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# Pterosaurs Were Monsters of the Mesozoic Skies

Fossils and mathematical modeling are helping to answer long-standing questions about these bizarre animals

BY MICHAEL B. HABIB

Credit: Chase Stone

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Evolution

The Mesozoic era, which spanned the time from 251 million to 66 million years ago, is often referred to as the age of dinosaurs. But although dinosaurs reigned supreme on land back then, they did not rule the air. Instead the skies were the dominion of an entirely different group of beasts: the pterosaurs.

Pterosaurs were the first vertebrate creatures to evolve powered flight and conquer the air—long before birds took wing. They prevailed for more than 160 million years before vanishing along with the nonbird dinosaurs at the end of the Cretaceous period, around 66 million years ago. In that time, they evolved some of the most extreme anatomical adaptations of any animal, living or extinct. The smallest of these aerial predators was the size of a sparrow. The largest had a wingspan that rivaled that of an F-16 fighter jet. Many possessed heads larger than their bodies, making them, in essence, flying jaws of death. Pterosaurs patrolled every ocean and continent on Earth. No animal in the Mesozoic would have been safe from their gaze.

Unlike dinosaurs, which are survived today by birds, pterosaurs left behind no living descendants. As a result, all that paleontologists know about pterosaurs comes from the fossil record. And that record has been frustratingly fragmentary, leaving us with just a glimmer of their former glory and a host of questions about their bizarre anatomy and ill fate. Paleontologists have scratched their heads over these mysteries for decades. Now new fossil discoveries, combined with mathematical modeling methods in which anatomical structures are simplified just enough that equations of physical properties can be applied to get best estimates of strength, weight, speed, and so forth, are finally generating insights. And what scientists are finding is that pterosaurs were even more extraordinary than we ever imagined.

## WINGED LEVIATHANS

One of the enduring mysteries of pterosaurs is how the largest members of this group became airborne. Giants such as *Quetzalcoatlus*, first discovered in Texas, and *Hatzegopteryx*, from modern-day Romania, stood as tall as a giraffe and had wingspans of more than 30 feet. These animals possessed jaws twice the length of those belonging to *Tyrannosaurus rex*. Their upper arms would have been nearly as large around as the torso of an average-sized adult human. They were true behemoths, attaining weights exceeding 650 pounds. For comparison, the largest bird to ever take to the air—*Argentavis*, living six million years ago in Argentina—most likely weighed less than 165 pounds.

The discrepancy between the biggest members of each of these groups is so vast, in fact, that multiple researchers have suggested that the largest pterosaurs could not fly at all (although this would be puzzling given their many anatomical adaptations for flight). Others have suggested that they could fly but only under very special air and surface conditions—if the atmosphere in their day were denser than it is today, for instance. After all, it seems unfathomable that birds of such sizes could fly. In fact, recent power-scaling studies from several researchers, including me, have demonstrated that supersized birds would have insufficient power to launch themselves into the air in the first place.

But pterosaurs were not birds. Indeed, over the past decade my colleagues and I have carried out numerous calculations of pterosaur launch and flight power, showing not only that giant pterosaurs could launch and fly but also that they probably did not need any special circumstances to do so. In line with these conclusions, we now know from geochemical analyses of sedimentary rocks and microanatomical analyses of plant fossils that air and surface conditions in the Late Cretaceous—the heyday of enormous pterosaurs—were not remarkably different from what we experience today. What was different, and unique, was the anatomy of pterosaurs.

There are three things that an animal needs to be able to fly at gigantic sizes. The first is a skeleton with a very high ratio of strength to weight, which translates to a skeleton with large volume but low density. Pterosaurs and birds both have such skeletons: many of their bones are quite hollow. The walls of the upper arm bone of *Quetzalcoatlus*, for example, were about 0.12 inch thick—comparable to an ostrich eggshell—yet the bone had a diameter of more than 10.5 inches at the elbow.

The second thing that a giant flier needs is a high maximum lift coefficient. This number describes how much lift the wings produce for a given speed and wing area. At a high lift coefficient, an animal can be heavier because its wings will support more weight at a lower speed. This relation, in turn, means the creature needs less speed on takeoff, which makes a huge difference in the muscle power required for launch. Membrane wings, such as those of pterosaurs and bats, produce more lift per unit speed and area than the feathered wings of birds. This additional lift improves slow-speed maneuvering capability, which for small animals helps with making tighter turns and for big animals facilitates takeoff and landing.

The third and most important prerequisite is launch power. Even with very efficient, large wings, a big flier still needs to produce lots of leaping power to become airborne. Flying animals do not flap their way into the air or use gravity to take off from an elevated location such as a cliff. Wings do not produce much lift at low speeds, and gravity launching would mean trying to take off by accelerating in the wrong direction—a dangerous prospect. Instead, a powerful jump provides critical speed and height to begin flight. Increased leaping power yields better launching power. Large fliers therefore need to be good jumpers.

Many birds can manage impressive leaps. They are constrained by their heritage as theropod dinosaurs, however: like their theropod ancestors, all birds are bipedal, meaning they have only their hind limbs to use for jumping. Pterosaurs, in contrast, were quadrupedal on the ground. Their wings folded up and served as walking, and therefore jumping, limbs. Numerous exquisitely preserved fossil trackways confirm this odd aspect of pterosaur anatomy. Being quadrupedal drastically changes the maximum size of a flying animal. Pterosaurs could use not only their hind limbs for launch but also their much larger forelimbs, thereby more than doubling the available power for takeoff. They had the perfect combination of adaptations to become aerial behemoths.

Previous studies have modeled bipedal launches for giant pterosaurs. For example, in 2004 Sankar Chatterjee of Texas Tech University and his colleague worked out how *Quetzalcoatlus* could propel itself into the air using only its hind limbs. But the researchers determined that for that approach to work, the animal could not weigh more than 165 pounds and had to run downhill into a headwind. The quadrupedal launch allows for more realistic body weight and less restrictive environmental conditions.

## HEAVY-HEADED

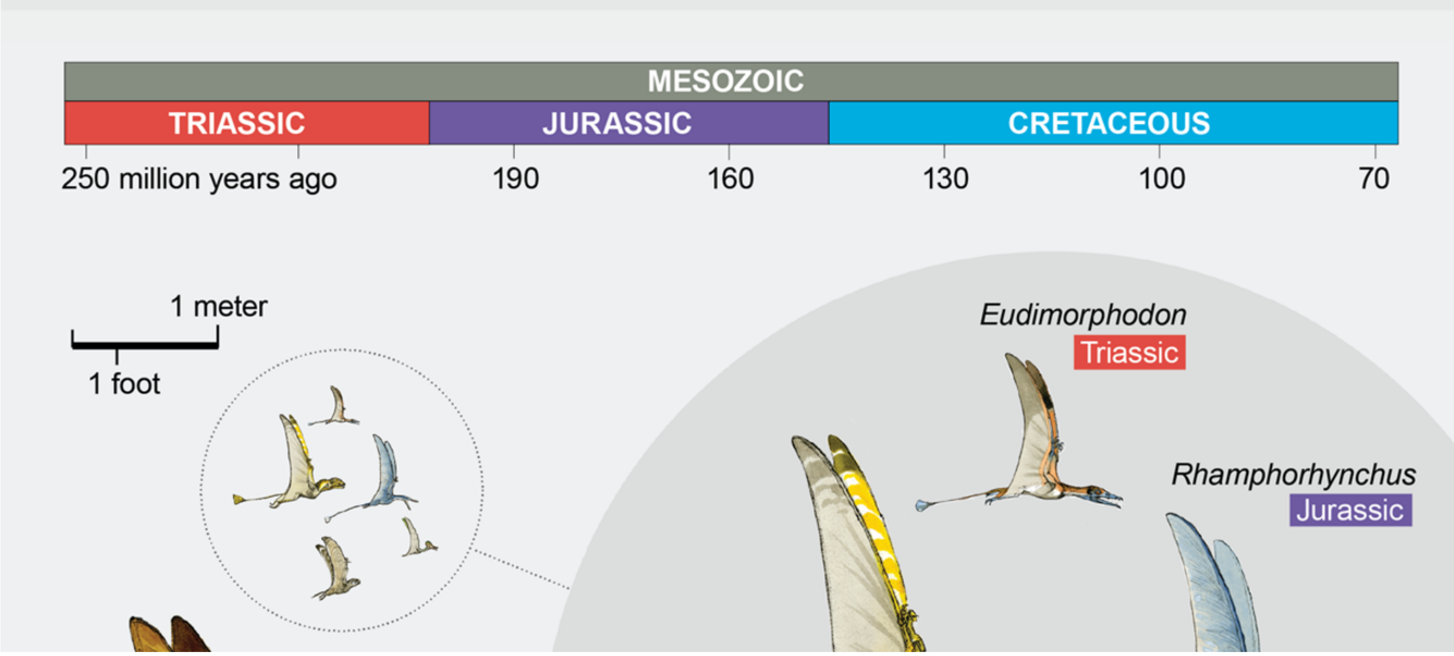
Although the great mystery of overall pterosaur size may finally be largely resolved, the relative sizes of their body parts continue to vex researchers. The proportions of pterosaurs are downright bizarre. All pterosaurs had oddly proportioned limb elements. Their hands, for example, are probably the most specialized in all of the vertebrate world, with an immense fourth finger that supported the wing. Yet this is not especially surprising in and of itself because that unusual hand was intrinsic to the pterosaur wing and the animal's ability to fly. What really confuses scientists and enthusiasts alike is not the wings of pterosaurs but the heads.

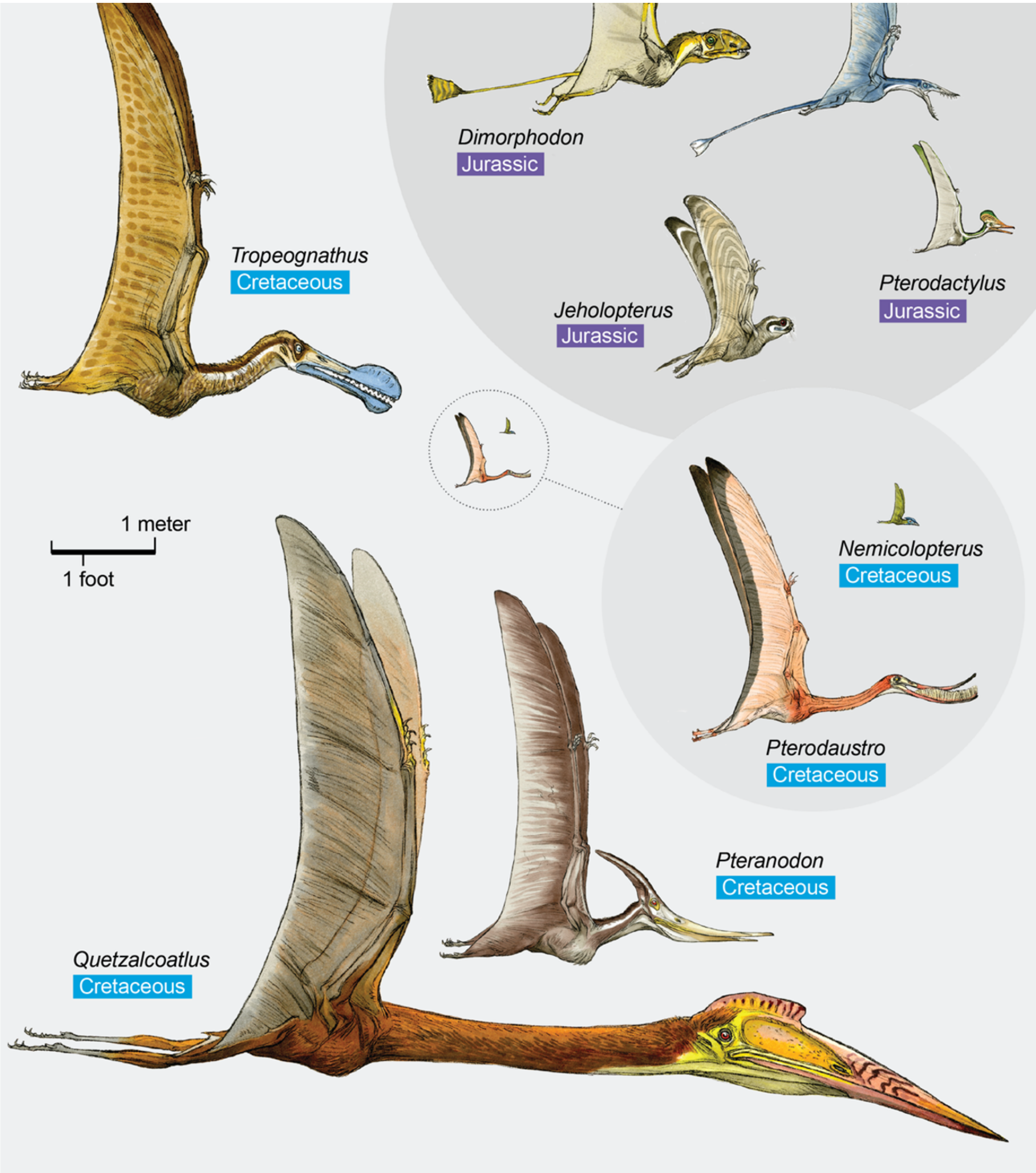
Even early pterosaurs had decidedly large noggins. The head on *Rhamphorhynchus,* a representative species from 150 million years ago, in the Late Jurassic period, was nearly as long as its body. Then in the Cretaceous head size got even more extreme. Fossils of species such as *Quetzalcoatlus,* as well as *Anhanguera* from Brazil, show that pterosaurs got bigger on average, but their heads became proportionately gigantic. The skull on a rather typical

Cretaceous pterosaur might be two or even three times the body length (usually taken as the distance between the shoulder and hip). Some had skulls surpassing four times the length of their bodies. The braincases on these animals were not terribly large, though. It is mainly the faces and jaws that expanded to an outrageous degree. Bony flanges under the jaw, towering crests atop the cranium and other elaborations further exaggerated pterosaur skull anatomy. In all, the head could almost seem like it was from a different animal than the body.

## Going Big—and Weird

All pterosaurs had strange proportions. Their hands were highly modified to support wings, and their heads were large relative to their bodies. Later pterosaurs evolved even more extreme body plans with proportionately gigantic heads. In some forms from the Cretaceous period, such as *Quetzalcoatlus*, the head and neck could make up more than 75 percent of the animal's total length. Ultimately the pterosaurs' tendency to grow large may have contributed to their demise at the end of the Cretaceous.






Credit: Terryl Whitlatch; Source: FLYING MONSTERS, DESIGN STUDIO PRESS

The oddities do not end there. Whereas in most animals, including humans, the bones of the neck are among the smallest in the spine, the neck vertebrae in pterosaur specimens are often the largest. In fact, the neck vertebrae are often twice the volume of the vertebrae in the torso. One of the newest additions to the pterosaur family tree offers a great example of this trend. David Hone of Queen Mary University of London, François Therrien of the Royal Tyrrell Museum in Alberta, Canada, and I will soon unveil fossils from this species, found in Alberta, in a paper in press at the *Journal of Vertebrate Paleontology*. We have given it a name that means "frozen dragon of the north," which is officially a reference to where it was found but reflects personal inspiration by the *Game of Thrones* dragon Viserion. It has neck vertebrae that are nearly as long and twice as strong as its humerus, the wing bone to which most of the flight muscles attach and that does most of the work to keep the animal up in the air. In some species the neck is triple the length of the torso, with the head size triple again, such that the head and neck could make up more than 75 percent of the total length of the pterosaur. Why would any animal be so ridiculously proportioned? And how could such a body plan possibly work for a flying creature?

Specialists are still working out why pterosaurs ended up with such crazy anatomy, but one probable explanation is what I call the "if it were easy, everyone would do it" hypothesis. In short, having a big set of jaws to eat with and a big face with which to signal to mates and rivals might be a great option for a lot of animals if the costs associated with these traits were not normally so prohibitive. For example, mammals have big braincases, so mammal heads become very heavy as they grow larger in overall dimensions. Pterosaurs might have stumbled into a developmental zone where the proportions of the face were less coupled to those of the back of the skull. This would have allowed them to evolve a giant set of jaws without having a huge braincase.

Pterosaurs also had extra openings in their skulls, the largest of which was an opening in front of the eyes known as an antorbital fenestra. Dinosaurs had this opening, too, but pterosaurs took it further, in some cases evolving an opening so large that the torso skeleton could have fit inside it. This opening would have been covered with skin and other tissues in life and probably would not have been visually obvious, but it made the skull quite light relative to its volume. The bones of the skull might also have had large air spaces within them, similar to the air-filled skull bones of some living birds.

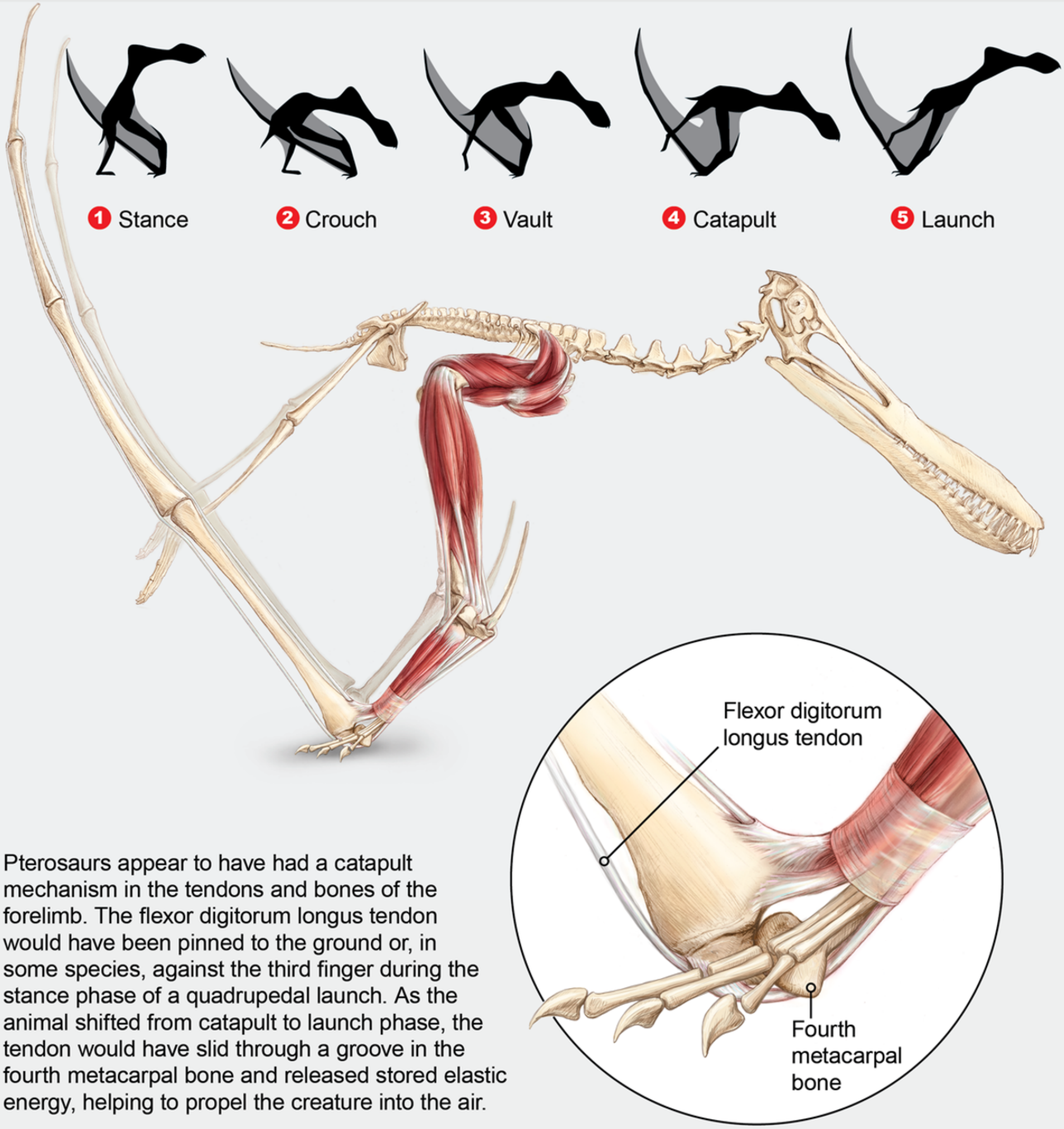
Even with these weight-saving features, however, pterosaurs' heads were often so colossal that they still would have been quite heavy. Perhaps counterintuitively, the fact that they were flying animals may have worked in their favor in this regard. The main problem with a heavy head is not the overall increase in body weight. Rather it is the disproportionate effect that the skull weight has on the animal's center of gravity. A huge head, especially if mounted on a huge neck, moves the center of gravity quite far forward. For a typical walking animal, this creates a serious problem with gait: the forelimbs have to move into an awkward forward position for the animal to be balanced. But pterosaurs had enormous forelimbs purpose-built for flight.

Gait reconstructions by Kevin Padian of the University of California, Berkeley, have shown that when a pterosaur was walking, those forelimbs were positioned just about right to take up the weight of the head, neck and chest. Most of the propulsion during walking came from the legs, so pterosaurs could hold the weight of their hefty heads on their extrabulky arms and push themselves along with their much more normal-sized hind limbs. Imagine using crutches to walk while minimizing the weight on both legs—you would advance both crutches simultaneously and let them bear all your weight, then swing your legs forward between them, touch down and repeat. This is what the gait would have looked like for the longest-armed pterosaurs. (During takeoff, incidentally, the legs would have pushed first, followed by the arms, for a perfect one-two push-off.)

This arrangement would not have made for the most efficient walking gait, but it was doable. And anyway, pterosaurs traveled primarily by flying. Pterosaur species with especially long, narrow wings, like those of some modern seabirds, might have flown continuously for months or even years, touching down only to mate or lay their eggs. The pterosaur *Nyctosaurus* may have had the most efficient wings—and thus the longest continuous soaring flight—of any vertebrate animal ever.

## Up and Away

The largest pterosaurs had clear adaptations to flight but probably weighed upward of 600 pounds—far more than the largest known flying birds. How did such behemoths become airborne? Unlike birds, which walk and jump into the air using only their hind limbs airborne? Unlike birds, which walk and jump into the air using only their hind limbs, pterosaurs walked on all fours, as evidenced from fossil trackways. Mathematical modeling indicates that launching from a quadrupedal stance—pushing off first with the hind limbs and then with the forelimbs—would have provided the leaping power that giant pterosaurs required for takeoff. Unlike a bipedal launch, a quadrupedal launch would have leveraged the powerful flight muscles and a catapult mechanism in the forelimb.




Pterosaurs appear to have had a catapult mechanism in the tendons and bones of the forelimb. The flexor digitorum longus tendon would have been pinned to the ground or, in some species, against the third finger during the stance phase of a quadrupedal launch. As the animal shifted from catapult to launch phase, the tendon would have slid through a groove in the fourth metacarpal bone and released stored elastic energy, helping to propel the creature into the air.

Credit: Julia Molnar

In the air, the center-of-gravity problem becomes much easier to deal with. For an animal to be stable in the air, its center of lift and center of gravity must be in alignment. This might seem like a difficult prospect for a creature with a supersized head and a correspondingly forward center of gravity. But a pterosaur's center of lift was close to the front of a wing, which means that the animal needed only to angle its wings moderately forward from the root to align the center of lift with the center of gravity, as Colin Palmer of the University of Bristol in England and his colleagues were first to point out. Forward-swept wings can themselves be sources of instability, but the flexibility of pterosaur wings and the rapid cerebellar reflexes that all vertebrate creatures possess could have compensated for it.

Stability challenges aside, forward-swept wings can offer some serious benefits. One is that their tips tend to be the last part of the wing to stall. During a stall, which typically occurs at low speed, the wing suddenly loses much of its lift. Tip stall is especially catastrophic because it quickly disrupts the wake of the wing, severely compromising thrust and control, and sharply increasing drag. The ability to delay that loss of lift makes landing and takeoff much gentler, which is important for big animals. In this sense, a giant head could actually be advantageous for a large flying animal with flexible wings: it moves the center of gravity forward, which moves the wing sweep forward, which makes it harder to stall the wing, which means the animal can fly more slowly and grow larger.

## DEATH OF A DYNASTY

Pterosaurs were the only vertebrates with powered flight for about 80 million years. Then around 150 million years ago, in the Jurassic period, a second group of backboned animals started to take wing: feathered dinosaurs. This group included four-winged creatures such as *Microraptor* and *Anchiornis*, as well as the most accomplished fliers of the bunch: birds. By the Early Cretaceous, a wide variety of birds shared the skies with pterosaurs. Despite this shakeup in the aerial niche, pterosaurs continued to dominate among the medium to large fliers, particularly in open habitats. Birds were mainly restricted to vegetated areas where their small body size and agility were advantageous. Pterosaurs were thus able to maintain supremacy as the rulers of the open sky.

But when an asteroid crashed into Earth 66 million years ago, killing all the nonavian dinosaurs, the pterosaurs' reign also came to a close. Paleontological discoveries so far indicate that not a single pterosaur species made it across the End Cretaceous boundary; they all perished, as did the majority of birds. Only one lineage—the neornithines, or "new birds"—made it through. (Nevertheless, that single lineage was enough. It went on to produce thousands on thousands of new species, and today neornithine birds represent the second-largest group of vertebrates, behind only the bony fish, with more than 12,000 recognized species.)

Why did pterosaurs suffer a fate worse than that of the birds at the end of the Cretaceous? One reason might be their tendency to grow large. Hardly any land animals with an adult body mass of more than 44 pounds survived that apocalyptic time. And being not only large but also volant might have been particularly costly, because big fliers tend to rely on soaring flight for much of their travel. Soaring is dependent on the right weather conditions. When the asteroid struck, it vaporized part of Earth's crust, along with much of itself, and the reentry of this superenergized rock-metal cloud essentially set the sky on fire around the world. Soaring experts such as Jim Cunningham, an independent industry engineer with decades of experience with aircraft design, have pointed out that global soaring conditions might well have been ruined for a month after the impact—enough time to starve every pterosaur that needed to soar to eat.

Clearly, just being a small flier did not cut it either, given that most birds perished as well. The ones that survived might have been able to eat foods that could withstand a nuclear-style winter, such as seeds. They might also have been able to burrow out of harm's way, just as many modern-day birds do. Pterosaurs do not seem to have been seed specialists, nor do they appear to have been capable of burrowing. And why should they have been? A dinosaur-munching, 14-foot-tall, flying monstrosity does not need to dig its way out of danger—it *is* the danger.

Although it ends with extinction, the story of pterosaurs is one of success: they were the ultimate aerial giants, having evolved a dazzling array of extraordinary anatomical features not seen in any other group before or since. From them we have learned much about the limits of animal form and function. Those lessons help us understand the history of Earth and the complexity of ecology. They are even inspiring new technologies, including novel aircraft designs. Their fossil record is a thrilling window into a bygone world filled with real flying monsters. Pterosaurs were not just extreme—they were exceptional.

**MORE TO EXPLORE**

**On the Size and Flight Diversity of Giant Pterosaurs, the Use of Birds as Pterosaur Analogues and Comments on Pterosaur Flightlessness**. Mark P. Witton and Michael B. Habib in *PLOS ONE*, Vol. 5, No. 11, Article No. e13982; November 2010.

**The Wingtips of the Pterosaurs: Anatomy, Aeronautical Function and Ecological Implications**. David W. E. Hone, Matt K. Van Rooijen and Michael B. Habib in *Palaeogeography, Palaeoclimatology, Palaeoecology*, Vol. 440, pages 431–439; December 2015.

***Cryodrakon boreas*Gen. et Sp. Nov. a Late Cretaceous Canadian Azhdarchid Pterosaur**. David W. E. Hone, Michael B. Habib and François Therrien in *Journal of Vertebrate Paleontology* (in press).

**FROM OUR ARCHIVES**

**Giants of the Sky**. Daniel T. Ksepka and Michael Habib; April 2016.

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More by Michael B. Habib


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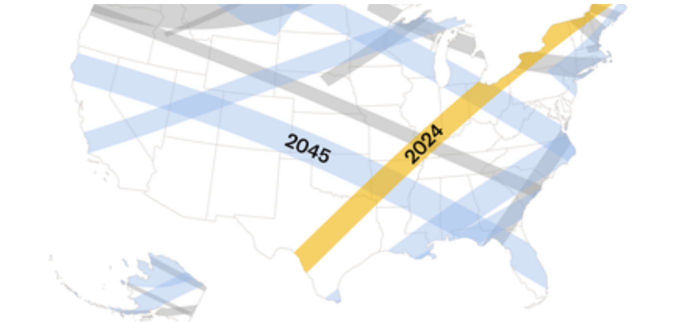


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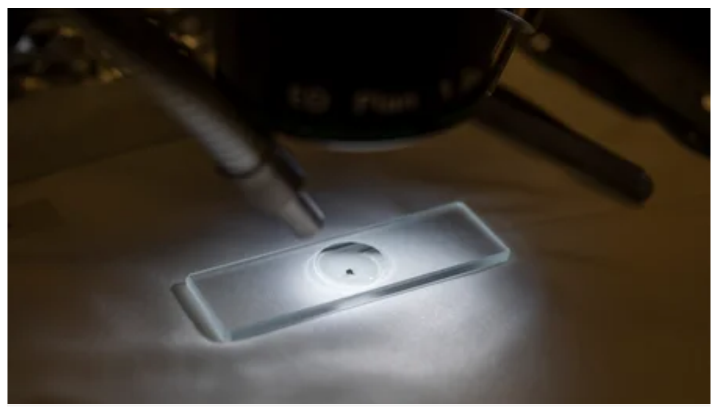

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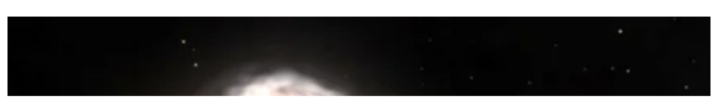

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