fore-and-aft in the membrane, behind the ulna, without attaching to the skeleton at either end. In gliding flight, these muscles flatten the cross section at higher speeds, and relax to allow the membrane to bulge upwards into a more cambered shape at low speeds. A similar arrangement in hang gliders is called "variable billow". Figures 6.8 and 6.9 show contour maps of the wings of a gliding bat, at speeds near the minimum and maximum at which it would fly in a wind tunnel. Changes of profile shape and angle of attack at different speeds can be seen (Box 6.1). These maps were made by photogrammetry from stereoscopic photographs like those of Figure 6.5.

BOX 6.1 Bat contoured plots.

Figures 6.8 and 6.9 were made from two stereo pairs like the lower pair in Figure 6.5, taken by transmitted light (Pennycuick 1971, 1973). Enlarged positive transparencies were made from the original negatives and placed

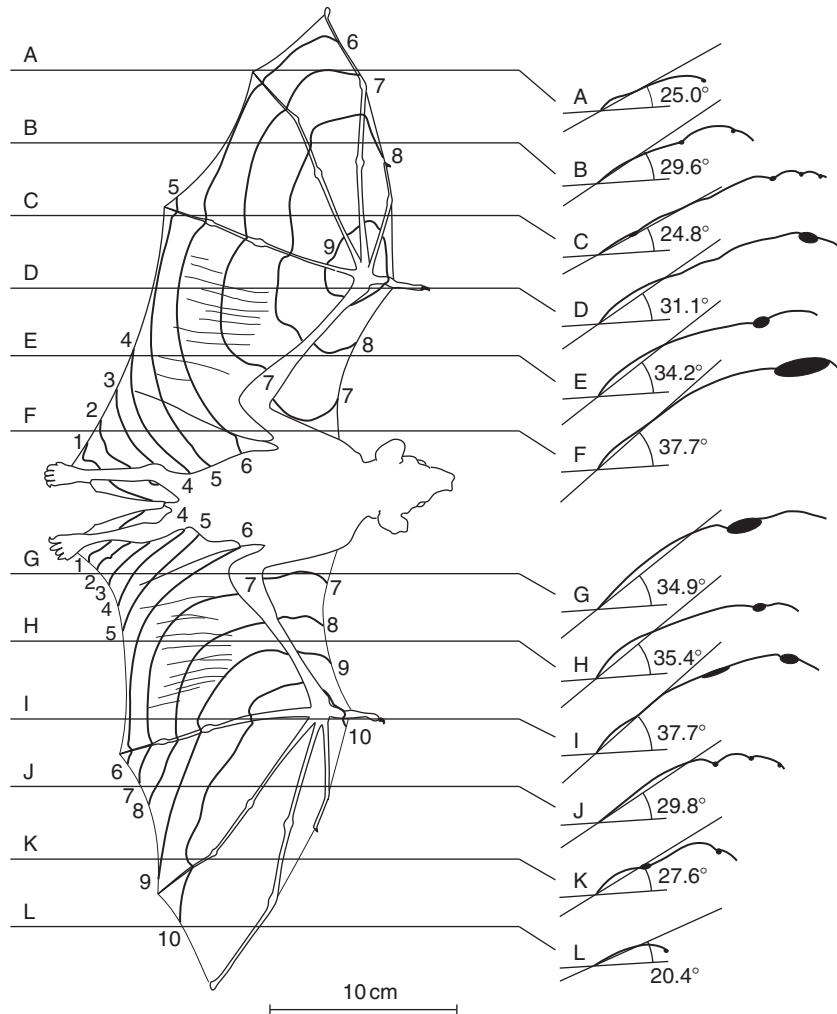


FIGURE 6.8 Contour map of a *Rousettus* fruit bat gliding steadily in a tilting wind tunnel at an equivalent air speed of 5.5 ms^{-1} , from a stereo pair of photographs taken by transmitted light, as in Figure 6.5. The thick contour lines are numbered with the height in centimetres above a datum plane just below the bat's feet. The thin lines marked A–L are the positions of profiles whose upper surface is shown on the right, with the cross-sectional shapes of the bones filled in approximately. The zero-lift line through the trailing edge of each profile was calculated from thin aerofoil theory according to the method of Pankhurst (1944), and as this bat was gliding, the angle of attack was measured relative to the axis of the wind tunnel. Data for the bat are in Table 6.1. From Pennycuick (1973).

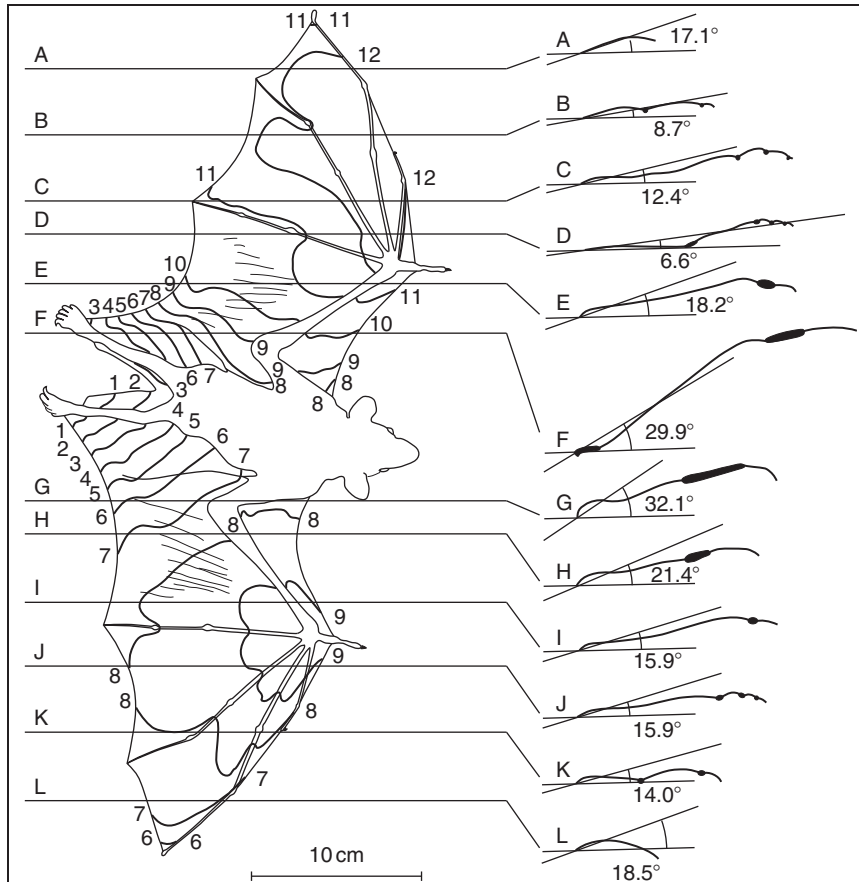
BOX 6.1 *Continued.*

FIGURE 6.9 Contour map as in Figure 6.8, but at a higher speed (9.0 ms^{-1}). The bat reduces its wing span and area slightly, flattens its profile by tightening the plagiopagial muscles, and reduces its angle of attack. From Pennycuik (1973).

in a map-making machine, normally used for making contour maps from pairs of vertical aerial photographs. A spot that appeared to the operator to float at a constant (but adjustable) height was steered by hand along the three-dimensional surface, while the machine reproduced its track on a drawing. The resulting contours (thick lines) are numbered with the height of the membrane in centimetres, above a datum level just below the bat's feet. In Figure 6.8 the highest level is Contour 10 on the outer part of the right wing, which is 10 cm above the datum level, that is, nearer to the camera.

Besides drawing the contours, transects were taken along each of the 12 chord lines A–L, and plotted as wing profiles on the right of each figure. The cross-sectional shapes of the bones are approximate, as these are seen in silhouette by transmitted light. The profiles from the upper surface can

BOX 6.1 *Continued.*

be considered according to the classical theory of thin wing sections as explained by Abbott and von Doenhoff (1959). A practical numerical method due to Pankhurst (1944) allows the zero-lift angle of attack to be calculated (see Chapter 3, Box 3.5). This is the angle between the chord line and the direction of the incident air flow, which would make the lift coefficient zero if this were a rigid profile made of, say, sheet metal. The chord line is not shown in the profiles in Figures 6.8 and 6.9 (it joins the leading and trailing edges), but they show an estimated zero-lift line drawn through the trailing edge, and a line which is parallel to the axis of the wind tunnel, and assumed (as the bat was gliding) to represent the incident air flow. The angle between these two lines is an estimate of the local angle of attack.

TABLE 6.1 Data for *Rousettus* contour maps.

	Figure 6.8	Figure 6.9
Body mass (kg)	0.120	0.120
Lift (N)	1.14	1.16
Wing span (m)	0.523	0.500
Wing area (m ²)	0.0495	0.0484
Aspect ratio	5.52	5.17
Lift coefficient	1.27	0.485
Equivalent air speed (ms ⁻¹) ^a	5.45	9.00
Tunnel tilt (°)	13.50	9.00
Downwash angle (°)	4.18	1.71
Reynolds number (mean chord)	34,000	57,000

^a Reduced to sea level air density 1.22 kg m⁻³.

6.1.4 FLIGHT MUSCLES OF BATS

The downstroke in flapping flight is powered by the paired pectoralis muscles, which originate over a wide area of the ribs and sternum, much like those of birds. The sternum of bats does not have an expanded curved dorsal plate like that of birds, because bats breathe with a diaphragm, not with a sternal bellows. Bats also lack the prominent ventral keel of the bird sternum, having only short bony sections at the forward and aft ends of the sternum, with a median ligamentous sheet stretched longitudinally between them. A bat's pectoral muscles originate on either side of this sheet of connective tissue, through which the left and right muscles pull directly against each other. No bony keel is needed for the muscles to flap the wings. The keel of the bird sternum serves a different function that does not apply to bats, allowing evaporative cooling directly from

cavities in the pectoralis muscles (Chapter 5). As in birds, the pectoralis of bats inserts on the underside of a ridge that projects forwards from the head of the humerus, so applying a nose-down moment to the wing, which is necessary for the same reason as in birds (Figure 5.5). Bats elevate the wing with the deltoid group of muscles, which originate on the side of the vertebral column, and pull upwards on the dorsal side of the humerus (Norberg 1970, 1972a).

6.1.5 THERMOREGULATION AND RESPIRATION IN BATS

When a bat's wing is not tensioned, the sail hangs loose with little contraction of its area. It does not fold in the fanwise manner of a bird's wing, or contract in the manner seen in pterosaur fossils (below). Bats cannot stand upright on their back legs, and they roost by hanging head-down from the feet, with the sail wrapped around the body. The sail has a vast surface area and a copious blood supply, which can be controlled in flight to dispose of heat by convection, provided that the air temperature is below that of the bat's blood. In sunlight, the wing collects heat if the blood supply is turned on, and this may be the main reason why most bats are nocturnal, or at least crepuscular. Bats can also dispose of heat to a limited degree by fluttering the sail when roosting, but they have no system for evaporative cooling, either internal like the air sacs of birds, or external like the sweat glands of many other mammals. Their last resort in a thermal emergency is to lick their chests, and use saliva for cooling.

The lungs of bats are like those of other mammals, but very different from those of birds (see Chapter 7, Box 7.7). Oxygen diffuses into the blood from the gas in the blind cavities (alveoli) that line the wall of the lung, and carbon dioxide diffuses out. The lungs are ventilated by contraction of a muscular diaphragm which closes the posterior end of the thoracic cavity, as in other mammals. Bats' lungs are no more effective than those of mountaineers at high altitudes, unlike the lungs of birds, which can maintain blood oxygen levels sufficient for strenuous activity, at lower atmospheric pressures. Some bird species routinely migrate at heights above 6000 m ASL, whereas bats are confined to more modest altitudes, perhaps 2000 m.

6.1.6 TAKE OFF AND LANDING IN BATS

Most bats roost in places like trees or the roofs of caves, where they can take off by dropping into a clear space, although a few (vampires) can take off by jumping upwards from a level surface. Landing involves

attaching the claws to a suitable toe-hold, and rotating the body from the flight attitude to the head-down roosting position. Small bats can land on a vertical or inverted surface, either by hooking the thumb claws on to the surface and swinging the feet up, or by rotating in the air and attaching the feet directly. Fruit bats have a somewhat different technique for landing on branches. The bat approaches slowly above the branch, with its feet trailing, and hooks the branch with its downward-curving claws, then swings over forwards into the head-down posture, furling its wings as it does so.

6.2 — PTEROSAURS

Pterosaurs are an extinct order of reptiles. They belonged to the archosaur branch of the Class Reptilia, which comprises birds, crocodiles and the two orders of dinosaurs, Saurischia (which were closely related to birds) and Ornithischia which were somewhat different. The archosaurs may be considered a sub-Class, or a super-Order, depending on how you look at it. The relationship between the different archosaur orders is that they all sprang from a common ancestor. That was a long time ago, but not so long ago as the still earlier ancestor that the archosaurs as a whole shared with other branches of the reptiles, such as turtles, lizards and the synapsid line that eventually led to mammals (including bats and ourselves). The common ancestor of birds and pterosaurs was not a flying animal. Birds and pterosaurs each evolved flight separately, in different ways, from an ancestor that did not fly (Chapter 16). Neither group inherited any flight adaptations from the other, or from a common ancestor.

The first pterosaur fossils are the most ancient known flying vertebrates, dating from Triassic times. Wellnhofer (1991) has written an authoritative account of their history, with sketches of all known genera drawn to the same scale. In terms of general shape, pterosaurs were like frigatebirds, with large wings relative to the size of the body, not like swans or guillemots. Early pterosaurs, characterised by a long, bony tail with a paddle on the end, are assigned to the suborder Rhamphorhynchoidea, which survived until late in the Jurassic. Some of the best-preserved rhamphorhynch specimens were found in the famous upper-Jurassic Solnhofen limestone formation of south Germany, alongside the first members of the other pterosaur suborder (Pterodactyloidea) which differed in having very short tails that could not have been used to balance the body weight about the hips. The loss of the balancing tail typical of dinosaurs was not accompanied by any drastic modification and expansion of the pelvis, like that seen in birds (Chapter 5), presumably because rhamphorhynchs had given up bipedal walking long before, when they modified the legs to

support the inner end of the wing (below). The Solnhofen formation also yielded several specimens of *Archaeopteryx*, the first bird known to have had a wing that (more or less) fitted the description in Chapter 5, although the rest of its skeleton did not yet show the characteristic modifications of the limb girdles and tail that distinguish birds from dinosaurs. Pterodactyls flourished until the last days of the Cretaceous, when they disappeared along with the dinosaurs and many other groups of animals. Birds later reappeared and prospered, but pterosaurs sadly did not.

6.2.1 MECHANICS OF THE PTEROSAUR WING

Pterosaurs are known only from their fossilised skeletons, and from surface impressions of the wing membranes in the relaxed (dead) state. As there is no prospect of observing pterosaurs in flight, still less of flying one in a wind tunnel, the way that their wings worked has to be inferred from the similarities and differences between their wings and those of birds and bats. The pterosaur skeleton was basically dinosaur-like, and to that extent it resembled a bird more closely than a bat. However, while birds retained the bipedal stance of their dinosaur ancestors, the legs of pterosaurs were modified like those of bats to support the inner end of a flexible sail, with only a limited capacity for walking.

The wing skeleton of pterosaurs differed from those of both birds and bats, in that there was a single, jointed bony spar, running all the way to the wing tip (Figure 6.10). Wellnhofer (1991) illustrates a sectioned pterodactyl humerus, which is a thin-walled tube very similar to the swan humerus of Figure 5.5, complete with internal trabeculae. The cavity may have been connected to the respiratory system and filled with air, as in birds. The radio-ulna was quite similar to that of bats, but instead of dividing into five digits at the carpal joint as in bats, the spar continued with four tightly bundled and partially fused metacarpals. These are thought to represent Digits 1–4, while Digit 5 is presumed to have been lost at an early stage of pterosaur evolution. The metacarpal unit was short in rhamphorhynchids, but in the later pterodactyls it was longer, and formed a prominent section of the spar. Three short, clawed digits (1–3) projected forwards from the outer end of the metacarpal unit, while the spar continued along the leading edge of the wing to the tip as a

whales (Figure 6.14), becoming prominent when the membrane is fully contracted. (D) *Rhamphorhynchus* foot after Wellnhofer (1991). If the feet were simply rotated back in C, the soles would be upwards, and Digit 1 would be on the inside. Outward rotation at the hip brings the dorsal side of the foot upwards, with Digit 1 on the outside. Digit 5 still supports the trailing edge tendon, as in the unrotated ancestor, and therefore has to be modified so that the tendon can pass over Digits 1–4 to the outside.

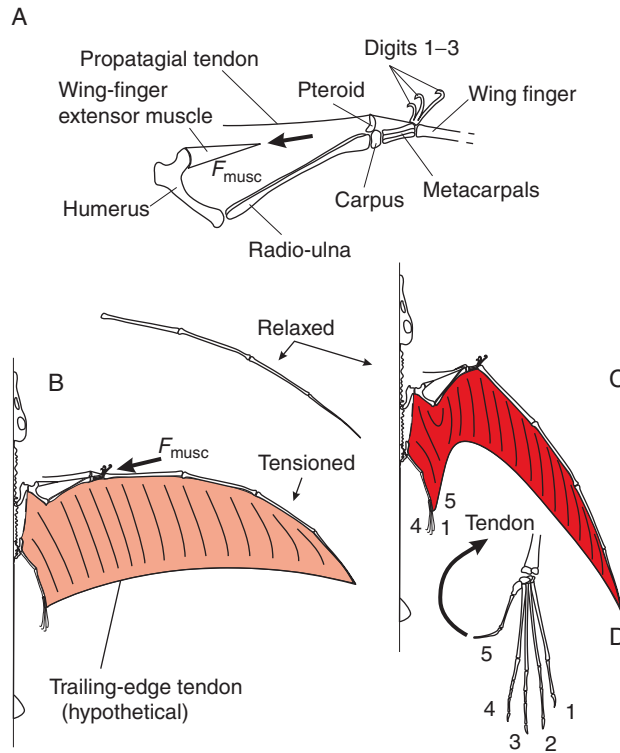


FIGURE 6.10 Pterosaur reconstruction based on *Rhamphorhynchus muensteri*, a small, tailed pterosaur from the Upper Jurassic Solnhofen limestone of southern Germany, as described by Wellnhofer (1975). The hypothetical elements of this reconstruction are from Pennycuik (1988b). (A) Arm skeleton (enlarged from (B) below). The distinctive hammer-headed humerus articulates with a straight radio-ulna (not curved like the ulna of birds). The pteroid, projecting forward from the carpus, is a bone that is peculiar to pterosaurs. The metacarpals are bound together to form a single structural unit. Beyond them the phalanges of Digits 1–3 form fingers with hooked claws, while Digit 4 is the hugely elongated “wing finger”. (B) To spread the wing, the elbow joint would have been fully extended, and the wing finger fully protracted. It is proposed that a muscle originating on the head of the humerus exerted a force F_{musc} to pull the wing-finger forwards, against the pull of elastic fibres in the membrane. A hypothetical trailing-edge tendon connects the fifth toe with the tip of the wing finger. The joints between the wing-finger’s phalanges are assumed to be bound by elastic material, so that the finger as a whole would flex like a bow when the wing was tensioned. The isolated wing-finger above the diagram is copied from (C), where the tension is partially relaxed, allowing the joints to straighten. (C) When the pull of the extensor muscle was relaxed, the elastic membrane would have been free to contract, pulling the wing finger back, reducing the wing’s span and area. The fully relaxed wing would contract so that its planform would be similar to that seen in the dead wings of fossils. The contraction would cause wrinkles to appear on the surface (thin black lines), which have been interpreted as structural “fibres”, although they are strictly surface features seen in casts of dead wings. More probably they are analogous to the “pleats” seen in the throat pouches of orquid

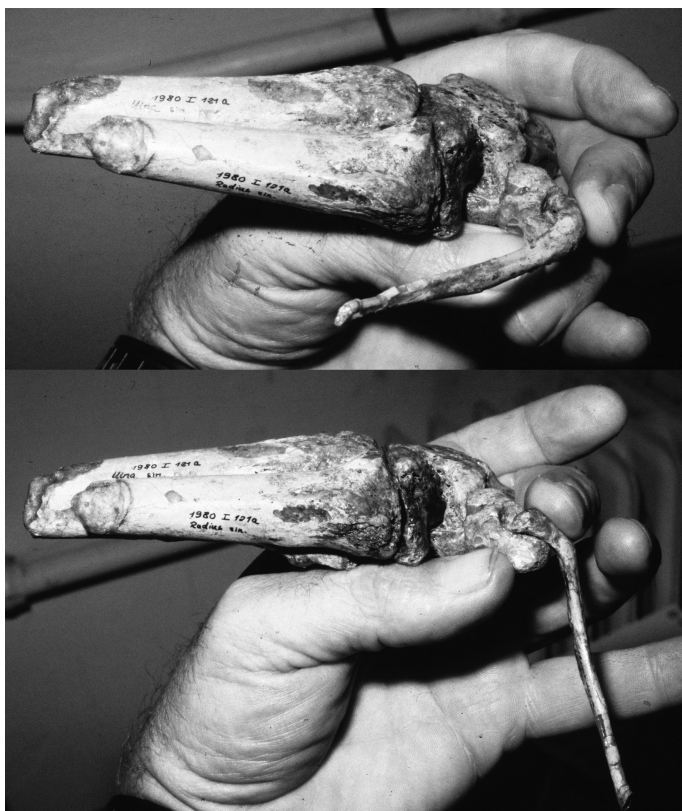


FIGURE 6.11 Two photographs of the carpus, and the outer end of the radio-ulna, of a Cretaceous pterodactyl *Santanadactylus spixi*, held by Prof. Peter Wellnhofer to show that the pteroid can be articulated with the carpus in two alternative positions. It is proposed here that extension of the wing caused the pteroid to “snap” from the upper to the lower position, so deploying the propatagium as a drooped leading edge. Photos by C.J. Pennycuik.

single, vastly elongated “wing-finger” with four phalanges, believed to be Digit 4. A small *pteroïd* bone, peculiar to pterodactyls, projected from the wrist, usually pointing inwards in fossils, towards the shoulder. Its function is uncertain, but it most probably controlled the leading edge of a propatagium that stretched from the shoulder to the inner end of the wing finger (Figures 6.11 and 6.12).

The nature of the wing membrane is known from a few fossils in which surface impressions of dead wings have been preserved, especially a number of famous late-Jurassic specimens of both rhamphorhynch and small pterodactyls from the fine-grained Solnhofen limestone. These show the outer part of the wing contracted into a narrow, sharply pointed shape which some authors (not very imaginatively) have assumed was also their

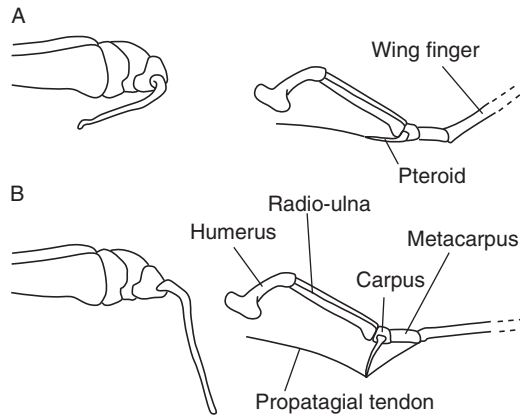


FIGURE 6.12 (A) Pteroid pointing inwards towards the shoulder, in the position normally seen in the contracted wings of fossils. (B) Pteroid in the "down" position proposed for the extended wing, deploying the leading-edge tendon to droop the propatagium.

shape in flight. In a few specimens, especially the famous "Zittel wing" now in Munich (Figure 6.13) a pattern of fine surface ridges can be seen, which were first described in 1882 as "Fasern" (fibres), and have been widely assumed ever since to be stiff structural elements made of keratin. The pattern of these "fibres" is vaguely reminiscent of the fan-like arrangement of flight feathers of a bird's wing, but there are far more of them, and they are much thinner—far too thin to be spars like feather shafts. They are also closely packed side by side, and as they radiate towards the trailing edge of the wing, new ones are interpolated between those that start further forward. At the forward end, they peter out, and there is no sign of any mechanical attachment to the wing bones. In the inner part of the Zittel wing, the "fibres" wrap around the elbow joint, appearing soft and flexible at that point, which suggests that they might have been soft and flexible over the rest of the wing as well.

It has been claimed that the "fibres" must represent solid structures, because they are so regular and sharply defined. However, elsewhere in this same Solnhofen limestone, fossilised medusae have been found, showing patterns of wrinkles where the surface contracted as the animal died in hypertonic brine. Such a soft creature would have to be preserved in a two-stage process, whereby some encrusting microorganisms such as blue-green algae first deposited a hard, negative "mould" on the surface, and mud particles were later compacted into the mould, after the organic remains had decayed away. The preservation of surface detail implies nothing at all about the mechanical strength of the original jellyfish, or about that of the Zittel wing's membrane. These pterosaur fossils were revealed when a slab was split from its counter-slab.

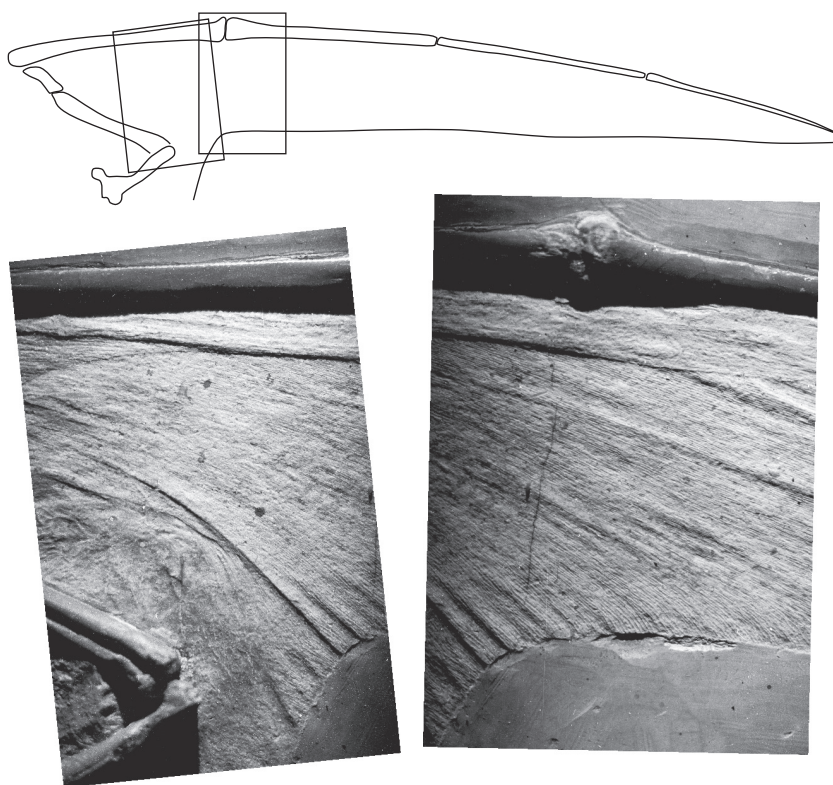


FIGURE 6.13 The Zittel wing from which the supposed “fibres” were first described. The sketch shows the contracted outline of the wing, with two rectangles corresponding to the photographs below. The ridges are even and regular in the right-hand photograph, but in the left-hand one they fold around the elbow joint. Additional ridges are interpolated as the wing widens towards the trailing edge. There is no separation or fraying of the ridges at the trailing edge, as might be expected if they were stiff fibres. Photos by C.J. Pennycuik.

Bones may be preserved in one slab or the other, but no internal structure is preserved in the wing membranes. They are strictly surface impressions, positive in one slab and negative in the other.

6.2.2 TENSIONING THE PTEROSAUR WING MEMBRANE

If we doubt the assumption that the surface ridges represent “fibres”, then we may ask whether anything that resembles them is known in living animals. There is actually a striking resemblance (albeit on a larger scale), with the throat pouches of rorqual whales, the group that includes Blue, Fin and Humpback whales, whose feeding methods have been described by Minasian et al. (1984). When relaxed, a rorqual’s throat

pouch has prominent, closely packed, parallel ridges, running in a fore-and-aft direction. Whale biologists refer to the pattern of ridges and grooves as “pleats”. Despite their robust appearance, the pleats do not contain longitudinal stiffening elements of any kind, and their function has nothing to do with resisting bending forces. They are a by-product of the internal structure of the wall of the pouch, which is highly elastic in the direction transverse to the pleats, but not in the longitudinal direction. The whale feeds by taking in a huge volume of water through its mouth, so expanding its throat pouch into an enormous balloon (Figure 6.14). The pouch then slowly contracts, expelling the water through the baleen plates along the sides of the mouth, while any fish, squid or krill that it contained go down the whale’s throat. The pleats flatten out as the pouch expands, and reappear as it contracts. If this was also the basis of the ridges on pterosaur wing membranes, then the implication is that the membrane (unlike a bat’s wing) was highly elastic, in a direction transverse to the ridges, and that the ridges (or pleats) appeared on the surface when the wing was relaxed, allowing the elastic membrane to contract. Of course, all the fossil wings are relaxed.

The outer part of the relaxed, dead wing of a pterodactyl fossil has much the same narrow, sharply pointed shape as the outer part of the wing of a dead bird, or of a living one in fast gliding flight, or during the upstroke of flapping flight. The corrugated surface and narrow planform shape of the relaxed (dead) membrane suggest that it contained much stronger elastic fibres than are present in a bat wing, and was expanded in flight by the outward pull of the wing finger, which was much thicker than the fingers of bats, and raises the possibility that this expansion and contraction might have taken place during each wingbeat cycle, as it does in birds (Figure 6.7). A bird can expand its wing to its full span and area without exerting any large forces, but a pterosaur, constructed as suggested, would have had to do work against the elastic fibres when expanding the wing at the beginning of the downstroke. However, this work would have been temporarily stored in the elastic fibres, and could in principle have been converted into aerodynamic work, when the wing was allowed to contract at the end of the downstroke. In that case, pterosaurs would have been able to vary their wing span and area in flapping flight in the same manner as birds, which is something that bats cannot do, or only to a small extent. If the implication of this kind of motion for long-distance migration, as suggested in Chapter 5 is correct, then it is possible that some pterosaurs could have been long-distance migrants, with all the adaptive opportunities that migration opens up for birds but not for bats (Chapter 8).

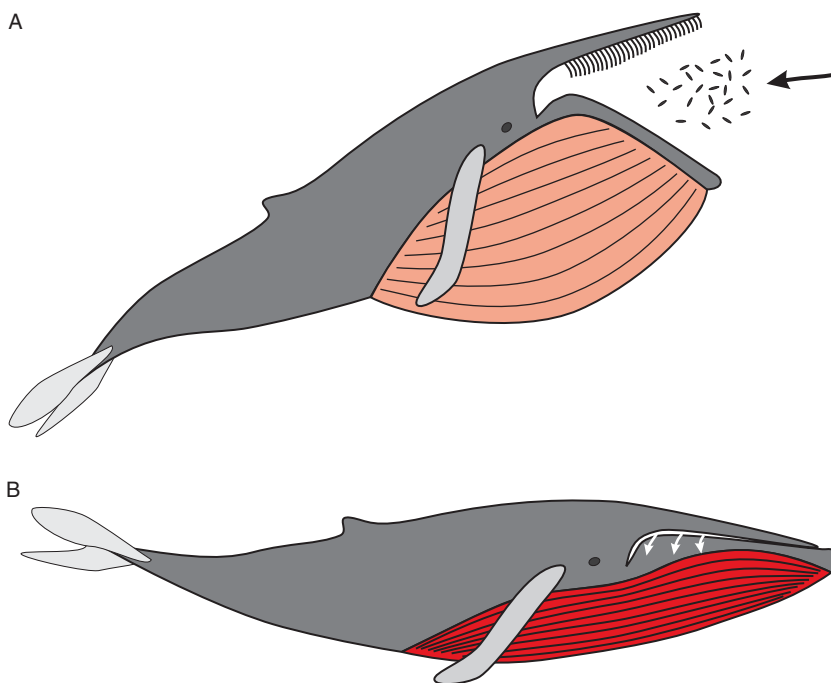


FIGURE 6.14 (A) Rorqual whales (*Balaenopteridae*) feed by engulfing prey in a highly distensible throat pouch, then closing the mouth and contracting the pouch, so that the water flows out through the array of baleen plates along the sides of the upper jaw. The name of the sub-order to which rorquals belong (*Mysticeti*) refers to the baleen plates (Greek *mystax*: moustache). (B) The contracted throat pouch fairs into the streamlined shape of the whale's body, and the contracted membrane surface then shows prominent longitudinal "pleats". It is argued here that these are directly analogous to the parallel "fibres" seen on the surface of the contracted (dead) wing membranes of some pterosaur fossils, implying that the membranes were stretched in flight to a much larger area than that seen in the fossils. See also Figures 6.10 and 6.13.

6.2.3 THE TRAILING-EDGE TENDON AND THE FIFTH TOE

The reconstruction shown in Figure 6.10, based on an elastic membrane, requires a tendon that runs from the foot to the tip of the wing finger, and pulls the trailing edge of the elastic patagium back when the wing finger is protracted. No such tendon is visible in any of the fossils, but that is not a compelling argument against its existence, as no other tendons are preserved in these fossils either. Pterosaur feet have an unusual feature, which at first sight appears to conflict with existence of a trailing-edge tendon. Digits 1–4 of the pterosaur foot are slender like the toes of bats, with hooked claws that look suitable for hanging up, but for little else, whereas Digit 5 is different, more robust than

the other toes, and with a bend at the joint between the first and second phalanges. This looks like the anchorage for the inner end of the trailing-edge tendon, but there is a difficulty. Because of the rotation of the thighs to make the knees project dorsally, as they do in bats, the fifth toe lies on the *inside* of the foot in flight, towards the centre-line. Some authors have argued that the fifth toe supported a “uropatagium” between the legs and the tail, but have not explained why such a sturdy support would be needed for this, even if a uropatagium existed. A more likely interpretation is that the tendon originated at an early stage of evolution, at a stage when the pterosaur ancestor’s fifth toe was still on the outside of the foot, as it is in flying squirrels. Subsequent rotation of the leg in the course of pterosaur evolution meant that the tendon crossed from the fifth toe above the other toes, so requiring the toe skeleton to be modified to control it.

6.2.4 MECHANICS OF THE WING FINGER

The pterosaur patagium was a single expanse of membrane, without any bony supports running through it, as Digits 4 and 5 do in a bat’s wing. These two digits are loaded in compression, and serve to turn the direction of the tension paths in the membrane (Figure 6.4). Most reconstructions of pterosaur skeletons show the wing finger sticking straight out from the body, but this overestimates the wing span, as the wing could not have been tensioned in this position. The tension paths in a pterosaur’s wing would have had to run directly from the inner edge of the membrane to the wing finger, without any corners, and this would mean that the wing finger had to bend back when the wing was fully extended. The wing finger was made up of four phalanges, each of which had oblique and slightly expanded end plates at both ends (except at the wing tip). The phalanges were connected by butt joints where the end plates met. If these joints were bound together by elastic ligaments, the finger as a whole would bend like a bow when tensioned, and this is shown in the greater curvature of the wing finger in Figure 6.10B than in C.

6.2.5 LARGE AND GIANT PTEROSAURS

Wellnhofer (1991) gives wing span estimates for a number of pterosaur species throughout the history of the group, and these include large pterodactyls with estimated spans between 5 and 6.2 m, throughout the Cretaceous. These estimates are based on the assumption that the wing finger ran straight out to the wing tip. The span would be less if the wing finger were bowed as in Figure 6.10A, but even so it seems

that the largest Cretaceous pterodactyls had functional wing spans which were greater than those of living vultures and albatrosses, both of which reach about 3 m in the largest species. Some tertiary fossil birds such as *Teratornis* and *Argentavis* may have had larger wing spans but this depends on extrapolating from the skeleton. This is unreliable in birds, because much of the span is made up by primary feathers, which have not been preserved in these fossils.

At the extreme end of the Cretaceous, something seems to have changed with the brief appearance of the giant pterodactyl *Quetzalcoatlus northropi*. The enormous size of this animal may be judged by comparing its humerus (Figure 6.15) with that of the little rhamphorhynch in Figure 6.10. Both humeri have the same distinctive, hammer-headed shape, but the one in Figure 6.10 is only about 4 cm long, a convenient size to handle with tweezers. The *Quetzalcoatlus* remains are fragmentary, but Chatterjee and Templin (2004) estimate from the size of the known bones that the mass of *Q. northropi* was 70 kg, its wing span

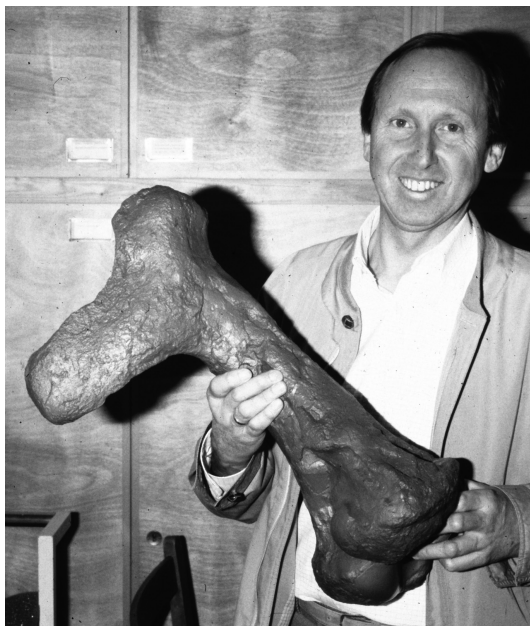


FIGURE 6.15 Prof. Peter Wellnhofer, Director of the Bavarian Museum of Palaeontology, where many of the most famous pterosaur specimens from Solnhofen are kept, holding a cast of a humerus of the giant end-Cretaceous pterodactyl *Quetzalcoatlus northropi*. The hammer-head shape of the humerus is similar to that of the little *Rhamphorhynchus* illustrated in Figure 6.10, but that humerus is about 4 cm long, and if it were free from the matrix, it could be conveniently handled with tweezers. Photo by C.J. Pennycuik.

was 10.4 m, and its aspect ratio 11.3, i.e. around twice the linear size of the “standard” large Cretaceous pterodactyls.

If Chatterjee and Templin’s numbers are input to *Flight*’s power curve calculation, together with a flight muscle fraction of 0.15 and today’s sea-level air density and gravity, its maximum rate of climb would be negative, meaning that it would not be able to maintain height when flying at its minimum power speed and exerting full power. This is a mechanical argument, not a physiological one. It makes no assumptions about the availability of oxygen, but assumes that the sea-level *density* of the air was much the same as in modern times. However, it seems likely that the atmosphere was denser throughout Mesozoic times than it is now (Budyko et al., 1985; Dudley, 1998), and there may also have been an episode of extremely high air density right at the end of the Cretaceous, when *Quetzalcoatlus* lived, caused by outgassing associated with the prolonged and massive volcanic eruptions that created the Deccan Traps (Officer and Drake, 1985). Increasing the air density reduces the minimum power speed, and also the power needed to fly at that speed, in inverse proportion to the square root of the air density, whereas the power available from the flight muscles is proportional to the wingbeat frequency, which varies in inverse proportion to the 3/8 power of the air density. These two graphs are shown in Figure 6.16B, representing nine power-curve runs, in which the air density was increased in steps of 0.5 kg m^{-3} from 1 to 5 kg m^{-3} , while everything else was held constant. The maximum rate of climb (Figure 6.16A) is initially about -0.1 m s^{-1} , but increases through zero when the air density is just below 4 kg m^{-3} . This is 3.25 times the sea-level air density in the International Standard Atmosphere, and would correspond to an altitude of 14,000 m *below* sea level today. It is not inconceivable that Earth could retain such a dense atmosphere, considering that Venus currently retains an atmosphere whose surface density is more than 90 times ours, even though its gravity is weaker, and its surface temperature is much higher. So long as sufficient oxygen is still present to support the reduced level of metabolic activity needed to fly, any gas that is not actually toxic or corrosive will serve to increase the air density (see also Chapter 2, Box 2.4).

6.2.6 WATER PTEROSAURS?

It is a common idea that many of the larger pterosaurs were fish-eaters, although no known pterosaur shows a body form like that of wing-swimming birds such as auks. If any pterosaur could swim with its bat-like legs, then one would expect some bats to be able to swim too, but they do not. Pterosaurs did, however, fly with toes 1–4 of each

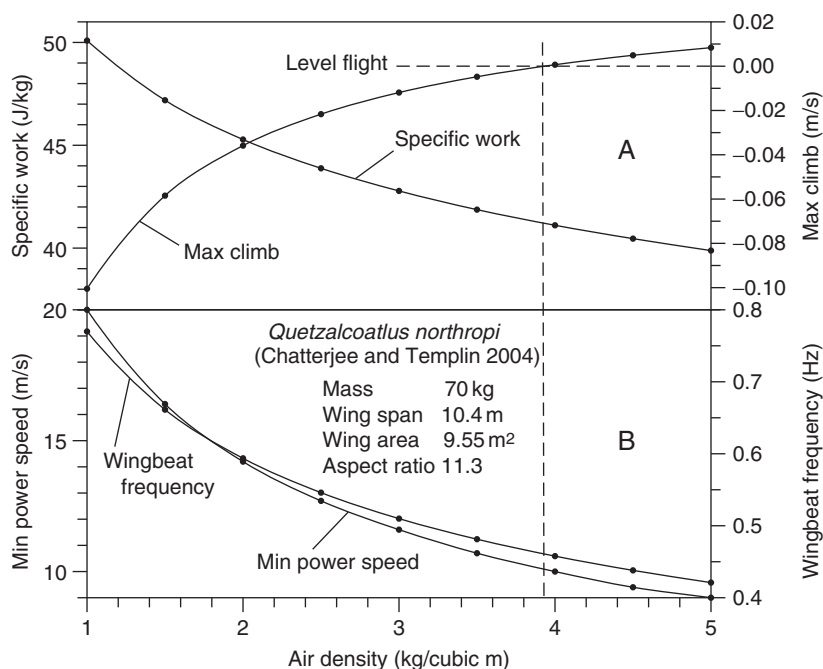


FIGURE 6.16 Output from nine runs of *Flight*'s power curve calculation for *Quetzalcoatlus northropi*, using estimated mass and wing measurements from Chatterjee and Templin (2004), with the flight muscle fraction set to 0.15, gravity to 9.81 m s^{-2} , and all other input variables set to default values, including the isometric stress for the myofibrils at 560 kN m^{-2} (Chapter 7). (A) Rate of climb according to the calculation of Chapter 7, Box 7.5 rises above zero when the air density is just below 4 kg m^{-3} . As the air density increases from 1 to 4 kg m^{-3} , the specific work decreases from around 50 J kg^{-1} (too high), to about 42 J kg^{-1} , which is only a little over the value for delivering maximum power (Chapter 7). (B) The minimum power speed (and with it the power required to fly) drops by a factor of 2.2 when the air density increases from 1 to 4 kg m^{-3} , whereas the wingbeat frequency, which determines the power available, drops by a factor of only 1.7. This is the reason for the increasing power margin, which permits the maximum rate of climb to increase.

foot curled downwards, which raises the possibility that they could have caught fish that were swimming just below the surface, by trailing their claws in the water like the fishing bat *Noctilio leporinus* (Novick and Leen, 1969). Some raptors such as ospreys and fish eagles, which snatch fish in their talons without actually entering the water, are fish-eaters without being true water birds, and the same may have been true of some pterosaurs. Such a lifestyle would be sufficient to explain the occurrence of fish remains, apparently in the body cavities of pterosaur fossils, without necessarily implying that any pterosaur could actually swim.