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flight held up the front end of the animal by holding the humerus constantly close to horizontal. That would use a fraction of the muscular work produced by the pectoralis during powered flight. Most of the fore-and-aft arm rotation occurred at the shoulder joint using the same wing-pitch-altering muscles used during flight to rotate the humerus along its long axis. The large, downward-projecting pectoral crest of the humerus was used as a back-and-forth muscle lever near the shoulder. Swinging the elbow end of the humerus a little back and forth could have added a corresponding amount to the length and power of the propulsive stroke. Adjusting the horizontal angle of the humerus would have placed the elbow at the changing heights needed as the lower arm and inner hand swung from forward at the beginning of the propulsive stroke, to vertical at the middle, and backward at the end. At the end of the propulsive stroke the downward motion of the humerus would have added to the power of the final push-off. It is possible that the wrist helped compensate for the elbow height changes that occurred during the propulsive limb swing by flexing in the middle of the stroke. On the other hand, in tetrapods the wrist is typically held straight during the propulsive stroke and is flexed only to help keep the hand clear of the ground during the recovery swing. The latter would also be facilitated by lifting the elbow higher during recovery than during the propulsive stroke.

The shoulder joints of most pterosaurs were more open at the back than are those of birds. This is a major reason that some argue that pterosaurs had an erect arm posture, but it may instead reflect other differences between the two groups. Being quadrupedal, pterosaurs could probably take off with a push from their arms (Habib 2008; Witton 2013), which probably required the humerus to swing farther back than the humerus of bipedal birds, which never push off the ground with their wings. Also, when folding their wings, birds have to point the stiff inner wing feathers downward rather than inward to keep them from being compressed against the body wall. In order to do that, a very unusual and complicated system evolved in which, as the arm folds against the body, the humerus rotates along its long axis so its back edge and the feathers anchored on it are directed downward. What is the lower side of the humerus when the wing is held out for flight now faces to the side, and the radius and ulna fold up alongside that. During this operation, the long-axis rotation of the humerus allows its head to remain in articulation with the sideways-facing shoulder joint. Because the pterosaur inner wing membrane was highly flexible, there was no need for the humerus to rotate along its length, so the wing folding was much more straightforward, consisting of just the arm being folded, with the lower surface of the humerus continuing to point in that direction. That required the pterosaur shoulder socket orientation to include a strong backward component.

As far as the prints left by pterosaur hindlegs, the variation in the lateral gauge of the foot trackways is not as extreme as that of the hands. That is because there is no example of extreme leg sprawling. The foot gauge width was usually moderate in rhamphorhynchoids and pterodactyloids alike, the feet being laterally separated by five to eight foot widths even when the hands were splayed much wider. Exceptions were the giant azhdarchid prints, as well as the even larger Early Cretaceous pterodactyloids in Asia, with wingspans of up to perhaps 10 m (30+ ft) (Kim et al. 2012), whose feet were separated by one-half to two foot widths, a fairly narrow gauge similar to that of the hands in the case of the quadrupedal azhdarchid tracks. In some other cases, the hands and feet also follow much the same gauge, albeit broader, while in others the handprints are well outside those of the feet.

The typical pterosaur combination of semierect femora with a vertical shank posture kept the feet from sprawling far out to the sides, but the result was the considerable distance between the left and right feet preserved in most pterodactyloid trackways. In azhdarchids, if not in the azhdarchoids they were within, the more erect leg posture allowed by their more downward-oriented hip socket is in line with the narrow gauge of their trackways.

Pterosaur hindprints show a very long heel pad pressed into the ground behind the toes, key evidence that their feet were plantigrade rather than digitigrade, as were the feet of their avian archosaurian relations, which also have a simple hingejoint ankle. This is somewhat perplexing because, aside from how carrying the ankle high off the ground would reduce the common disparity between the length of the arms and legs, pterosaurs lacked the backward-projecting Achilles heel that provides leverage for the flat feet of bats, humans, bears, and crocodilians, but flat-footed lizards also lack such a heel lever. The trackways also affirm that the foot was directed predominantly forward, often with a sideways splay to varying degrees, a normal tetrapod orientation quite unlike that of bats, whose feet are oddly directed straight to the side like their hands.

Being front heavy, the hindlegs bore less of a pterosaur's weight when walking than did the more robustly boned and powerfully muscled arms. That was most true in the often bigheaded, sometimes long-necked, and always short-tailed pterodactyloids. Because pterosaurs were not bipedal the way birds are, pterosaur leg muscles were correspondingly probably not as bulging and powerful as those of avepods and were more like those of humans. With the rather short pelvis, the thigh was fairly narrow, although the platelike ischium below and behind the hip socket supported strong leg-pulling muscles. Pterosaurs lacked the very prominent forward projection of the tibia at the knee found in avepods, including birds, so the shank muscles did not form as prominent a drumstick shape. The feet were operated largely by tendons coming down from the shank.

Trackways and anatomy reveal that pterosaurs were not outright fore-and-aft sprawlers like lizards, nor were the tracks generally as broad gauged as those of the bats best adapted for getting around on the ground, the vampires. Neither were most pterosaurs as erect legged and narrow gauged as dinosaurs, including birds, that sport very narrow-gauge trackways—this being true even of waddling ducks, geese, and pigeons—or many mammals, humans among them. Any who disagree need to produce detailed restorations of undistorted pterosaur limbs with fully articulated joints that actually fit into the trackways. Most pterosaurs were somewhat like crocodilians, which often use a semierect high walk that produces a trackway of similarly moderate breadth. The pterosaurs most like erect-gaited quadrupedal dinosaurs and mammals were the exceptionally terrestrial azhdarchids, although even they do not appear to have had tightly tucked-in elbows and knees. Note that differing limb postures and designs-sprawling versus erect, flexed versus straight jointed, short versus long limbed, heavy versus light footed, bipedal versus quadrupedalhave remarkably little effect on the energy cost of moving a given distance for any given body mass (Paul 2002, 2012). So pterosaurs were likely to have been typical in this regard. Nor does walking or running a given distance make much difference as far as energy loss. The cost is similar regardless of speed, although the effort per unit time rises with speed. What does make a difference is moving on land versus in air-the former is rather costly on a distance basis, burning about three times as much energy as does power flying the same distance.

In pterodactyloid trackways, the hindprint is set a little ahead of the foreprint, while for dinosaur trackways, the opposite is true. This is probably because pterodactyloid limbs were so long relative to their short bodies that as the hand lifted off the ground just before the forward-swinging hindfoot on the same side was set down—the normal footfall pattern of walking animals—the hindfoot overstepped where the hand had just been. The footfall pattern of rhamphorhynchoids was less consistent, and sometimes the foreprint was placed ahead of the hindprint. That may have been because the short-limbed long-tails had fewer problems with leg interference.

The length of the stride compared to the height of the hips two to four times the length of the foot in pterosaurs—can be used to approximate the speed at which the track maker was moving via a formula that indicates that the known pterosaur fossil trackways were laid down at speeds of 4–14 km/h (2.5–9 mph).

That pterosaurs were at least strongly quadrupedal makes sense because, as in bats, their arms were more powerfully muscled and stronger boned than their legs and usually bore hands, which exclusively bipedal birds lack. There is no known pterosaur that could not go on all fours. But with a long tail to better balance a usually smaller head, an always short neck, and the body, it is possible that rhamphorhynchoids were more prone to progressing bipedally, including when running without the intention of taking off. It is possible that the more frontheavy pterodactyloids were able to go on two legs by standing erect, as well as or better than apes and bears. The extremely marine nyctosaurs, lacking even the free fingers found in all other pterosaurs—though these were very small in their fellow oceanic ornithocheiroids—are particularly likely to have gone about on their hindlegs alone. They may have spent at least a



Quadrupedal and bipedal pterosaurs

portion of the limited time they moved on the ground during breeding season walking on the big knuckle of their wing fingers, rather like the knuckle walking of big apes. Potential direct evidence for bipedal pterosaurs comes from the hindprint-only trackways—that the hindfeet stepped on the foreprints cannot be ruled out, but no handprints are known in any of the sets of tracks of the giant Asian pterodactyloids (Kim et al. 2012).

Most land animals can run, as can many birds on their hindlegs, including many fliers from strong to weak, but a few such as tortoises can only walk. The ground agility of bats that are specialized for hanging under branches and rocks varies from often minimal to well developed in the prey-stalking vampires, which can even achieve a bounding run to flee discontented victims. Lacking terrestrial speed specialization, pterosaurs could not match fast-running birds, but some should have been able to achieve a fairly good clip. The pterodactyloid trackway with the sprawling arms has the longest recorded stride length, so the animal was either walking fast or barely running on all fours and was doing so by striding rather than bounding, although it is possible that faster-running pterosaurs bounded. The wide gauge of the arms may have been a means to prevent the unsplayed legs from getting tangled up with the folded wings, which is the practice of running bats. High-speed trackways are always scarce because animals make the intense effort needed to run usually only when necessary.

Pterosaur ground locomotion abilities varied widely. The scarcity of rhamphorhynchoid foot traces leaves open the possibility that they spent very little time on the ground, which is perplexing because many of them look as though they should have been competent on terra firma. Certainly they were not out there feeding on the sand and mud flats that most readily preserve prints, as were the later pterodactyloids and especially shorebirds. It is notable that the earliest pterosaurs, the preondactylans, had long legs that suggest good terrestrial abilities (Witton 2013). Conversely, the classic rhamphorhynchoid Rhamphorhynchus had exceptionally short legs compared to its relatives, indicating notably limited ground performance. Also interesting is that the most aerially adapted continental pterosaurs, the anurognathids, look more terrestrially capable than swifts, nighthawks, and the like, which either avoid ground contact altogether or do not walk about.

As for the pterodactyloids, it makes sense that the gigantic oceanic ornithocheiroids had limited ground locomotion abilities because they spent their time either soaring over the waves or breeding on isolated islands, neither of which required exceptional ground performance. The ornithocheirids and pteranodonts were not awkward on the ground as much because their legs were exceptionally short relative to the body as because the legs were so much shorter relative to the arms that even with the humerus held horizontal, the body would have been pitched very strongly upward with the outer arms and inner hand directed downward. The difference could have been reduced, however, by holding the elbow a little above the level of the shoulder. The fore-aft disparity was taken to an extreme in the nyctosaurs, which also lacked free fingers. Perhaps the sheer awkwardness of being all on fours caused the long-armed ornithocheiroids to sometimes walk on two legs, although this too would have been rather awkward, as seen in rearing bears or apes. Alternatively, they may have splayed their arms well out to the sides with the hands following a wide gauge, as the trackway of a running pterosaur shows it did.

Most pterodactyloids had less disparate fore-aft limb ratios and should have been able to progress readily across the ground, in some cases across wet flats in search of prey items, in other cases across dry land in search of food items, as in the assorted azhdarchoids up to the biggest giants. Perhaps the pterosaurs best adapted for walking about were the dsungaripterids. Their legs were not only the longest relative to their bodies among the great group but were also as long as the inner wings, eliminating any awkward slope of the trunk when the humerus was held horizontal. That makes biosense since dsungaripterids appear to have been dashing about on shoreline flats and streambeds as they searched for mud- and sand-boring invertebrates to dig up with their heavy spiked beaks.

Because many pterosaurs were small and lightly built and had grasping, claw-tipped fingers and toes, they had the potential to be arboreal to some degree. The long limbs, webbed feet, and rather short toes typical of pterodactyloids indicate they were not spending much time scrambling about within bushes and trees. The combination of shorter upper arms and inner hands, as well as legs with fairly long fingers and toes bearing large hooked claws, suggests that at least some of the lowslung rhamphorhynchoids with squirrel-like proportions were adept climbers-which might help explain why they did not leave lots of footprints on flat ground. If, as is uncertain, some wukongopterids had the opposable thumb ascribed to them (Zhou et al. 2021), then that is evidence for arboreality in a few derived rhamphorhynchoids. The anurognathids are particularly interesting because the tucked-up posture in which some specimens have been found suggests that they lay flattened out along the tops of broad branches, or on the ground like some nightjars, to remain inconspicuous when resting (Witton 2013). If some anurognathids had a reversed inner toe similar to those of birds, they could have used the digit to help grasp branches when climbing (Lü et al. 2017). The toes of a hanging bat all share the same subequal proportions, allowing them to readily wrap around a perch, but the toes of pterosaurs were too asymmetrical to do that (Witton 2013). There is currently no evidence that any pterosaurs lived or nested in burrows or caves like some dinosaurs, including a number of birds, and many bats. This may not have been feasible because of their gangly folded wings, but the possibility cannot be ruled out.

Many pterosaur hindprints are webbed, which is in line with the soft tissue webbing preserved in some fossils. This may have been true of all pterosaurs or at least all pterodactyloids, but it is possible that some pterodactyloids and/or rhamphorhynchoids were not web footed: the few known rhamphorhynchoid footprints seem to lack webbing (Mazin and Pouech 2020). The highly terrestrial anurognathids were apparently web toed. The webbing of the hindfeet helps explain why some pterosaur trackways show only handprints. Because the fingers were short and webless, they bore more weight than the much biggersurfaced webbed feet, which therefore enjoyed a much higher surface-area-to-weight load. As a result, the hand fingers tended to sink deeper into soft sediments than the flat feet, and the arms bearing more weight than the legs enhanced this effect. If the sediments were barely soft enough yet sufficiently firm, then only the fingers would leave an impression. Or it is possible that the trackways that have been found are an underimpression rather than a surface impression, and only the fingers sank far enough to disturb the muds or sands a short distance under the surface. Another possibility is that the pterosaur was floating in water to at least some degree and poling along the bottom with its inner arms, which were longer than the legs and so could reach the bottom while the hindfeet could not. A few trackways appear to record floating pterosaurs scraping with feet and/or hands along the shallow bottom (Lockley and Wright 2003).

Whether pterosaurs, especially the giants, could readily dive and swim underwater is problematic. Partly because they lacked a dense, smooth covering of feathers, their heads, necks, and bodies were not streamlined in a hydrodynamic manner. Nor do the gangly wings appear suitable for underwater propulsion any more than those of bats, which never dive, or for being smoothly tucked out of the way. Water is nearly 800 times denser than air, and big, flat beaks and especially head crests would have caused steering issues. The slightest deviation from the intended course would have resulted in a strong hydrodynamic deflection off course. And while the modestly muscled legs and webbed feet were sufficient for surface paddling, they lacked the power and other specializations seen in birds that swim mainly or entirely with their hindlimbs.

## **Pterosaur Pneumatics**

Further contradicting deep-swimming pterosaurs, among the pterodactyloids especially, is their light, airy, and correspondingly buoyant construction, including sometimes very thin-walled pneumatic bones and air sacs. These should have especially precluded the high-velocity splash diving performed by some birds such as gannets and boobies, but some small pterosaurs might have been divers like the big-headed kingfishers. Having descended from nonpneumatic mammals, bats show that internal air spaces other than lungs are not necessary for high-performance flight. Birds, having descended from already pneumatic avepod dinosaurs, integrated internal air voids into their flight systems. Deep-diving birds are notably less pneumatic than the avian norm. Because the preflight ancestors of pterosaurs are poorly known, it is not certain how much of their pneumaticity they inherited—it may have been none, little, or substantial—versus how much evolved in the group independently. In basal rhamphorhynchoids, the pneumatic structures were limited to the skull and vertebrae. These expanded somewhat to the shoulder girdle and inner wing in more derived rhamphorhynchoids, tended to be further expanded in pterodactyloids, albeit with a few exceptions, and were taken to an extreme in some pterodactyloids such as azhdarchids, and especially pteranodonts and nyctosaurs, in which most of the arms and the upper hindlimbs were air filled (Witton 2013; Larramendi et al. 2021). That marine soarers are so exceptionally buoyant is specific and good evidence that pterosaurs were not underwater swimmers as opposed to floaters.

The pneumatic bones of pterodactyloids could be amazingly thin walled, just a few millimeters even in the gigantic forms. Strength was maintained in part by internal struts in an evolutionarily selective parallel to stress analysis, in which a supporting structure is placed only where stress loads required its presence. Some birds have the same. But whether pterosaur skeletons were exceptionally lightweight in order to reduce overall mass is open to question. The pneumatic skeletons of birds are not lighter than those of other tetrapods relative to overall heft, according to some accounts (as noted by Witton 2013), and the quality of the data used in those studies is questionable (Larramendi et al. 2021), so whether simple weight reduction is or is not a primary selective factor behind the evolution of nontrachea/lung internal air spaces is not certain; respiratory functions may have been the driving evolutionary factor. Filling bones with air does balloon the surface area available for adding muscles without adding weight, so that may be a selective factor. And filling big beaks with air allows them to be very large without making the animal front heavy.

In addition to bones filled with air, pterosaurs probably had air sacs filling parts of the head, neck, and trunk similar to those present in avepod dinosaurs, as well as the highly pneumatic sauropod dinosaurs, and those in the main body could have been particularly large. Most land animals float, albeit barely enough to allow them to swim. Their density, or specific gravity (SG), is just a little less than that of water because the air inside the lungs counters the density of their soft tissues and bones,



Longitudinal section of large pterodactyloid humerus

which are denser than water. Bats have SGs barely below 1.0. In birds, all the combined air spaces can make up to around a third of internal body volume when at maximal expansion during the peak of inhalation, but this can be misleading because the respiratory tract is only half-filled with air on average during the inhalation-exhalation cycle. In many flying birds normal SG is around 0.9, ranging from about 0.85 to over 0.95, higher than has usually been thought. Large-beaked birds such as toucans, sporting big bills with SGs of around 0.1, have overall densities of around 0.75. This is not as surprising as it might seemmammalian fliers do not have reduced density, and fliers can actually degrade flight by being overfilled with air because the resulting ballooning of the body threatens to unduly increase frontal area, which increases drag. Back in the last century when it was assumed that pterosaurs had to have been soaring ultralight air beings, SGs were estimated to have been absurdly low, 0.2 to 0.5. This is abjectly impossible because it is not biologically practical for animals to consist largely of air-like inflated balloons, nor is it aerodynamically efficacious. Current restorations of pterosaur SGs indicate they were even denser than has recently been thought, ranging from about 0.95 in rhamphorhynchoids, to 0.9 in the more pneumatic small pterodactyloids, down to 0.75-0.85 in giant pterodactyloids that sported the most pneumatic and biggest heads and arms (Larramendi et al. 2021).

## Skin, Feathers, and Color

So far, the only scales on pterosaurs have been found on the underside of the hindfeet, where they formed a pavement of small, polygonal scales (Witton 2013). It is possible but not certain that the tops of the feet also bore scales. Where other bare skin is preserved, it is fairly smooth.

A modest number of pterosaur specimens record the presence of filamentary body coverings (Witton 2013; Yang et al. 2020). These are not fur, the fibers not being the same as the hair that adorns the unrelated mammals. What they appear to be are feathers. The filament shafts are hollow, which is true of feathers but not of normally solid-shafted mammalian fur. And pterosaur filaments are in at least some cases branched (Yang et al. 2018, 2020), a characteristic of feathers but not fur. The branching is fairly simple, like the feathers adorning some nonavian dinosaurs as well as birds, although the ultrasophisticated contour feathers common to many birds are not seen in pterosaurs. These pterosaurian pycnofibers, or pycnofeathers, were usually short, at 5–10 mm, but were sometimes longer atop the necks of some pterosaurs. Aside from bare horny beaks, the fibers covered much or all of the head-except in the beakless anurognathids, which were pycnofibered from the tip of the snout to the neck, body, wings, and hindlegs down to the ankles. So far, no example of pycnofeathers forming display structures such as cranial crests or anything elsewhere on the body has been discovered.



Examples of pterosaur fibers

The body coverings of flying birds are almost always smoothly streamlined to minimize drag, but in slow-flying bats the body fur is sometimes more erect and fluffy, and that may have been true of some of the aerially less capable pterosaurs such as Pterodaustro. Drag minimization is always critical for soarers to maximize their glide ratios, so all soaring pterosaurs should have had smooth pycnofiber coverings. Being as aerodynamically sleek as possible is also important for any aerial giant whose ability to get its massive body into the air might be marginal, as in the azhdarchids. Flying birds with short necks can pull the highly flexible neck back into a strong U curve that brings the head close to the body. The broad contour feathers emerging from the back of the head and neck then form a smooth aeroshell that blends the head into the body. Pterosaur necks were not flexible enough to do that, nor could the short, simple pycnofibers form a continuous aeroshell. So pterosaurs were more comparable to long-necked birds, in which the slender form of the neck remains obvious during flight.

Because hollow, branching fibers also covered a variety of dinosaurs, it is a reasonable scientific bet that ornithodiran fibers evolved once (Paul 2002, 2012, 2017a, Yang et al. 2018, 2020). If so, then pterosaurian pycnofibers and dinoavian feathers are truly the same thing. The absence to date of fibers from Triassic and Early Jurassic protodinosaurs and dinosaurs is the kind of negative evidence that is no more meaningful than the lack of fossil scales, and it is likely to be corrected by the eventual discovery of fibers in basal examples if sufficient fine-grained sediments that could preserve them are found. However, it cannot be ruled out that fuzzy body coverings evolved more than once in ornithodirans.

One question is why pterofeathers, and for that matter any external insulating fibrous body covering, appeared in the first

place. The first few bristles must have been too sparse to provide insulation, so their initial appearance should have been for nonthermoregulatory reasons. One highly plausible selective factor is display purposes. As the pycnofibers increased in number and density to improve their exposition effect, they became thick enough to also help retain the heat generated by the increasingly energetic archosaurs. Also plausible is an initial sensory function, as in the whiskers of mammals. Pycnobristles adorning the jaws of anurognathids may have been for tactile purposes. As insulation became the primary function of pterofuzz-because hollow-feathered pycnofibers enjoyed a significant heat retention advantage over solidfibered fur-the air contained within the feathers made them as much as twice as efficient as fur at trapping warmth for a given mass of insulation. And insulation can work in both directions: under certain conditions feathers and fur can help keep an animal cooler than it would otherwise be in a very hot place. The thick pycnofeather coats that have been preserved adorning the bodies of some specimens are fully characteristic of thermal insulation.

Apparently because pterosaurs had bat-like main wing membranes, it became an arbitrary convention for paleoartists to color them rather like bats, largely in drab, fairly solid blacks, dark grays, browns, or gray browns. There was never a good reason to do so in such a near-universal manner, because the largely daylight-flying archosaurian pterosaurs were not close lifestyle analogues to or phylogenetic relatives of the more nocturnal, mammalian bats. Being more closely related to their fellow ornithodiran birds, and largely sharing daytime skies with them, pterosaurs more likely were often or always colored more like birds. Because bird eyes can see ultraviolet light, their color patterns include ultraviolet patterns that humans cannot perceive, and presumably the same was true of pterosaurs. As for what we can see of avian coloration, it is highly variable, ranging from drab to brilliantly colorful—sometimes this extreme occurs within a species, the female being the former and the male the latter. That may have occurred among some pterosaurs if the males needed to stand out for reproductive competition, and the females needed to be able to hide as well as possible.

If the anurognathids were cryptic branch and ground huggers like nightjars, they may have been similarly camouflaged. This appears to be supported by the brownish coloration with a red component indicated by melanosome capsules within pycnofeather specimens that can be assigned to *Dendrorhynchoides*. Whether a speckled pattern was present is not apparent. One caveat is that some researchers question the ability to restore the colors of fossils via their pigment capsules.

Another example of preserved pterosaur color patterning records dramatic subvertical banding on the soft tissue head crest of the rhamphorhynchoid *Pterorhynchus* (Czerkas and Ji 2002). The observed banding records the pattern of the coloration, not specific colors. It is quite likely that such bold coloration was widespread among pterosaurs, especially in the crests, whose primary function was probably display. The deep snouts and big beaks of various pterosaurs also may have been bold patterned, as they sometimes are in birds, such as auks.



Aeroshell necks

It is very possible that shore and marine pterosaurs were colored like birds with similar habits, in attractive patterns of pleasing whites, grays, and browns. Topsides could have been darker to protect against chronic exposure to ultraviolet radiation, undersides lighter to decrease their visual profile when silhouetted against the bright sky. It has recently been suggested that dark wing tops also increase lift by heating the air flowing over the wings, decreasing its density and further reducing air pressure, which helps create more lift without drag (Rogalla et al. 2019). The effect is enhanced by a light-topped inner and dark-topped outer wing; the differential seems to enhance lateral airflow in a manner that improves lift efficiency. Or, the wing tops may have been light toned in order to minimize heat overload from the sun in the living membrane tissuesoverheating is not a problem for inert bird feathers. Other pterosaurs may have been a single solid color top and bottom, perhaps solid black in some examples, or solid white in others. It is common for the tips of bird wing feathers to be darker on the trailing edge than farther inward on the airfoil. This is at least in part because the dark pigment capsules that provide the color also serve to strengthen the feather ends against wear and abrasion. Whether the trailing edges of pterosaur membranes exhibited the same adaptation is not known. Because pterosaur eyes were like those of birds or reptiles, not mammals, they lacked white surrounding the iris. Pterosaur eyes may have been solid black or brightly colored, as in many reptiles and birds.

## Flight

As important as walking and the like was for pterosaurs, they were adapted above all else for progressing through thin air, which is why they all had large wings. In order to understand pterosaur flight, we must first address a basic question.

#### How Wings Really Work

The popular explanation for how wings work goes as follows. Wing tops are more curved than the bottoms. As a result, the air traveling over the top has to travel farther in order to meet up with the air moving along the flatter and therefore shorter underside. Because it has to travel farther, the topside air has to travel faster. The faster a fluid moves along a surface, the lower the pressure, which is called the Bernoulli effect. This is why, if two boats are moving close alongside one another, they are in danger of being sucked into one another and colliding; the water being squeezed between the vessels moves faster than the water on the outer sides of the hulls, so the water pressure is lower between them than on their outer hulls. The boats will therefore be pulled together and collide along their inner sides if the helmsmen are not careful; this is a problem when ships are engaged in refueling and supply operations. Because the pressure is higher on the bottom of the wing than on the top, lift is generated, and up it supposedly goes. Note that the same applies to horizontal helicopter rotors, which produce both lift and thrust, as well as vertical propeller blades, which produce forward thrust.

The above explanation cannot be and is not correct. At air shows when a plane flies upside down, it does not come crashing to earth. Nor do all wings have the standard shape. The stunt planes common at air shows have symmetrical wing cross sections that provide the same aerodynamics whether the plane is upright or rolled onto its back. The wings of some recent airliners, such as the gigantic Boeing 777 and the superjumbo Airbus A380, are actually flatter on the top than on the bottom because such supercritical wings reduce drag as they approach the speed of sound. Some wings—those of early flying machines, hang gliders, and many ultralights, bats, and pterosaurs—are arched sheets in which the bottom follows the same dorsally convex arc as the top. Paper airplanes tend to have flat wings, and it is easy to produce lift with a flat piece of cardboard.

In a standard wing, the extra distance the air needs to travel from the leading to the trailing edge on the curved top compared to the air flowing along the straighter bottom is just a small percentage more, not close to substantial enough to produce the dramatic speed differential needed to generate



the big pressure difference required to produce enough lift to allow flight. To produce lots of lift, the air going over the top has to move a whole lot faster than that going underneath the wing. Also, pressure differentials alone cannot produce lift. In the end, it all comes down to Newtonian physics. In accord with an action requiring an equal reaction, in order to sustain a body of mass denser than air in the air, enough air must be projected downward with enough velocity to equal the mass of the object. You can observe the latter effect by watching a bee or wasp flying just above grass or loose soil. In order to keep the insect off the ground, the buzzing wings must produce a notably strong downdraft that bends grass blades and scatters dirt and dust. Helicopters from small drones to large machines produce downdrafts that in the latter case can easily knock down a person. This happened to Julie Andrews near the beginning of The Sound of Music every time the camera-bearing helicopter roared directly over her head to shoot the alpine pasture scene.

A key requirement for a wing—including a chopper blade—to work is that it needs to have an angle of attack. If the aircraft, whether biological or artificial, is to maintain a constant altitude, the leading edge of the wing needs to be higher than the trailing edge. This helps produce the downward rush of air that keeps a B-52H or *Pteranodon longiceps* in the air, but it is much more complicated—and fascinating—than that.

As air is approached by the leading edge of a wing with the proper angle of attack, the air does not remain undisturbed until the wing's leading edge cuts into it, as one might expect. Instead, the air begins to lift upward when it is still about half a wing chord ahead of the leading edge. This happens because the bottom of the wing, which projects downward toward its trailing edge, acts like a bit of a dam, obstructing the airflow below the wing, slowing it down, and causing it to pile up in front of the leading edge. This also leaves a deficit of air behind the trailing edge of the wing. In order to compensate for the latter, the air flowing over the top of the wing has to speed up greatly, flowing along the wing's surface half again or more as fast as that along the bottom. The dramatic speed difference is most easily seen in online videos in which smoke streams showing the flow of air are pulsed to show how fast the two bodies of air are moving. Because the top air is moving so much faster than the underside air, the big speed differential produces the big pressure difference needed to deliver abundant lift via the Bernoulli effect. In addition, the topside air arrives at the trailing edge long before the bottom air. This creates a standing vortex above and behind the wing, rather like the standing wave downstream of a boulder in the rapids of a fast stream. Because the air at the trailing edge of the vortex is moving downward, and because the downward and backward bottom surface of the wing also pushes the air down, the resulting downwash of mass provides the Newtonian equal action and reaction that keeps the mass of the wing from dropping earthward.

This not-simple set of effects works regardless of the crosssectional profile of the wing as long as it is sufficiently shallow relative to its chord length. The reason the bottom of standard wings is less curved than the top is partly because this causes the leading edge to be close to symmetrical relative to the airflow, reducing drag, and because the differential curves do produce a minor extra Bernoulli effect that increases lift efficiency a little at very high speeds when the angle of attack is at its bare minimum. The standard wing profile is a good generalized shape that, with appropriate modifications for specific needs, works well in a variety of types of aircraft. But the standard profile runs into problems near the speed of sound. When a wing is moving just below that speed, the faster-streaming air flowing over the top is racing at or above the speed of sound. That is a negative result because the fast-flowing top air produces minor shock waves that create extra drag, as well as potentially interfering with the control surfaces. By having a flatter top, supercritical wings slow down the top air enough so that it does not move at the speed of sound, eliminating the shock waves.

Producing lift always produces drag-the wing or blade that generates lift is a drag even when it is the thin blade of a supersonic machine such as the razor-winged F-104 Starfighter. This is exasperated by the angle of attack, which prevents the wing from presenting its minimal frontal profile to the air. In general, producing more lift produces more drag. High-camber wings consisting of strongly arced thin sheets produce a large amount of lift because the strongly downward-deflected aft portion of the curve directs air strongly ventrally, but there is also a lot of air resistance because the bottom air has to first flow hard up into the concavity before it continues aft. Plus, their thinness means that sheet wings cannot be as strong as thicker wings. They are therefore most suitable for slow fliers, such as many early aircraft, hang gliders, and bats. Because bird wings are sort of a cross between standard and sheet wings-fairly thick, curve topped, and flat bottomed forward, with sheetlike feathered trailing edgesand because they have less camber, they are somewhat better suited for higher speeds than are those of bats. That is why no bat can match the highway-like cruising speed of pigeons, much less the speedway velocity of diving peregrine falcons.

As complicated as the above aerodynamics are, there is yet more complexity involved with wing aerodynamics. When wings are viewed from top or bottom, the air flows straight back from the leading to trailing edge only if the wing is held straight out rather than swept back or forward, and only if there are no wing tips-in other words, the wing goes on forever laterally. But all real wings come to an end. In that case, the higher pressure of the air on the underside of the wing causes it to slide outward to the side toward the wing tip, while the lower-pressure air on the top slides inward. As the bottom air slides out from under the wing tip and the top air shifts in the opposite direction, a whirling wing-tip vortex is generated. This produces a large amount of drag without any compensating extra lift. The effect can never be entirely eliminated and is worst if the wing tip is simply squared off. One way to reduce the problem is with the winglets that adorn the wing tips of many airplanes. Another

way, which is used by many birds, is to have wing tips consisting of multiple feather tiplets, as this helps break up the vortex to some extent. A third option is to have a sharp tip. Used in a number of airplanes, including the semielliptical-winged Supermarine Spitfire and the new Boeing 787 airliner, it is also found in some birds, the fastest-flying bats, and all pterosaurs. Having the top of the outer wing darker and correspondingly hotter from sunlight makes the air warmer and therefore less dense than it is over the lighter-colored inner wing. In flight, that causes the air to flow more laterally over the wing top than it otherwise would if the wing top was all the same tone. That in turn reduces the wing-tip vortex and the resulting drag, which may be a reason some birds are colored in that manner. A small pycnofiber tuft lining the trailing edge of the outermost portion of the wing membrane of at least some anurognathids probably helped suppress the wing-tip vortex.

As bad as they are, wing-tip vortices can be exploited by formations of fliers. This is done by flying in the classic V formation used by the likes of geese and pelicans, as well as military aircraft-experiments flying airliners this way are being conducted. In this arrangement, all but one of the fliers in the flock fly just behind one another, with one wing tip flapping in coordination with the flier ahead in order to keep the tip in the outer, upward-rotating portion of the vortex coming off the end of the wing of the bird just ahead. This gives the follower free lift and reduces the work it has to do to maintain speed and altitude. Direct measurements show energy savings of a substantial 10 to 15 percent. The flier in front does not experience any loss in performance from the freeloading trailing flier, but that individual is not getting anything out of the formation. So it tires more rapidly, and when it has had enough it drops back and begins to trail another flock member, as another in the group temporarily assumes the lead until it too tires. This is done only by fairly large birds that power fly substantial distances in flocks. If any of the larger pterosaurs regularly did the same, they may have adopted V formations. This would presumably exclude the big wave soarers such as pteranodonts because, like albatrosses, they did not constantly flap and probably never flew in flocks.

#### Pterosaur Wings

The configuration of the pterosaur wing was anatomically based on the posture of the arm bones that supported the airfoil membranes. Although the precise poses will never be known and presumably varied to some extent, the always short humerus of the inner arm should have been swept backward to some degree, with the elbow correspondingly flexed forward, and the long radius-ulna unit of the upper arm also swept forward. In front view, when the wing was held out horizontally in neutral flight posture, the humerus was probably tilted upward a little, with the outer arm a little less so, producing a slight dihedral, which is common in aircraft. All this is similar to bats and most birds, the partial exception being big birds in which the humerus is very elongated along with the rest of the wing, as in the superwinged pelagornithids and albatrosses. In those, the inner and outer arms are nearly straight, with only modest flexion at the elbow, and it is unlikely any pterosaur was like this.

In birds and bats, the wrist, which is always the key rotation point for wing folding when not flying, is always flexed fairly sharply so that the hand is straight or swept backward somewhat during flight relative to the outer arm. In front view, this is where the wing may slope outward and downward some, producing an anhedral, which is found in some aircraft. The bestdeveloped familiar avian example of an inner dihedral and outer anhedral is the gull wing. The situation with pterosaurs, whose flight wing configuration is not likely to be reliably preserved in the fossil record, and whose main wing folding occurred farther out at the finger base, is more ambiguous. It is possible that the wrist was flexed significantly backward and downward, causing the main wing flexion at this joint. The alternative is that the wrist was nearly straight, and, with the most flexible joint being the wing base, the main wing flexion was there, which seems more likely. The fossil big finger bones of at least some ornithocheirids appear to have been dorsoventrally curved to give the outer wing a shallow arch, and this may have been true of other pterosaurs. That any pterosaurs had a wing dihedral/anhedral is highly plausible but somewhat speculative. The rest of the wing finger followed the general direction of the innermost element in a gentle backward arc.

Operating the wing skeleton, held together with bone-to-bone ligaments and joint capsules, was a set of muscles, sometimes attaching to bones via tendons. Easily the biggest arm muscle was the pectoralis, which did more than any other to power flight, achieving that by doing the great majority of the work of the downstroke that produced most of the forward thrust. The pectoralis spread over and was anchored on the entire sternum, from the front vertical keel across the big chest plate. Its outer end inserted on the large pectoral crest of the humerus just lateral to the shoulder joint. By increasing the leverage of the pectoralis on the wing, the pectoral crest improved the muscle's ability to pull the arm down during the downstroke. It also improved the ability of the pectoralis and other, lesser muscles to adjust a given wing's angle of attack relative to the body. That system worked automatically when flapping. On the downstroke, because the crest was at the leading edge of the wing base, contracting the pectoralis rotated the leading edge downward and increased its pitch in addition to depressing the overall wing. On the upstroke, the crest being at the leading edge meant that contracting the wing elevators also pitched the leading edge of the wing up a little, resulting in the liftgenerating wing also becoming a variable-pitch thrust-producing propeller. Pterosaurs could also voluntarily use this system to adjust wing pitch, symmetrically on both sides or differentially for maneuvering, to control flight. Because the shoulder joint was the only arm joint that could rotate in pitch many degrees, the otherwise stiff-jointed pterosaur wing could rotate extensively along its long axis. This wing pitch control point was vital to aerial power and maneuvering, as it is in birds and to a lesser degree in the more flexible-winged bats.

In modern flying birds the sternum is even larger than that of pterosaurs, with a very deep bony keel, but this does not mean that the avian pectoralis is correspondingly dramatically larger than that of pterosaurs. For one thing, the often very large sternal keel of birds helps support the supracoracoideus, a large muscle that loops up and over the shoulder joint to help elevate the wing during the upstroke. Pterosaurs, like bats, entirely lacked this unusual complex; the supracoracoideus was merely a small muscle that helped pull the wing down. Also, in today's birds the pectoral crest of the humerus is modest in size, and the bulk of the pectoralis volume is supported by the big sternal plate. But in basal birds, the sternum and pectoral crest were more like those of pterosaurs, with the first being a flat plate and the latter a very large hatchet-shaped blade. In pterosaurs and early birds, more of the mass of the pectoralis was supported by the pectoral crest than it is in derived birds, rather than by the sternum. This meant that the pterosaur shoulder region was flattened out and somewhat broader from side to side than those of deeper-bodied birds, somewhat like late-generation fighter jets.

Opposing the pterosaurs' downward-flapping pectoralis was the upward-flapping latissimus dorsi. Anchored on top of the rib cage and the neural spines of the chest vertebrae, it inserted on top of the humerus. Because it took much less work to lift wings that already wanted to rise up under the combined upward push of wing lift and the mass of the body suspended between the wings, the latissimus dorsi was not nearly as large as the pectoralis, although it may have been the second most powerful wing muscle.

Aside from the big pectoralis and latissimus dorsi muscles, the rest of the important flight muscles were positioned largely either in front of or behind the wing bones. This had the advantage of keeping the frontal area of the arm minimal, reducing aerodynamic drag. This meant that, as in birds and bats, the top and bottom of the arm bones from the middle of the inner arm out were largely bare of muscles. On the inner arm the stout biceps did the most to flex the elbow downward, thereby making an important contribution to the total downstroke, and to also flexing the elbow forward. The longer but less powerful triceps, positioned behind the humerus and wrapped around the elbow, performed the opposite actions. Farther out, the upper arm and beyond were worked by a complex of long, slender muscles, anchored in part at the elbow end of the humerus, and also on the radius and ulna, which operated the wrist and the rest of the wing via tendons, often very long-beyond the wrist there may have been no muscles.

Although pterosaurs used their arms for nonaerial locomotion, the primary evolutionary purpose of the arm skeleton and musculature was to support and power the wings, the airfoils of which were formed by three membranes, two supported largely by the arms. One is also present in birds and bats, the propatagium, which spreads across the space between the shoulder and wrist, in front of the backward-flexed elbow. This leading-edge airfoil broadens the chord of the inner wing and helps streamline the inner and lower arms into the airfoil. In



Pterosaur chest and wing frontal profiles compared with birds

pterosaurs, the leading edge of the propatagium approaching the wrist was supported by the pteroid bone. This was an elongated inner carpal (Peters 2009); there is nothing similar in bird or bat propatagia. Perhaps the pteroid was used to modify the camber of the propatagium to alter the lift capacity versus streamlining the inner wing, especially in those pterosaurs in which the bone was long. But in a number of rhamphorhynchoids—including, interestingly enough, the agile anurognathids—the element appears too short to have strongly altered the leading-edge membrane. Another wrist element, the preaxial carpal, projected a little forward of the joint and may have supported the inner end of the shallow outer propatagium, which could have helped streamline the leading edge of the fairly thin inner metacarpal.

By far the largest wing surface of pterosaurs was the brachiopatagium, which made up three-quarters to nine-tenths of the total airfoil area. From the tip of the big finger, it ran along behind the arm to anchor on the body and apparently on the legs, in some if not most or all pterosaurs. In rhamphorhynchoids, the front edge of the outer membrane could be anchored in the shallow groove on the back of the wing finger, but this is not present in pterodactyloids. Probably because the bat outer brachiopatagium is supported by four splayed-out fingers, of which the leading-edge digit is not the longest, the membrane of the flying mammals is consistently made up of thin, supple, stretchable tissue similar to a latex sheet. Apparently, because it was not supported by a series of digits, most of the pterosaur brachiopatagium was a thicker, stiffer, multilayered structure (Witton 2013). The underside had a dense vascular network that supplied the tissues with blood. Next and in the center was a thin sheet of connective tissue and light muscle. This sandwich was topped by a continuous sheet pavement of slender actinofibers that were oriented directly backward behind the inner arms, rather like the shafts of inner wing bird feathers, and beyond the wrist they were directed increasingly outward, again like the feather shafts of bird primary feathers. In small pterosaurs the actinofibers were a fraction of a millimeter wide; how thick they were in the giants is not known. On the inner wing the fibers were rather short, apparently fairly flexible, and covered only the membrane immediately behind the arm, leaving the rest of the inner membrane consisting of highly stretchable tissue as in bat membranes. Outside the wrist the actinofibers were very long, sometimes 2,000 times longer than wide, running all the way to the trailing edge of the brachiopatagium, and were markedly stiffer. Sometimes the filaments split into two as they progressed to the trailing edge. The fibers did not make the outer membrane as permanently flat and fixed as a sheet of thick paper; the membrane could fold, but only in fanlike pleats paralleling the fibers.

Wing membranes add mass to animals that need minimal weight, so evolutionary selective pressure works to keep them as thin as possible. Bat membrane thickness ranges from just 0.02 to 0.15 mm (0.00075 to 0.01 in) from the smallest to the largest species, leaving even the thickest membranes translucent.

The thickness of bat membranes stretched between their fingers tends to be fairly uniform. Pterosaur membranes, not being supported by multiple fingers, having multiple layers, and stiffened by actinofibers, should have become progressively thinner aft of the supporting arm and finger, and should have been thicker on average at a given body mass than those of bats. But because wing membranes are so large, their mass as a percentage of the total adds up surprisingly fast, depending on their thickness and chord (Larramendi et al. 2021). If average (thicker at the front, thinner toward the trailing edge) brachiopatagium thickness ranged from approximately 0.2 mm (0.0075 in) in the smallest to 4 mm (0.15 in) in the most gigantic, then the membranes would have made up about a tenth of the total mass of pterosaurs. That is more than the wing feathers of birds, or the wing membranes of bats, which are half as heavy. On the other hand, the multiple wing fingers of bats weigh more than the one pneumatic pterosaur finger, so it balances out. And because the main pterosaur wing membrane was thicker than the thinner membranes of bats and was reinforced by the actinofibers, it should have been less vulnerable to being torn than those of bats. The main membranes of pterosaurs may have been translucent like those of bats, especially those of smaller examples, but dark pigmentation could have rendered them opaque.

Although very large portions of the brachiopatagium have been preserved in a few fossils of small pterosaurs, in no case is its exact profile known. That is because the postmortem events that happened to the deceased pterosaur's body and the fossilization process always prevented the wing from being stretched fully out as it would be in flight; all fossil membranes are folded to some extent. The preservation of membranes is often patchy and ambiguous, and it does not help that different researchers' interpretations of the extent of a given specimen's fossil wing tissues can consequently differ dramatically. It is possible to readily restore the wing profiles of a number of extinct birds because if enough of the wing feathers are preserved in place and complete, even if the wing is partly folded, the dimensions and profiles of the stiff feathers can be used to map the overall wing profile during normal flight. No giant pterosaur wing membrane has been found anywhere close to intact.

Among bats, the high stretchability of the thin membranes between the wing fingers means that the trailing edges form prominently concave, stretched-out curves between each fingertip, creating the classic bat wing profile frequently reproduced in often sinister logos. It has been fairly common for artists to portray pterosaurs with similarly concave trailing edges on their wings, starting at the wing tip, and some researchers contend this is correct because the trailing edge of the pterosaur membrane should also have been under elastic tension (Palmer and Dyke 2012; Hone et al. 2015). However, the un-bat-like stiffening of the pterosaur's outer membrane out to the edges by the actinofibers should have allowed the trailing edge of the outer membrane to assume a convex curve, as is present in their preserved membranes (Bennett 2000).



The forward curvature of the tips of the wing finger of some pterosaurs should also require that the trailing edge of the membrane be convex. Some researchers propose that pterosaur finger bones were so flexible that the forward-curved wing bone was bent back and straight by the pull of the stretched-out membrane when the wing was under tension in flight (Hone et al. 2015). Whether ossified bones would be as bendable as fishing rods is dubious-if they were, the wing finger would be too floppy to produce an effective airfoil; it would be subject to severe flutter in the airstream. Also working against this idea is that bending the slender fingertip backward and only backward would work only if the cross section of the bone were shaped to limit flexion to that direction-the forward-swept tips of recurved archery bows bend only backward when the string is drawn because the bow's broad limbs are strongly compressed fore and aft. The front-to-back flattening relative to limb breadth prevents the tips of the arms from flopping to one side or the other as the bow is drawn, as the round cross-sectioned tip of a forward-curved fishing rod would do. Pterosaur wing finger bones, instead of being strongly flattened fore and aft-which would not be aerodynamic-were streamlined and transversely flattened, meaning that they would be twisted out of the flat plane of the wing if the forward-swept tips were pulled under the extreme tension of the membrane that would be needed to straighten the bone. It is concluded that the wing finger was moderately flexible, that the actinofibers meant that the internally stiffened outer wing membrane did not need to be under high tension during flight, and that pterosaur wing tips were often and probably always convex on their trailing edge.

The biggest issue yet to be fully resolved is how the inner brachiopatagium was anchored. In all bats the membrane is connected all the way along the leading edge of the hindlegs down to at least the ankle, in a few cases even farther. The membrane appears to have been attached to the ankle in at least some rhamphorhynchoid specimens, and possibly in some pterodactyloids, but that evidence is more ambiguous. In a specimen of the pterodactyloid Pterodactylus, the attachment appears to be on the thighs on both sides, above the knees, but this has not been confirmed by other specimens. That the brachiopatagium anchored on the legs is in accord with the pterosaur's bat-like ability to splay out the hindlegs on the same plane as the airfoil, if that is correct. But the folding of the membrane, and the possibility of displacement during the process of decay and preservation, render the apparent connections problematic. Perhaps the membrane actually attached to the ankle in Pterodactylus, and the seeming connection above the knee is an illusion because of the folding of the membrane across the splayed-out legs. Or perhaps the seeming ankle attachments are the result of postmortem displacements. Also complicating the situation is the argument that the hip socket ligaments

#### BIOLOGY





Recurve bow limbs and pterosaur wing tips

incorrect Rhamphorhynchus wing-tip membrane

bow limb tip can be pulled nearly straight because of front-backed flattened limb cross-section probable convex convex Bellubrunnus Rhamphorhynchus wing-tip wing-tip membrane membrane as behind recurved preserved fingertip

> does the calcar spur in bats that have it. Because the fifth toe was the outer digit, and it was on the topside of the foot when the legs were spread to support membranes during flight, the two outer legs formed inverted, airflow-channeling walls below the level of the interleg membrane; in bats, the legs are simply lateral to the uropatagium. In *Sordes* the trailing edge of the inner portion of the uropatagium was a concave aft shallow V; this may have been true of some or all other rhamphorhynchoids. Lacking the splint-like fifth toe, the pterodactyloid uropatagium was less extensive; that of *Pterodactylus* was a subtriangular sheet on each leg running from behind the hip to the ankle. How true this was of other pterodactyloids is uncertain, as it is possible that the specialized pteranodontid tail was somehow involved in the interleg membrane.

> When rhamphorhynchoids stood on all fours, the membranes would have formed a sort of tentlike configuration, with the brachiopatagium making up the side walls much of the way to the ground, and the extensive uropatagium making up the back wall, while the front would be open. The much more limited and posteriorly open uropatagium of pterodactyloids should have produced a less pronounced tent effect.

> With the three flight membranes described, it is time to look at the overall wing and tail section profiles in plan view. Supported along much of their length by a series of long wing fingers, bat wings have a broad chord that tends to promote turning more than speed even among the narrowest-winged examples, the molossids. As a result, the trailing edge of the inner brachiopatagium usually runs in a fairly straight line or a gentle curve out from the ankle to the similarly broad outer wing. Exceptions are some fruit bats, which hold the hindlegs straight back during flight, and the inner brachiopatagium sweeps strongly back toward the ankle.

> More brachiopatagia are preserved for *Rhamphorhynchus* than for any other pterosaur, and some appear to be spread out close

prevented pterosaur legs from being sprawled out horizontally. It is quite possible that the exact nature of the leg attachment varied among pterosaurs, perhaps between rhamphorhynchoids and pterodactyloids, or within one or both groups.

Pteranodontid tails may be significant because they ended with elongated rods, which suggests that some form of airfoil was attached, perhaps the inner trailing edge of a brachiopatagium that did not attach to the legs. Of related interest are azhdarchids, because the significant possibility that they could not splay out their hindlegs sideways implies that their situation was markedly different from that of other pterosaurs. They may have had a distinctive leg posture during flight to hold the membrane, perhaps with the legs stretched straight back as in fruit bats. Possibly the brachiopatagium-leg connection was lost and the membrane was attached to the tail, as it may have been in pteranodontids. If the latter was true, then what was the leg pose during flight? Were the legs directed straight backward from the hips, or did they fold up fully or partially, as is common in flying birds?

Bats, but not birds, feature a third, rear-end uropatagium membrane. Anchored on the hindlegs, it has quite a variable configuration in bats, ranging from a very large, broad sheet if the legs are held widely splayed out and the twin membranes run along the entirety of a fairly long tail; to narrow, subtriangular bands behind the legs if the tail is very short or much of the tail is free of the uropatagium, and if the legs are held nearly straight back, leaving little space between them. Pterosaur uropatagia appear to have been similarly variable, with the interesting proviso that they apparently did not attach at all to the long tails of at least some rhamphorhynchoids even at the base—this makes sense in that it allowed the tail to be entirely unlinked to the legs, so both could operate independently either on the ground or in flight (Witton 2013).

The splint-like fifth toes of rhamphorhynchoids helped support and manipulate the trailing edge of the interleg membrane, as



Pterosaur wing profile compared with birds and bat

to full chord breadth. If the wing membrane is drawn from the wrist out so that it is a little broader than that of the specimen, the chord is narrow along the outer wing from the tip to behind the wrist. That means that the main membrane was far from being so broad chorded that the inner trailing edge emerged straight out from the ankle. That in turn indicates that the trailing edge of the inner brachiopatagium swept strongly back to the ankle, which some specimens suggest it anchored to. In an anurognathid rhamphorhynchoid, the fore-aft chord of the membrane behind the elbow appears to be preserved, according to some researchers' interpretation. Again, the inner trailing border of the main membrane appears to have swooped dramatically forward like that of fruit bats from the ankle of the long leg out to the rest of the brachiopatagium (Larramendi et al. 2021).

In pterodactyloids the wing chord was fairly narrow at the base because the main membrane probably emerged well forward, off the lower thigh. If the brachiopatagium was not attached to the legs in some pterodactyloids, then the wing chord must have been narrow. It therefore appears that, from a gentle convex trailing edge at the wing tip, the main wing membrane of pterosaurs was fairly to quite narrow chorded, promoting speed over agility. Although broader wings cannot be entirely ruled out based on the limited data on hand, such wide chords would have significantly added to the total mass of the animal. The propatagium provided a gentle concave leading edge to the inner wing and broadened its chord, contributing to the overall wing area. Almost certainly the overall chord of the wings would have been the least in the very long-winged, short-bodied, and short-legged oceanic ornithocheiroids, nyctosaurs most of all. The sometimes even bigger azhdarchids had markedly shorter and correspondingly probably somewhat broader wings relative to their bodies. The wing chords restored herein produce wing area to mass ratios close to the avian norm, supporting their validity. Between the legs were the uropatagium sheets, apparently much more extensive in rhamphorhynchoids than in the pterodactyloids lacking the outer splint-like toe.

Viewed overall, the restored pterosaur wing was an evolutionary work of simple, clean elegance in top or bottom profile view, much more so than the creepily irregular rear edges of bat wings, and exceeding the attractiveness of even most birds' airfoils. The extraslender wings of the big marine pterosaurs may have been the most aesthetically graceful, being similar to those of albatrosses.

The camber of the bat brachiopatagium is strong because it is maintained by the two strongly arced midwing fingers, a configuration that favors agility via lots of lift over speed via low drag. The camber is the least in the faster bats such as molossids. The shallower feathery camber of bird wings favors speed over maneuverability. Presumably the cross section of the pterosaur brachiopatagium followed a dorsal arch maintained over most of the span by the stiffening of curved actinofibers. Lacking the long fingers to maintain a strong camber and ease the turbulence of airflow during slow-speed flight, pterosaur wings should have had more modest camber than those of bats and should have favored speed over agility, although this balance probably varied considerably among pterosaurs.

Along the outer pterosaur wing, especially the wing finger, the aerodynamically flattened leading edge bone, tendon, and ligament struts were so slender that they would not have seriously interrupted the frontal streamlining of the airfoil. The three joints between the four wings formed minor bulges, which were reduced to two in the extra-high-performance nyctosaurs and an anurognathid to bring the drag of the outer wing down to a bare practical minimum.

Farther inward on the wing is a different matter. In order to provide sufficient bending strength and muscle power for flapping flight, the bones and muscles of the inner arm from the wrist inward have to be fairly robustly built in bats, pterosaurs, and birds, producing considerable frontal area that generates drag. In birds this is not as much of a problem because the progressive reduction of layers of feathers toward the trailing edge allows the inner wing arm to be smoothly integrated into a gently cambered teardrop shape well suited for minimal drag. The resulting wing cross section is similar to that of moderately fast planes like biplane fighters during and after the World War I. The leading edge of the propatagium further reduces the problem of smoothing airflow over the humerus, radius, and ulna and their muscles but does not entirely solve it.

For bats and pterosaurs, smoothing out the connection between the very thin fore and aft wing membranes and the thick inner arm was not so readily solved. Mostly rather slow fliers, bats usually accept the imperfection-in fact, the resulting irregular top surface of the outer wing created by the multiple fingers may improve airflow during slow flight by helping to keep airflow from breaking away from the top of the wing and creating an unwanted stall during slow flight. The exception are the fast-flying molossids, in which carpet-like strips of short fur are used to blend the top of the propatagium with the inner arm and both sides of the brachiopatagium. Although preserved pterosaur membranes usually lack evidence of pycnofiber coverings, there is some fossil evidence of such carpeting; hence it is possible that some pterosaur wings minimized drag via pterofuzz. Also possible is that air sacs filled out the wing membranes close to the wing bones to help smooth out the surface profile. Blending via pycnofeathers and/or air sacs may have been particularly necessary among giants in order to smooth out hefty inner wing bones, and such should have been an aerodynamic priority. Almost certainly pterofuzz helped smooth the base of the inner brachiopatagium, as is true in bats. Because pterosaur legs were slender, they would not have produced serious drag as they anchored the rear of the inner brachiopatagium and the uropatagium.

Pterosaur wings lacked a feature of bird wings, the leadingedge alula or bastard wing. This is a set of small feathers supported by the freely moving thumb splint. When a bird is flying slowly to turn hard or land, it can lift the alula a little above the leading edge of the main wing, allowing air to flow between the two airfoils. This creates a leading-edge slot, similar to those used on some airplanes, that alters airflow over the top of the wing in a manner that allows the wing to adopt a higher angle of attack and generate yet more lift, rather than accidentally stall out and suddenly lose all lift. The improvement in lift improves turning ability at low speeds and slows down landing speeds. Because pterosaurs lacked a similar structure, as well as the higher camber that can be adopted by bat wings, pterosaurs were probably not as maneuverable when flying slowly, nor were they able to fly as slowly, as birds and especially bats.

#### Flight Control

Now that we have detailed the anatomy and basic actions of the pterosaur wing, the next task is to look at how it generated and controlled flight.

During the late 1800s, when increasingly serious attempts were being made to produce powered, winged planes that could carry humans, it was widely assumed that controlling a flying machine would be a lot like steering an automobile, a boat, or even, more appropriately, a lighter-than-air ship or submarine. Turning right or left would be a simple matter of moving the rudder in the correct direction. Going up and down would require using a movable elevator. It was the Wright brothers who first realized that this simplistic view of aviation was errant, and that flying through thin air that is 800 times less dense than water is inherently dynamic. That the Wrights were mere bicycle makers is actually key to their realization. On a bike, one does not merely turn the front wheel as in an auto; one banks into the turn-cycling is dynamic. To stay in the air is more than a matter of sufficient lift and power; it requires control of orientation in upward-downward pitch, right-left yaw, and right-left roll. The latter realization in particular is what allowed the Wrights to first get into the air in 1903, albeit in a misdesigned Flyer 1 that they accidently made so extremely unstable that it was barely controllable. That is why their first flights were so short-there was fuel enough to go a few kilometers, but the pitch controls were oversensitive so the machine kept semicrashing, until on the fourth flight one of the brothers managed to squeeze a few hundred meters out of it. It was not until 1905 that they got the bugs worked out and could stay up in the air under full maneuvering control as long as the fuel did not run out. In 1906 Europeans started flying, but without dynamic controls they could barely steer in the air and were amazed when in 1908 one of the Wrights showed how their machine could fly like a giant bird, under complete command by the pilot.

What the Wrights realized is that, like bicyclists, birds dynamically bank into a turn. If a winged flier tries to turn by simply kicking over the rudder while keeping the wings level, it will skid and end up going partly sideways while barely beginning to make the turn. And in any case, few if any biofliers have a prominent vertical rudder. When banking, the wings are not just generating vertical lift: the lift is now directed partly away from the direction the flier wishes to go, producing a dramatic sideways thrust that pushes the flier into a tight turn-the steeper the bank, the harder the turn. Hang glider pilots bank by shifting their weight left or right. Most aircraft use ailerons or other hinged flap-like mobile panels on the outer wings. But the early Wright Flyers used a bat-like wing warping in which the lightly built, thin-sheeted, flexible wings were flexed along their long axis, so that the angle of attack was higher on one side than on the other. The greater the angle of attack, the more lift an airfoil produces-as long as the attack angle is not too steep-so the angled-up wing lifts up, the other tilts down, and banking is produced, which automatically generates the turn. Interestingly, many airplanes, including airliners, rarely use the rudder when turning; like a flying animal, they rely entirely on wing banking to produce smooth passenger- and cargo-pleasing turns. The rudder is used only in particular situations, including emergencies such as an engine going off-line. In the Wright Flyers and some other early planes, the wing warping caused the attack differential to gradually increase toward the outer wings. The more complex wing warping enjoyed by multifungered bats helps them make sudden hard turns. Because the main rotation of wings along their long axis is limited to the shoulder in flying birds and pterosaurs, the entire wing on a given side is pitched up or down as needed for banking. This aerodynamically simpler, stiffer scheme, though not used in any piloted aircraft, limits the turning ability of birds and presumably pterosaurs relative to chiropterans. On the other hand, the bat-like minimuscles that were probably within and helped finely manipulate pterosaur membranes should have improved their agility vis-à-vis birds to some degree. Another item that may have helped pterosaurs turn was their small free fingers. Presumably these were normally folded tight during flight to maximize streamlining, and extending or flexing the short fingers up or down to project into the airstream on just one wing would have created some drag on that side. The turbulence created by the splayed fingers would have disrupted the air flowing over the downstream area of the airfoil and enhanced the amount of drag on that wing, further turning the creature in that direction. Somewhat similar to the drag-inducing split flaps used for turning on some aircraft such as the B-2, this limited form of pterosaur yaw control would have worked better when the free fingers and their claws were relatively bigger.

Flying craft need to control orientation on all axes—roll along the long axis of the main body, left and right yaw, and up and down pitch. Although flying is dynamic, the degree of dynamism is quite variable. A priority for small private planes is to make them as easy and safe to fly by amateur pilots as is practical. To do that, they are made as stable as possible—so stable that if the pilot lets go of the controls the plane will naturally assume a steady, horizontal path. This is why when the pilot of a private plane becomes gravely disabled the plane often cruises along until the fuel runs out. One way to achieve high stability

is to simply place flat wings atop the fuselage, so the low-placed mass of the latter provides stabilization. If, on the other hand, the wings are attached to the lower fuselage, then the wings are given a strong dihedral, with the tips markedly higher than the bases to form a shallow V. If the plane starts to tilt to the right, then the right wing now being more horizontal relative to the ground produces more vertical lift, while the left wing being more steeply angled away from horizontal, and with the high-pressure bottom air more easily spilling off the wing tip, produces less vertical lift, so the craft automatically rights itself. During World War II the P-51 fighter was given a little extra dihedral because it was designed to fly farther than other single-seat, single-engine fighters, and the improved stability reduced the fatigue imposed on the pilot by long missions.

A high degree of stability is not ideal for some aircraft because it makes it harder to maneuver, so stunt planes and most fighters are designed to be at most moderately stable. To do that, the wing dihedral is modest, absent, or reversed via an anhedral if the wing is mounted high on the fuselage, as seen in the Harrier jump jet. When stability is low, the pilot has to constantly fly the plane—unless autopilot is available—to keep it straight and level. Some modern jet fighters, starting with the F-16, are so aerodynamically unstable that a human pilot has no hope of keeping them in control for even a few moments, so computers are in constant use to keep the machines from tumbling through the air.

The neural networks of flying insects and vertebrates are de facto expert computer controls that allow them to constantly and without specifically thinking about it keep stable at all times regardless of the individual's aerodynamic stability or lack thereof at a given moment, within reason. None of these networks possess the high automatic stability of a private plane. Even so, a pterosaur would not have cruised far with its wings assuming so much anhedral that if it began to unintentionally tilt right, the right wing would become increasingly vertical and generate less lift, while the increasing horizontal left wing would produce ever more lift and threaten to flip the ancient flier over. To keep from rolling, the pterosaur would have had to struggle, with physical and mental difficulty, to constantly adjust its wing controls to keep on an even keel, wasting energy, tiring itself out, and risking loss of control. Instead, cruising animal fliers tend to put their wings in a posture that provides easy-to-adjust-for stability. A notable example is the way that many vultures, which soar with little or no flapping for hours at a stretch, habitually pose their wings in a distinctive shallow V dihedral.

Among animals that fly, only one group apparently had potential flat vertical tail rudders: the long-tailed rhamphorhynchoids. Because preservation of soft tissue vanes is very spotty, it is quite possible that some portion of rhamphorhynchoids lacked the vanes. Some, most notably *Rhamphorhynchus*, had a short deep vane adorning the tail tip. Others had a series of shallow vanes along a long portion of the tail. That the vanes are asymmetrical indicates that they were vertical in the living animals. The shallow vanes do not appear highly aerodynamic, so they are candidates for display rather than aerodynamic purposes. The same may have been true of the deep tail-tip vanes, but it is also possible that the use of a vertical rudder was variable in rhamphorhynchoids in accord with the different aerial needs of different species; we will likely never know. What is certain is that the long tails impacted the flight of the pterosaurs that had them one way or another, as did the lack of them in other pterosaurs. The long tails of rhamphorhynchoids made up a nonnegligible twentieth of their total mass. With such a significant mass placed well away from the body center, the tail could be used to help quickly change direction along all axes, especially in yaw if the vanes acted like air rudders. On the other hand, long tails, vaned or not, would also tend to provide more stability than in pterosaurs that lacked the distally placed inertial mass and vertical aerosurface. That most rhamphorhynchoids retained the long tail for some 90 million years indicates it was a successful adaptation for aerodynamic purposes, for reproductive display, or both. On the other hand, many of the exceptionally high-performance anurognathids lost the long tail, and the short-tailed pterodactyloids replaced all the long-tailed rhamphorhynchoids and often became oceanic and/or enormous. This indicates that lacking a substantial mass well away from the body center was overall superior to having it, probably by increasing dynamic agility by concentrating mass more toward the body center. The simple reduction in total mass was also an advantage. The absence of long tails in dinoavian fliers after the Mesozoic, and the similarly short tails of bats, support this dynamic flight hypothesis.

That the atypical rod at the end of the pteranodontid tail sported a vertical rudder surface is highly speculative but cannot be ruled out.

Many and perhaps all pterosaurs had another potential vertical rudder, the head crest. For that matter, the big beaks or deep snouts of some archosaurian fliers had aerodynamic steering potential. Very few aircraft have a rudder in front of the wings. A very large surface area well ahead of the central axis of the body would produce tremendous bending forces on necks, which would have been problematic, especially among pterosaurs with longer and more slender necks. Birds-including those with head crests, as far as we know-and bats turn without the use of vertical rudders, which favors pterosaurs not doing so either. A related matter is the little-considered issue of how pterosaurs oriented their head during banking turns. Birds tend keep the horizontal plane of their head and eyes level with the ground as the following body and wings roll into a turn, even a hard turn. Presumably this differential improves spatial orientation as the bird's flight direction rapidly changes-doing so is possible in birds because their neck vertebrae are so numerous and rotationally flexible relative to one another. Bats, with their shorter, stiffer necks, seem less prone to this action. Because pterosaur neck vertebrae were not highly rotationally flexible and were few in number even in long-necked pterodactyloids,

they must have kept their head tilt much the same as their body tilt, hard banking both head and body into tight turns. This point reduces the possibility of the use of head crests as rudders. If a pterosaur were steeply banked in a turn, the head included, then turning the head strongly into the turn so that the head and its crest were acting as a rudder in the airstream would not only produce sideways thrust, but the tilt would also make the crest into a partial front elevator that would produce significant downward thrust, causing the pterosaur to go into some degree of dive. The downward force would be all the more disadvantageous because when a winged craft is banking in a turn, the reduction in direct vertical lift from the wings tends to cause the craft to lose altitude, costing critical maneuvering energy. On the other hand, if a crested pterosaur wished to make a descending turn, the head crest may have been useful.

Another viable set of potential rudders that has received little attention are the webbed feet. In birds that have them, foot webs can be and often are used for aerodynamic purposes, especially as air brakes when landing. If pterosaur legs were sprawled out to the sides to spread out the trailing portions of the inner brachiopatagium and the uropatagium during ordinary flight, the trailing feet were automatically held vertically so that the outer side of the foot was on the top edge and the inner side on the bottom edge. This is not the case with bats and birds, in which the trailing feet are more horizontal. The toe webs therefore could have acted as vertical air rudders. That could have been done either by swinging the lower leg inward or outward at the knee, and/or by swinging the foot outward at the ankle-the foot could not be flexed inward because the ankle would not allow it. The rudder effect could have been enhanced when needed by spreading out the toes to maximize the area of the webbing. Although in most pterosaurs the modest size of the feet would have kept the resulting rudder effect from being especially powerful, it would have helped produce a turn by pushing the rear of the pterosaur to, say, the right in a left turn, pointing the body in the direction the pterosaur wished to go-something that wing warping alone has trouble doing. Foot rudders could also have been used to help maintain a straight course via small, quick corrective movements, including helping to counter any accidental turning movements produced by head crests. The feet of some pterosaurs were too small to be effective rudders or air brakes. On the other hand, the presence of large, webbed feet in anurognathids despite their dry-land lifestyle supports the use of such appendages as auxiliary airfoils.

Now that we have dealt with roll and yaw, it is time to look at pitch control. The latter is linked to distribution of mass, specifically the center of gravity, relative to the axis of lift produced by the airfoils at any given moment. Those who design and operate fixed-wing aircraft must be very careful to ensure that the distribution of weight in the fuselage and of the engines, whether it be the permanent structure or the internal contents—humans, fuel, cargo, ammo—always produces a center of mass that correctly matches up with the axis of lift. Failure to do so will result in the plane not being able to successfully take off if front heavy, or to stall on takeoff and crash if rear heavy. However, the two factors need not always be exactly aligned. In some cases the center of gravity is set somewhat ahead of the axis of lift so that the rear elevators have to be set to produce a downward force during level flight; doing this reduces the danger of stalling out, while improving sudden evasive dive performance in fighters. Biofliers, with their multijointed wings that are more flexible in their configuration, have even more room for slack.

With long tails aft balancing modest-sized heads fixed to short necks in the front, the fore-aft weight distribution looks well balanced relative to the wing base in rhamphorhynchoids. With big and sometimes enormous heads at the ends of sometimes long necks in front of the wing base, and hardly any tail behind, pterodactyloids appear much more front heavy, in a way not seen in similarly short-tailed bats and birds, big-headed toucans and hornbills excepted. Nor could the stiff, long necks of pterodactyloids that had them be pulled far back, as they can be in flexible-necked birds such as egrets and pelicans. Large-beaked pterosaurs were not as front heavy as they appear because their big bills were, like those of similar long-snouted birds, highly pneumatic-filled largely with air, they sported very low densities around a tenth that of normal tissues, about the same as extrastrength Styrofoam (Larramendi et al. 2021). Even so, large-headed pterodactyloids were more front heavy relative to the wings than were rhamphorhynchoids. Yet this was not a problem because the more forward weighted a pterosaur was, the more it could sweep its wings forward to shift the axis of lift far enough forward to match up with the forwardly placed center of mass. This was most especially the case in the very longnecked azhdarchids. How dramatic the difference in forward wing sweep would have been in more front-heavy pterosaurs compared to the rest is not firmly determinable and may have been visually subtle.

Because it is so easy for flying creatures to rapidly adjust the sweep of their wings at their many mobile arm joints, they can use that action to very quickly control pitch in order to climb, remain in level flight, or dive. To climb, sweep the wings forward the pertinent amount and the tail end will drop, so that the resulting upward pitch will cause a climb-temporary if no increase in power from increased flapping is applied, steady if it is not. Return the wing sweep to normal, and level flight resumes relative to the surrounding body of air if sufficient power is maintained. Sweep the wings back, and the nose pitches down and the flier descends regardless of whether flapping power is used or not. Wing sweep alteration is used by all biofliers-it is the primary or sole means of pitch control in aerial insects. In a high-speed dive, partial folding of the wings could reduce the frontal drag of the airfoils by up to half. Even so, no pterosaur had the ultrastreamlined body and wing form that would have allowed it to fast dive like a stooping falcon.

Another major means of pitch control is horizontal elevators. In conventional aircraft, movable panels provide such control.

These elevators can be placed in front of the wings, as in the earlier Wright Flyers and other planes over time, including some recent advanced designs. But in most, the elevators are either well behind the wings, or on the trailing edges of delta wings and flying wings. In the last situation, the aerodynamics can be dangerously tricky. The famed Northrop flying wing bombers—the piston-powered B-35 and its direct descendant, the B-49 jet—had so little distance between the center of mass and the elevators that they were too short coupled and at risk of tumbling end over end, which one of the B-49s did and crashed. It is computer stabilization that makes the Northrop B-2 and robotic stealth flying wings practical.

All bats and most birds have dedicated elevator control surfaces. The rare exceptions among birds are some Mesozoic examples, the fossils of which show very short tail feathers, too short for effective pitch control, so they had to rely on wing sweep alteration and thrust adjustment alone. Other birds use their tail fans as elevators in coordination with wing sweep alteration. Bats do much the same, except that their elevators consist of the combination of the rear inner membrane of the main wing and uropatagium attached to the legs. The same would have been true of pterosaurs with their uropatagia and the trailing portions of their inner brachiopatagia. Rhamphorhynchoids could have attained some pitch control with their long tails. Quickly swinging the tail up would have pitched the nose up into a climb, and a downward swipe of the tail would have helped point the nose down into a dive. Because the articulations of the forward vertebrae of the rod-tipped tail of Pteranodon tail appear to favor an up-and-down motion, it appears to have been part of an elevator complex. It might have supported an independent elevator surface or may have been integrated into the uropatagia.

The combination of immobile shoulder girdles; a fairly narrow-chorded main wing membrane that was supported by a single finger upon which stiff actinofibers were anchored, probably creating a shallow camber; the absence of boundarylayer airflow control interruptions on the wing tops; the absence of a long pteroid in some examples; and the presence of long tails in some indicate that pterosaurs as a whole were faster and less maneuverable than are mobile-shouldered, broad-chorded, multifingered, wing-warping bats in general. Yet pterosaurs were likely to have been somewhat slower than birds and more agile, especially when large pteroids were present and long tails were not.

#### Wing Power

In fixed-wing powered aircraft, the sources of lift and thrust are separate in that the rigid wings generate the lift while the engine's pistons or turbines produce the thrust. Most helicopters use the main, subhorizontal rotors to produce lift and thrust at the same time, although some have additional thrust-generating engines, and tilt rotors transform them from helicopters to winged machines pulled by vertical propellers. Attempts to produce human-carrying flapping machines have been made for engineering sport, but there are serious efforts to use flapping wings to create both lift and thrust in small drones. The latter are modeled on powered flying animals that are somewhat like helicopters in that the same airfoils produce both lift and thrust, but in their case the arm-borne airfoils are large horizontal wings that also act as vertical propellers to generate thrust.

Within the context of powered flight, using wings as propellers is marvelously energy efficient. Force equals mass times velocity squared, so velocity is the most important factor. That means that to generate a given amount of thrust, it costs less energy to slowly accelerate a large mass of air than to rapidly accelerate a small volume of air. World War II fighters pulled by big propellers accelerating large volumes of air, such as the P-51 Mustang, P-47 Thunderbolt, and P-38 Lightning, had very large flying ranges (when fitted with droppable external fuel tanks). Contemporary Me-262s, Meteors, and P-80 Shooting Stars, which were pushed along by turbines rapidly accelerating small volumes of air into the narrow intakes of their turbojets, had notoriously short ranges. Jet turbines have become fuel efficient by their transformation into turbofans that slowly accelerate the bulk of the air that passes through them-thus the plump engines suspended below the wings of late-generation airliners. Using entire wings to slowly move very large masses of air is about as fuel efficient as powered flight gets.

Bat flight can be extra energy efficient because the aerial mammals use their multiple, jointed, membrane-supporting fingers to semifold the wing inward during the upstroke such that it saves a third of the power. Because pterosaur archosaurs had a single stiff finger supporting an actinofiber-stiffened membrane, it is doubtful that they could fly as efficiently as bats. As for whether bats or birds are more energy-efficient fliers, there have been contradictory studies, with birds apparently having the advantage according to the most recent work, at least when comparing small examples of the two groups (Johansson et al. 2018). As one can see when watching small songbirds, they use an energy-saving, sort of bouncing flight in which they repeatedly cycle between a burst of lift and thrust-producing, power-demanding flapping followed by a period of no-cost streamlined ballistic travel with the wings fully folded. Bats are not able to do that. And because they were neither small enough nor able to tightly tuck up their wings, pterosaurs were not able to either. Although it does not save energy over a given distance traveled or a given period, some birds minimize flight muscle fatigue by repeatedly alternating flapping with gliding. That allows the flight muscles to rest somewhat before the next power burst, which pterosaurs of all sizes could do.

As efficient as wing propulsion is, much more so than walking the same distance, powered flight places high demands on the metabolic complexes of animals; it requires intense muscular exertion and corresponding energy expenditure per unit time, as well as possibly resulting in fatigue.

It is therefore not surprising that flight muscles make up almost a third of the total mass of some birds and bats, though

15 to 20 percent is more typical. But some birds with decent powered flight performance and acceptable flapping climb rates consist of only 6 percent flight muscle (Paul 2002). Ironically, the largest flight muscles are found in short-range birds such as fowl, including turkeys, chickens, partridges, and pheasants, which use their powerful, anaerobic-dominant and therefore whitish arm muscles to achieve very rapid, subvertical takeoffs to escape ground predators, and to travel short distances when flying fast is more suitable than walking or running the same distance. Some long-range flapping fliers such as ducks, geese, and swans actually have modest-sized flight muscles. These deep red, myoglobin-filled muscle fibers emphasize sustained aerobic power over long periods so they can power through the air for many hours. But with modest-sized flying muscles that do not have much anaerobic burst power, geese and swans have to use a laborious running takeoff followed by a gradual rate of climb to the desired cruising altitude. Pigeons are remarkable fliers because they can use their relatively big flight muscles to cruise at interstate speeds for long distances, and they are also able to take off vertically. They do the latter by wing clapping, which you can hear when they take off. Bringing the wings together directly over the body and then rapidly separating them at the beginning of the downstroke creates strong vortices that generate a dramatic increase in lift. The same aerodynamic trick is used by many insects such as bees-flying bees buzz because they are slapping their wings together at the top of each upstroke. Wing clapping is why bees and some other insects can fly with wings whose area would otherwise be too small to sustain flight using conventional aerodynamics. Whether any pterosaurs known or unknown were fast-takeoff wing clappers is not known, but anurognathids are possible candidates. Because some small bats can hover using wings that are not radically modified like those of the theropod hummingbirds, it is possible that some similar-sized pterosaurs did the same, perhaps unknown terrestrial examples. On the other hand, their multifingered wing membranes may allow bats to hover, and some flying mammals and dinosaurs hover in order to feed on the nectar of flowering plants, which were not available until the late Cretaceous, if then.

A caveat: the details of how the wings of small birds with their sophisticated feather airfoils, and of bats with their multifingered wings, work when producing thrust via flapping are very complicated and remain poorly understood. Studying the highly dynamic wing action of flying creatures is inherently taxing, and there has not been much money invested in the effort, although using bioflight as a source of ideas for improving the abilities of drones is changing that. Bird and bat flapping is so complex because it probably improves the efficacy of their flight in various ways. It would seem that the simpler, one-bigfinger wings of pterosaurs would not have been as complex in action when flapping. If so, then they may indeed have been less efficient in terms of energy use and maneuvering, although the minimuscles within their membranes should have made up for some of their deficiency. Exactly how remains obscure and, in view of our inability to study pterosaur wings in action, will always be so. At larger sizes the complexity differences would become less—the action of the steadily extended wing of a marine soaring albatross is not nearly as complicated as that of the flapping appendage of a robin, and probably not more multiplex than that of a wave-skimming ornithocheiroid. Ergo, there should have been less or no divergence in wing performance among the wings of the archosaurian titans.

#### Pterosaur Flight Repertoires

It is often said that animals that only glide—flying lizards, snakes, squirrels, and such—are not actual fliers because they do not power fly. This is silly. An albatross that is wave soaring for days on end over countless kilometers without flapping its wings is most certainly flying. As is a vulture using thermals. Same for a sailplane breaking a record in gliding height or distance. If something, animal or otherwise, has airfoils that allow it to at least glide, it is a flier. Flight comes in many forms, expressions, and variations.

The earliest-known pterosaurs were already fully developed fliers, and most were probably generalists with modest flight performance and correspondingly modest flight muscle mass. Many small and medium-sized pterosaurs, rhamphorhynchoids and pterodactyloids alike, appear to have been good performance generalists (Witton 2013; Venditti et al. 2020). But it is often hard to be sure about pterosaur flight performance estimations. Pterosaur aerodynamics are so distinctive from those of birds and bats, they often complicate figuring out what pterosaurs were doing in terms of aerial performance and habits. Most studies of pterosaur flight have focused on the giants, and the work has often been contaminated to uselessness by unrealistically low estimates of pterosaur masses (Witton 2013). Another vexing problem is that we do not know the actual wing plan profile for any pterosaur and probably never will-all wing restorations are speculative to a degree, and as a result, so are all flight performance estimates, which should be presented as a range of possibilities depending on varying possible wing areas and so on, rather than as firm conclusions. Also impossible to reliably restore are the details of the streamlining of the wing surface, such as the blending of the arm elements with the membranes. We do know that pterosaurs usually had wingspan to total mass ratios that either exceeded those of birds or were in the upper avian range, though a few were near or below the median. Pterosaurs were more like birds in that, if they had the narrow-chorded wing membranes restored herein, their wing area to total mass ratios were always well within the normal avian range for wing loading.

We also know that as pterosaurs evolved, so did flight specializations, notably in the anurognathids. Sporting welldeveloped wings and lacking tail stabilization, they should have been powerful flappers able to remain airborne for hours at a stretch, and fast and agile enough to capture flying insects on



the wing with ease (Witton 2013; Venditti et al. 2020). Whether anurognathids fully matched birds with comparable habits is problematic. Did anurognathids drink on the wing, like aerial insect-hunting and other birds and bats? This is possible and indeed probable.

For anurognathids, power flapping for hours was worth it despite the considerable energy costs because-like many bats and some anti-insect birds as well as dragonflies-by doing so they captured enough calories and other nutrients in the form of aerial insects to cover the energy expended in flight, plus maintain their bodies and reproduce. Some flappers even have enough energy left over from foraging that they engage in intense powered flight for no apparent reason. Flocking pigeons and starlings are prone to fly about in swirling, hard-turning flock formations for no apparent pressing reason-aerial predators are usually not present, so it may be a form of fitness testing, navigation orientation, or quite possibly social play. Mass crow flocks spend a portion of the evening irregularly flying from one location to another prior to roosting. So some fliers are able to acquire enough energy to burn some of it off in mass aerial relocation and acrobatics. Whether any pterosaurs did so is unknown.

It appears that the largest a bioflier can be and persistently power fly for many hours is about 20 kg (45 lb), the size of swans, which may be the largest birds to have evolved sustained power flying. Continuous cruising flight—energetically similar to walking at a very good clip or slow running—has to be powered aerobically, with the animal burning only as much oxygen at any given moment as its respiratory system can constantly provide without undue effort. But flapping flight can also power short anaerobic bursts, which are also used during fast running, including galloping. More than that and intense fatigue quickly sets in. Anaerobic power can also be used to get amazingly large animals off the ground and up to a substantial altitude, or over a few kilometers. Just how large a creature can be and still be at least a short-range power flier is not entirely clear; the biggest pterosaurs may well have been pushing the biological limits.

Also uncertain is how big a bioflier can be if it is mainly a glider. If a flier needs to spend a long time in the air on a daily basis for at least part of the year and is not hunting aerial prey, it would be to its selective benefit to minimize its flight costs by keeping powered flapping to a minimum. The way to do that is by gliding. By using gravity as a power source, a flier can travel a substantial distance at no more cost than is needed to hold the lift-generating wings in position. The last can be reduced to nearly nothing by an arm-locking mechanism in which the configuration of the bones, muscles, tendons, and ligaments allows the bioflier to make the wing semirigid. Gliding can cost dozens or more times less than power flying the same straight-line distance. If done in air that is not providing lift, the distance that can be traveled before the flight path coincides with the ground is limited. But if the aerialist has a sink rate that is less than that of the rising body of air it is in, then it will rise, which is passive soaring. Dynamic soaring does not rely on rising air but exploits the fact that when a strong wind blows, the air is slower close to a fairly flat surface such as a large body of water than it is a few meters higher up. When a flier flies into the wind, the faster air flowing over the top of the wing has lower pressure than the slower air below-the Bernoulli effect is achieved without the flier's wings producing it-and after rising as much as 15+ m (60 ft), the flier turns around and shallow dives to near the surface, repeating the procedure as often as needed. If this is done in a region of perpetual sufficient winds, it is possible for a soarer that can pick up food from the surface without landing to remain airborne with very little flapping for years. All forms of soaring are powered by a combination of gravity and the solar heating that produces rising air or wind.

Note that as energy efficient as soaring is, in practical terms it can be less so. That is because soaring usually requires not flying in a simple straight line from one place to another. So, unless they fly over suitable geography that coincidently matches the course they need to take, continental soarers traveling to a particular final spot may have to do so in a very erratic course that greatly increases the total aerial distance traveled and the time needed to make the journey. Even so, the overall reduction in energy expenditure via soaring during migration remains substantial in a number of birds that migrate primarily by soaring, storks and raptors being examples. But most migrating birds minimize travel time by power flying most or all of the way, including across oceans they cannot land on, geese and swans being large-bodied examples. If, on the other hand, a soaring animal is looking for sustenance, the erratic course of soaring can actually aid the search, as in flying scavengers and fishers.

Sources of rising air include solar-powered warm-air thermals, which are common over nonmountainous terrain with sufficient sunlight impacting the ground. Having exploited one thermal, the soarer can glide to the next-sometimes sighting in on the fluffy cumulus clouds that often mark a thermal's top-and so on from midmorning to late afternoon. When a general wind is blowing over ridges, hills, mountains, cliffs, and large waves in a direction not too parallel to the long axis of landforms, the resulting standing waves on the upslope side and over the top can provide a sustained updraft. In the case of hill and mountain ranges, this can be dozens to many hundreds of miles long, as long as suitable winds are in force. Direct sunlight is not required. Winds blowing steadily over large tracts of seas and oceans produce waves that act as miniridges-the resulting updrafts are all temporary, but new ones are constantly being formed. Dynamic soaring can be done over vast tracts of open seas and oceans day and night, though it does require that the

soarer fly in constant tight loops about 50 m (150 ft) across. When the air is still, waves themselves push on the air, their leading slopes forming small updrafts that fliers can exploit to reduce or eliminate the need for flapping while cruising barely above the rollers (Stokes and Lucas 2021). Such wave-slope soaring includes breakers along a coast, helping explain why birds often fly low along the shoreline.

Human-carrying soaring gliders range from hang gliders that weigh about half again as much as those who hang from them, to modest-performance slender-wing gliders with spans of 12-13 m (40-43 ft) that weigh 250 kg (550 lb) with the pilot, to ultra-high-performance sailplanes with 15 m (50 ft) wings that weigh over 500 kg (1,200 lb) fully loaded with pilot, possible passenger, and water ballast and can achieve remarkable distance/descent ratios of 45/1. Note that the highest-performing soaring gliders are not designed to be as lightweight as possible because their power source is gravity, and to glide requires that the glider weigh something-because a gas-filled airship weighs nothing, it cannot move through the air unless it is powered. Because gliding requires negative buoyancy in the air, if gliders are too light, then being insufficiently dense and wing loaded ironically leaves them with too low a mass relative to their drag to achieve the high gliding speed needed to produce the best overall performance. At the other extreme, being too heavy will make a glider sink too fast. So sailplanes are loaded to up to their optimal maximum design mass with water, which can constitute almost half the weight of the machine (Larramendi et al. 2021), or in some cases an auxiliary engine that is revved up only when needed. Some gliders join soaring birds in using temporary thermals as power sources. Ridge soaring is common and in the case of mountain ranges can allow extreme altitudes to be achieved, as well as tremendous distances. Dynamic soaring and wave soaring occur in a zone so close to the surface-birds occasionally incidentally dip a wing tip in the water, and the same was probably true of wave-skimming pterosaurs-that human-carrying machines do not soar this way, though there is an effort to apply this form of air transport to research and other drones.

The ultimate modern wave soarers are albatrosses; among birds over time they were the even more gigantic pelagornithids. With distance/descent glide ratios approaching 24/1, albatrosses and giant petrels combine dynamic soaring with wave-slope soaring. With their wings locked, the soaring energy expenditure is not much above the resting metabolism, and this is the most efficient form of nondrifting travel known among animals. That is all the more true because the near-zero cost of soaring occurs while the soarer is wandering about looking for food, rather than as part of a deliberate migration, in which not flying a straight course while not spending much time eating can pose a problem regarding energy in versus energy out. Although the oceanic soarers have very long wings, they are not lightly loaded. The slender wings are so narrow chorded that their area is not high compared to the mass of their large bodies. The

#### BIOLOGY



Giant pterosaurs compared to large birds and sailplane

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high wing loading is important to their ability to use gravity to power the high-speed downwind descents, often over 60 km/h (40 mph), needed to kinetically power the upwind climb in order to produce free lift via the surface wind-generated Bernoulli effect. Using near-surface soaring allows some albatrosses to stay at sea for up to five years at a stretch, flying 160,000 km (100,000 mi) in a year, not counting the dynamic soaring loops, at top speeds of 100 km/h (65 mph). The soaring performance of the often even more enormous pelagornithids was even more extraordinary in at least certain regards. Aside from the even greater dimensions, the faux-toothed birds had extreme winglocking mechanisms that may have severely limited flapping. But critical details of pelagornithid soaring are obscure. Their massto-span ratio seems less than for albatrosses, and if their wings were correspondingly narrow chorded then they were probably not the high-velocity dynamic soarers that current albatrosses are. Less powerful oceanic winds prior to the exceptionally steep latitudinal global temperature gradient of the Late Cenozoic could have favored some form of slower soaring, perhaps putting more emphasis on wave soaring than on dynamic soaring.

The albatrosses and pelagornithids of pterosaurs were the great pterodactyloid ornithocheiroid ornithocheirids and pteranodonts of the oceans in the last two-thirds of the Cretaceous. The ornithocheiroid arm shows specializations for wing locking. Like those of modern maritime soarers, their inner arm bones are slender in front view, minimizing the frontal drag that is antagonistic to a very high distance/descent glide ratio. Calculations indicating that the marine pterosaurs were extremely lightly loaded because of probably excessively large wing membrane restorations and/or unrealistically low body mass estimates can be discounted. If they had narrow-chorded wings, then the relatively small-bodied ornithocheirids would have been a little less loaded than are albatrosses, suggesting flight dynamics more like those of pelagornithids. With a very low temperature gradient in the warm, nearly glacier-free Cretaceous, marine winds should have been mild by modern standards, so ornithocheirids look to have been slower soarers than albatrosses, and more prone to passive wave soaring than

dynamic soaring. On the other hand, *Pteranodon* had a relatively larger body than the ornithocheirids, and if its wing was narrow chorded it may have had more albatross-like wing loading, which suggests more dynamic soaring than that of ornithocheirids. It is possible that unknown ornithocheiroids were specialized for the deep oceans, especially the Pacific, which was even larger then.

Of particular interest are the pteranodontids' closest relatives, the nyctosaurids. Ossification of some arm tendons suggests wing locking approaching or reaching the pelagornithid level. With the longest wings relative to their exceptionally small bodies, they were very probably the most lightly wing-loaded pterosaurs. In addition to showing that they were the pterosaurs least well adapted for ground locomotion, the loss of the small fingers means that nyctosaurs had the most aerodynamically streamlined wings among the group. The extreme pterosaurs were most similar to the most extreme gliding birds, the frigate birds, which in turn are the most pterosaur-like of birds. Frigate birds are the most lightly loaded known flying dinosaurs, and their basic appearance is the most reminiscent of the pterosaurs, with their long, slender, strongly kinked wings. Frigate birds are extremely aerial, spending little time anywhere but the air. But they are not deep-oceanic birds; they remain near islands that are their home bases.

In whatever way oceanic pterosaurs soared over open water, when along cliff-lined coastlines they would have taken advantage of the updrafts generated by the steep terrain near the waterline to move about, and to climb up to high nesting sites if they were using such, with minimal effort.

Ornithocheiroids were the most evolved soaring pterosaurs, but they were far from the first. The lifestyle seems to have appeared in rhamphorhynchoids as early as the Triassic– specifically in the slender-inner-winged caviramians, and in the campylognathoidids, whose very long wings suggest soaring (Witton 2013), perhaps of a gull or frigate bird type. Soaring appears to have evolved in very early birds too, its energy efficiency having strong natural selective value. Being typically nocturnal, few bats soar, but some diurnal flying foxes use thermals and slopes to do so.

![](_page_24_Picture_8.jpeg)

Soaring versus flapping wing profiles compared

The flight type of the pterosaur group that included the most colossal fliers, the continental azhdarchids, has been the focus of much research and conflicting results. Because these were nonmarine pterosaurs, they were not very low-altitude soarers like the ornithocheiroids. The big question is whether they were passive soarers that used thermals and ridges, like vultures, condors, and the extinct and sometimes gigantic Teratornis, or powered fliers that rarely or never soared, like turkeys and bustards. Many have presumed the first was most true (Habib 2010; Witton 2013), on the theory that because big modern birds are energy-saving soarers, all the big pterosaurs should have been as well. But some of the heaviest living flying birds are actually nonsoarers that rely on flapping flight, and some of them are short-range burst fliers that use an intense spurt of anaerobic power to get into the air quickly and then rapidly tire and reland. The big azhdarchids were probably too large to power fly for long distances.

Azhdarchids were shorter winged relative to their mass than most pterosaurs, being the only members of the group whose span-to-mass ratios fall close to the avian median, so they were quite unlike the low-altitude ornithocheiroid soarers. Presumably azhdarchid wing chords were fairly broad by pterosaur standards; the wing area to mass ratio appears to be a little below the avian average but still well within norms. Azhdarchid wings were correspondingly so much more heavily loaded than those of soaring continental birds that the glide ratio should have been too steep to allow these superpterosaurs to be passive soarers (Goto et al. 2020; Venditti et al. 2020). Also antithetical to soaring azhdarchids is the robustness of the inner wing elements, astonishingly so in the giant examples. This could hardly have been more different from the dragminimizing frontal slenderization of the inner wing of even the biggest soaring ornithocheiroids, as well as avian soarers, which helped provide the streamlining needed to slip through the air and thereby maximize gliding efficiency. Especially notable is the azhdarchid pectoral crest, an extraprominent arcing structure indicative of what should have been the most powerful pectoralis musculature among pterosaurs, or for that matter any fliers. Also bulky were bulging Popeye-like elbows and wrists that would have interfered with the airstream atop and beneath those sections of the wings.

The azhdarchid combination of short wings; oversized wing musculature, which, as powerful as it was, probably could not propel long flights; and the thick, drag-inducing inner wing that the massive musculature and its robust supporting and strengthened bones required to exist indicates that the land dwellers' wings were adapted to maximize flapping thrust power production over static wing gliding, and therefore these were shortrange burst fliers (Paul 1991, 2002). If so, then the flight muscle cells should have been configured to maximize quick, high-intensity anaerobic power over a few moments, which would have restricted powered flight range, rather than longer-term but lessintense aerobic power, which could have sustained somewhat longer trips. This is adaptively logical in that as big as the azhdarchids were, they lived in a world infested with even larger and faster-running predaceous theropod dinosaurs, so they needed to be able to get their up-to-half-ton, bear- and horse-sized bodies into the air very fast when threatened. That the azhdarchids could not then flee tremendously far would not be important relative to the critical aerial escape mechanism. And the ability to spontaneously travel a few kilometers in a given trip in the air at substantially less total energy cost, at a much faster rate, and with no danger of being attacked than when walking would also have been a major advantage. The initial flapping to altitude could have been followed by a distance-lengthening glide, further extended by fatigue-reducing cycling between flapping and gliding before landing if desired-a technique used by some albatrosses when sufficient winds are not available. An advantage of short wings is that they would have facilitated low flight through narrow spaces between tall vegetation in the landscapes azhdarchids dwelled in, similar to the short, broad wings characteristic of forest birds. The common presumption that thickarmed azhdarchids soared to cover long distances appears to be no more applicable than it is to the big ground-foraging turkeys and bustards, which never soar.

About half of all bird species migrate, and the possibility that some terrestrial pterosaurs migrated is considerable. The very dark polar winters shut down plant productivity, and even during the warmer portions of the Mesozoic they were chilly enough for snow. During global climatic cooling, high-latitude winters were outright severe, with blizzards and extended frosts during parts of the Mesozoic. The pressure to fly equatorward during the fall and then return toward the poles for the late spring and summer when the sun was above the horizon for longer, even continuously, would have been compelling. However, with the global north-south temperature gradient much less in the Mesozoic than in the modern world, the pressure for species to migrate, and the distances traveled, may have been generally much less than is common today. Fliers can migrate long distances because flying costs only about two-thirds as much as walking the same distance, even less if soaring is exploited. If pterosaur flight was less efficient than avian flight, it could have decreased their migratory range, as may be true of bats vis-à-vis birds (Johansson et al. 2018). Migration also makes it possible to avoid geographical barriers and hazards, such as dangerous river crossings and the big predators that afflict terrestrial travelers. By making a few short flights amounting to some tens of kilometers a day, and feeding most of the day, short-flight azhdarchids could have traveled in the low thousands of kilometers in the spring and fall. Thermal and ridge soaring could have facilitated longer trips if any land pterosaurs practiced such energy-efficient flight.

It is tempting to assume that as pterosaurs evolved, their flight became progressively more sophisticated. That was true in broad terms as various pterosaur clades expanded into previously unfilled aerial niches over Mesozoic time (Witton 2013; Venditti et al. 2020). But evolution is not intentionally progressive; it is adaptive to the specific life circumstances of a breeding population at a given time. Many modern birds have limited flight performance compared to birds all the way back in the Mesozoic, to the point of being flightless in many cases. Among pterosaurs the flight abilities of Early Jurassic *Dimorphodon* appear to have been less impressive than those of known earlier Late Triassic eopterosaurs, indicating a decrease in aerial performance. Nor do the flight abilities of Early Cretaceous filter-feeding *Pterodaustro*, which lays claim to the lowest wingspan/total mass ratio yet known among pterosaurs, appear particularly impressive, although the ratio was still well up in the avian range.

#### Takeoffs and Landings

Like airplanes, pterosaurs and other aerial beasts are highly configured to fly, but as per the principle that—unless it goes into deep space—what goes up must come down, all aerial objects must at some time take off and land. As a result, fliers need to have the means to do so, and to get around to at least some extent when not airborne. Birds and bats in high places can just drop into the air and glide or begin flapping. Or they can start the flight with a leap. If a breeze is available, launching into the wind is preferable, unless doing so is not compatible with the direction a bioflier wishes to travel between trees, or when departing a cliff. These factors would also have been applicable to pterosaurs of all sizes when launching from high locations. More difficult is taking off from flat ground, against the gravity well of the entire planet. A few flying birds and many bats are not well adapted to do so. Even flapping wings can be hard pressed to produce enough lift at zero wind velocity to readily get a body into the air; an initial booster is needed to be adept at it. In biofliers the booster is a push-off from the limbs. These are the normally powerful hindlegs in bipedal birds, but the weak legs of some of the highest-performing aerialists such as swifts and frigate birds are not well adapted for taking off from flat ground.

Among bats, the group most adept at ground locomotion, the terrestrial prey-stalking vampires, need to be able to lift up fast. Mammalian quadrupedal walkers and fliers logically rely on a push-off more from their powerful arms than from their comparatively weak legs.

Because most pterosaurs were strong-armed walking and flying quadrupeds with relatively weak legs, they are likely to have used their forelimbs as the main push-off mechanism during takeoff, as do bats (Habib 2010; Witton 2013). This adaptation appears to have been taken to an extreme in the azhdarchids. Their exceptionally robust-boned and powerfully muscled inner arms were well adapted for combining a rapid leap off the ground followed by a rapid flapping flight to climb away from danger. A downside of this system was that the resulting thick inner wing—because it was well muscled and strong boned—interfered with high-performance soaring.

Although pterosaurs were probably practitioners of armassisted takeoffs, the inner arms of some rhamphorhynchoids

![](_page_26_Picture_9.jpeg)

appear rather short for this purpose. It is possible that some pterosaurs on occasion would push off with the hindlimbs if enough wind were available, or run into the wind, especially in the case of big pterodactyloids. The best candidates for bipedal takeoff in pterosaurs are caviramians; their humerus was exceptionally slender and only a little stronger or more powerfully muscled than the femur.

It has been plausibly argued that water-loving ornithocheiroids used the arm push-off to get off the surface of the water, in part because most of them had better-developed inner arms than expected in soarers-the nyctosaurs being an exception-and because the ability to get back in the air after a spashdown, intended or not, was important. But the idea of oceanic ornithocheiroids spending much time floating on deep-water waves fishing like pelicans and albatrosses is problematic because they would have been sitting ducks-or in this case sitting ornithocheiroids-for being picked off by the host of big marine predators lurking under warm Cretaceous salt waters. Floating albatrosses can seize prey on the surface with reasonable safety because they typically inhabit cool to cold waters where active large predators are not numerous. Warmer-water pelicans minimize the danger of attack from below by seizing prey from the surface of shallow waters (which also hinders the prey fish diving away). Because they were creatures of the Mesozoic tropics and subtropics-there is evidence that ornithocheiroids avoided chillier high-latitude waters-floating would have rendered the pterodactyloids vulnerable to the many species of deadly fish and reptiles that packed those seas. Even worse, at any given time much of the sea surface has little in the way of easy prey, so openocean birds search for spots where the surface is being churned up by frenzied schools and bait balls of fish trying desperately to escape underwater predators attacking from below-predators that would be as happy to consume floating pterosaurs as they would fish. Surface floating is all the more dangerous because it is very difficult for eyes barely above the water to see and thereby trigger escape from submerged predators, while the latter can readily see their targets silhouetted against the sky above and beyond. At the same time, float feeding involves the significant energy expense of powered takeoffs.

Their high wing loading prevents big albatrosses from flying slowly enough to readily pick up aquatic prey on the wing, and their short head-neck length further limits their ability to quickly reach out for a tasty fish on pitching waves from the air. The longer beaks and perhaps slower flight of pelagornithids should have allowed them to dip feed—their ability to relaunch from the water being limited, as it is for frigate birds. Slower airspeeds combined with beaks up to over a meter long should have allowed giant marine pterodactyloids to feed on the wing. Concentrations of fish driven to the surface by their underwater marauders would have been easy pickings, including inert body parts left behind by the swimming killers. Ornithocheiroids would have done best by slowly wheeling on their great wings over the reptiles and sharks in the sea as they went about their business, taking advantage of the submarine hunters driving small fish and cephalopods en masse to the surface to be snatched up by their sword-length beaks, all the while staying safe from the dangerous undersea predators. This was not a particularly hard life; weighing about as much as an adult female human, a gigantic yet energy-efficient soaring *Pteranodon* had to eat only a dozen or more foot-long fish a day, even if feeding its nestlings back onshore. As for the strongly muscled inner arms of the marine pterodactyloids, they may indicate that they did more flapping than their avian wave-soaring analogues.

Having been in the air from just a few moments to months, flying pterosaurs needed to land. Doing so requires a flier to slow down dramatically, sufficiently to avoiding a crash landing. One way to do so when landing on a high location is to bleed off speed by approaching it from below, in which case the final landing speed can be close to zero, with the free fingers perhaps making the first contact with the branch or rock edge, as in bats. This gravity-assisted landing option is not available when landing on the ground or water. In that case, the objective is to land as slowly as possible, even while traveling down the gravity well. One way to do that is via a controlled stall, approaching the landing zone with the leading edge of the wings strongly tilted upward to make their undersides into drag-producing air traps, while keeping the more rapid airflow over the top of the wings stable enough to still generate enough lift to prevent the stall from occurring too early and causing a sudden hard crash. Increasing the wing camber to maximize both lift and drag is of great advantage when landing. Jet airliners use leading-edge wing slats to help do so, and pterosaurs may have increased the fore-aft arc of the inner wing by depressing the propatagium. To produce extra drag, webbed feet could be deployed as auxiliary air brakes as discussed earlier, which is convenient in that putting the legs down vertically prepositions them to act as initial landing gear during touchdown. This is similar to some aircraft, in which the nearly vertically deployed wing flaps are entirely for generating drag during landing while producing no extra lift, as in those of the Spitfire fighter. Extending the free fingers could have added a little braking drag. As the feet get close to the ground, the wings' angle of attack is further increased to the point that the top airflow becomes too turbulent to generate lift, and the deliberately stalled animal drops the last very short distance to the ground.

Depending on various factors, including wind speed, the landing could be fairly static, with the feet contacting the ground and no further movement occurring, or it could include deceleration running for a short distance, as appears to be recorded by a pterosaur trackway (Mazin et al. 2009). In that example, the two feet made contact in parallel fairly close to one another, the toes dragged a little as the body bounced a bit, the feet made a second contact followed by the hands slightly out to the side, then another step with hands and forefeet, and then the pterosaur walked off. In a water landing, the webbed feet were used as water skis to help cushion the initial contact, as in waterbirds.

![](_page_28_Picture_2.jpeg)

Pteranodon feeding on fish and belemnite schools driven to the surface by the mosasaur Platecarpus (those and front pterosaur to same scale)

## **Respiration and Circulation**

The hearts of turtles, lizards, and snakes are three-chambered organs incapable of generating high blood pressures. Crocodilian hearts are incipiently four chambered but are still low pressure. Reptile lungs, although large, are internally simple structures with limited ability to absorb oxygen and exhale carbon dioxide. Although they have a dead end, the lungs of some lizards and crocodilians may have unidirectional airflow. Lizard and snake lungs are operated by straightforward rib action. Crocodilian lung ventilation is more sophisticated. Muscles attached to the pelvis pull on the liver, which spans the full height and breadth of the rib cage, to expand the lungs. This action is facilitated by an unusually smooth ceiling on the rib cage that allows the liver to easily glide back and forth. The presence of a rib-free lumbar region immediately ahead of the pelvis, and,

![](_page_29_Figure_4.jpeg)

Respiratory complexes of archosaurs

at least in advanced crocodilians, a mobile pubis in the pelvis– very unusual in tetrapods–enhances the action of the muscles attached to it.

Birds and mammals have fully developed four-chambered, double-pump hearts able to propel blood in large volumes at high pressure. Mammals retain fairly large dead-end lungs, but they are internally very intricate, greatly expanding the gas exchange surface area. The lungs are operated by a combination of rib action and the vertical, muscular diaphragm. The presence of the diaphragm is indicated by the existence of a well-developed, rib-free lumbar region, preceded by a steeply plunging border of the rib cage, on which the vertical diaphragm is stretched.

It is widely agreed that all dinosaurs very probably had fully four-chambered, high-capacity, high-pressure hearts (Paul 2002, 2012, 2016). Their respiratory complexes appear to have been much more diverse. Most researchers also agree that the theropod dinosaurs, especially the avepods ancestral to birds, evolved increasingly birdlike respiratory complexes. Birds have the most complex and efficient respiratory system of any vertebrate. Because the lungs are rather small, the chest ribs that encase them are fairly short, but the lungs are internally intricate so they have a very large gas-exchange area. The lungs are also rather stiff and set deeply into the strongly corrugated ceiling of the rib cage. The lungs do not dead end; instead, they are connected to a large complex of air sacs whose flexibility and especially volume greatly exceed those of the lungs. Some of the air sacs invade the pneumatic vertebrae and other bones, but the largest sacs line the sides of the trunk; in most birds the latter air sacs extend all the way back to the pelvis, but in some, especially in flightless examples, they are limited to the rib cage. The chest and abdominal sacs are operated in part by the ribs; the belly ribs tend to be extralong in birds with well-developed abdominal air sacs. All the trunk ribs are highly mobile because they attach to the trunk vertebrae via well-developed hinge articulations. The hinging is oriented at an angle that compels the ribs to swing outward as they swing forward, inflating the air sacs within the rib cage, and then the sacs deflate as the ribs swing backward and inward. In most birds the movement of the ribs is enhanced by ossified uncinate processes that form a series along the side of the rib cage. Each uncinate process acts as a lever for the muscles that operate the rib the process is attached to. In most birds the big sternal plate also helps ventilate the air sacs. The sternum is attached to the ribs via ossified sternal ribs that allow the plate to act as a bellows on the ventral air sacs, the sternum dropping to further inflate abdominal air sacs as the chest ribs swing forward. In those birds with short sterna, the flightless ratites, and in active juveniles, the sternum is a less important part of the ventilation system. Some Mesozoic birds with short sterna retained the dinosaurian gastralia between the pelvis and sternum, and these probably helped ventilate the abdominal air sacs.

The system is set up in such a manner that most of the fresh inhaled air does not pass through the gas-exchange portion of

the lungs but instead goes first to the air sacs, from where it is injected through the lungs in one direction on its way out. Because this unidirectional airflow eliminates the stale air that remains in dead-end lungs at the end of each breath and allows the blood and airflow to work in opposite, countercurrent directions that maximize gas exchange, the system is very efficient. Some birds can sustain cruising flapping flight at altitudes as high as Mount Everest, at 8,500 m (28,000 ft), and equaling those of jet airliners; more energy-efficient soarers can reach over 11,000 m (37,000 ft).

There is no reason to doubt that pterosaur hearts were fully four-chambered, high-pressure organs (Paul 2002, 2012; Witton 2013). Because the ancestors of pterosaurs are not documented, the evolution of their respiration cannot be detailed. What we do know is that their breathing apparatus appears to have paralleled or converged with, and combined features of, those of both birds and crocodilians, along with adaptations of their own (Paul 2002; Witton 2013). The birdlike attributes included the well-developed pneumatic complex in which abdominal air sacs helped ventilate the lungs, presumably with considerable unidirectional air flow. The small volume of the pterosaur body suggests that the lungs must have been small, as in birds, and possibly rigid. As for how the air sacs were ventilated, in basal pterosaurs the main ribs were fairly mobile, and they were joined to the sternum via mobile sternal ribs. This should have allowed the back end of the sternum to change the volume of the air sacs near that location, as in birds. But unlike in the latter, the extra ossified projections that improved the leverage of the respiratory muscles were not uncinate processes on the ribs; they were the sternocostapophysis projections on the sternal ribs. In derived pterodactyloids the ribs started fusing with the vertebrae, limiting and finally eliminating the ability of the ribs to operate the air sacs.

That is where the crocodilian aspect of pterosaur breathing comes in. The pterosaur pubis was not mobile as it is in crocodilians, but the unusual prepubis at the end of the pubis was movable. It probably acted like the crocodilian pubis to help change the volume of the abdomen (Witton 2013). In doing so, it would have ventilated the air sacs in that region in all pterosaurs, aided by the gastralia as in avepod theropods, including basal birds. Being predominantly like that of birds, the air sac-ventilated respiration of pterosaurs should have been almost or perhaps as efficient at oxygenating their blood.

But pterosaurs may have had an additional breathing apparatus, one that is not found in birds and is present in bats: the wings. In bats the ultrathin wing membrane makes up 85 percent of the animal's surface area and, perfused with blood vessels, may add a tenth or more to oxygen intake. In pterosaurs the top of the wing was probably sealed off by the actinofibers, but the dense layer of blood vessels under the membrane appears well suited for acting as auxiliary lungs.

Sporting avian-like respiration and bat-like wing lungs, pterosaurs should have been able to respire well enough to fly at extreme altitudes. Whether they could fly as high as birds we cannot know, but they may not have had to in view of the scarcity or absence of Mesozoic mountain ranges as tall as some are today.

Mammalian red blood cells lack a nucleus, which increases their gas-carrying capability. The red blood cells of reptiles, crocodilians, and birds retain a nucleus, so those of pterosaurs should have as well.

# Feeding Apparatus and Digestive Tracts

The beaks and conical teeth of most pterosaurs were adapted for grabbing and holding on to food items, which they would then have had to swallow whole. The simple spiky teeth could not reduce items, and their jaws were often too weakly built and muscled to do much food processing. A recent analysis has used tooth microwear patterns to help sort out what kinds of foods specific pterosaurs were chowing down on (Bestwick et al. 2020), and another focuses on the power of the jaws based on reconstructions of the bite muscles of various derived pterodactyloids (Pêgas et al. 2021; includes prior examinations of isotope ratios in teeth). These studies often affirm what is already thought, and in other cases the research may settle controversies-the results are integrated into the group and species descriptions herein. Tooth microwear has not vet demonstrated dramatic shifts in feeding style from juveniles to adults. It is possible that food items could have been held in the throat pouch, when present, for a time if there was not yet room in a full belly. The very large size of fish found in some body cavities, up to 60 percent of trunk length, shows that such pterosaurs could swallow enormous prey intact and let their digestive tract acids and enzymes take care of it (Witton 2013). Swallowing such big items would have required that the esophagus be very distensible, as it is in birds that swallow large prey whole. As well as fish, saltwater pterosaurs dined on unshelled cephalopods (Hoffman et al. 2020). A few early rhamphorhynchoid pterosaurs with multicusped teeth could chew prey and plant material to some extent; why this seemingly useful ability was quickly lost in the group is a mystery. Among Cretaceous pterodactyloids, the strong-jawed and exceptionally powerfully muscled dsungaripterids and perhaps chaoyangopterids could crush hard-shelled creatures. Tapejarids may have been able to do some food processing with their mouths, especially those with deeper skulls and more powerful jaw muscles. The teeth of istiodactylid predator scavengers were like animal traps and appear to have been able to cut up items before they were gulped down. Istiodactylid hyoids are similar to those of scavenging birds, which adds to the evidence that those pterosaurs fed on carcasses (Jiang et al. 2020). Filter-feeding pterosaurs used their combs of slender teeth to ingest very small items in very large numbers.

Because the abdominal regions of all pterosaurs were quite small, and because some of that internal space was occupied by air sacs lining the walls, pterosaur digestive tracts were always low in volume and short. Archosaurs are prone to having gizzards in about the middle of the digestive tract, after the stomach and before the intestines, and a wide variety, including many birds, deliberately seek out and swallow gizzard stones, or gastroliths, to help process food. The absence of such grit preserved with many pterosaur specimens indicates that such stones were not widely employed by members of the group. But they have been found within the flamingo-like filter-feeding *Pterodaustro*, the front teeth of which look as if they were strengthened for gathering up small gravel, which was then used to help grind up the small hard-shelled creatures it fed on.

The big fish found inside fossil pterosaurs could have powered the creatures for a day or more, so some pterosaurs did not necessarily have to constantly work hard to obtain sufficient sustenance. Any plant matter that pterosaurs consumed should have been relatively easy-to-digest components such as fruits and seeds, their digestive systems being too small to effectively process leaves. Fruit seeds have been found in the abdominal cavity of a tapejarid pterodactyloid.

Pellets that may have been retched up by pterosaurs suggest that they periodically unloaded indigestible items such as bones, as do some birds and cats; that the pellets contain bones indicates that pterosaur stomach acids were not extremely strong, as is true of birds. Unlike dinosaur fossil feces, or coprolites, which are fairly common, pterosaur examples are few. One had just been voided from a deceased individual. Pterosaur coprolites might be rare because their feces may have usually been too liquid and soft to readily fossilize, as is true of those of their avian relations. It is not surprising that the few other examples of pterosaur poop appear to be those of filterfeeding ctenochasmatid pterodactyloids found in association with their trackways; the feces are laden with a high density of hard bits of the small creatures they consumed (Qvarnström et al. 2019).

#### Pterosaurs as Food

For Mesozoic eaters of flesh, pterosaur necks, legs, and especially flight muscles would have been appealing meals, and a number of their skeletons show evidence of being bitten by large fish, sharks, marine reptiles, and dinosaurs (Witton 2013). Whether these particular specimens record scavenging versus predation is not determinable, but it is likely that both were involved. It is also likely that large predaceous and omnivorous pterosaurs picked up and put down smaller pterosaur species and juveniles, in some cases perhaps of their own species. Pterosaurs were very likely to have stolen food from other pterosaurs, again of their own species, when the opportunity arose—some birds such as sea eagles and frigate birds are frequent food stealers. Also on the menu of Mesozoic predators would have been pterosaur eggs and hatchlings, which is one reason many pterosaurs nested in isolated locations where there were few or no egg stealers.

### Senses

The usually large eyes and well-developed optical lobes characteristic of pterosaurs indicate that vision was their primary sensory system, as it is in all birds (Witton 2013). Bats are never blind; their vision ranges from poor to very well developed in some fruit bats. The poorly developed color vision of most mammals is a result of the nocturnal habits of early mammals, which reduced vision in the group to the degree that eyesight is often not the most important of the senses-the high-quality color vision of primates, humans included, is a mammalian anomaly. Reptiles and birds have full-color vision extending into the ultraviolet range, so pterosaurs almost certainly did as well. Reptile vision is usually as good as or better than that of mammals, and birds tend to have very high-resolution vision both because their eyes tend to be larger than those of reptiles and mammals of similar body size and because they have higher densities of light-detecting cones and rods than mammals. The cones and rods are also spread at high density over a larger area of the retina than in mammals, in which high-density light cells are more concentrated at the fovea (so our sharp field of vision covers just a few degrees). Some birds have a secondary fovea. Day-loving raptors can see about three times better than humans, and their sharp field of vision is much more extensive, so birds do not have to point their eye at an object as precisely as mammals to focus on it. Birds can also focus over larger ranges, 20 diopters compared to 13 diopters in young adult humans. The vision of the bigger-eyed pterosaurs, particularly the flying insect-pursuing anurognathids, may have rivaled this level of performance.

The pterosaurs' big eyes have been cited as evidence for both day- and night-dominant lifestyles. It is the structure of the retina and pupil (unknowable for pterosaurs) that determines the type of light sensitivity, but some researchers have used the differing configurations of the sclerotic rings to try to determine what some pterosaur eyes were optimized for. The results indicate that filter-feeding pterodactyloids were largely nocturnal, like some water-straining birds, and other pterosaurs had different light level preferences (Schmitz and Motani 2011), but these conclusions have been disputed. Not needing keen vision to see their food, some filter feeders look as if they had the smallest eyes among pterosaurs.

Birds' eyes are usually so large relative to the head that they are nearly fixed in the skull, so looking at specific items requires turning the entire head, although the larger retinal area of focus reduces this need. The same was likely to have been true of smaller-headed pterosaurs. Pterosaurs with larger heads should have had more mobile eyeballs that could scan for objects without rotating the entire head. Most pterosaurs' eyes faced to

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