Pterosaurs

Neither dinosaurs nor birds, these creatures were flying reptiles that endured for 135 million years. The ones with wingspans of 12 meters are thought to have been the largest animals ever to fly

by Wann Langston, Jr.

Few prehistoric animals have captured the imagination so completely as have the flying reptiles known as the pterosaurs. Extinct for the 64 million years that have passed since the end of the Mesozoic era, these dragons of the air have nonetheless figured prominently in man's view of the earth's distant past ever since Arthur Conan Doyle made them part of *The Lost World*. For almost two centuries paleontologists have been puzzling over the fossil remains of the pterosaurs, and surely others have wondered how the pterosaurs resolved the problems of powered flight. Hang-gliding enthusiasts might well be curious, because the larger pterosaurs weighed about as much as a human hang-glider pilot.

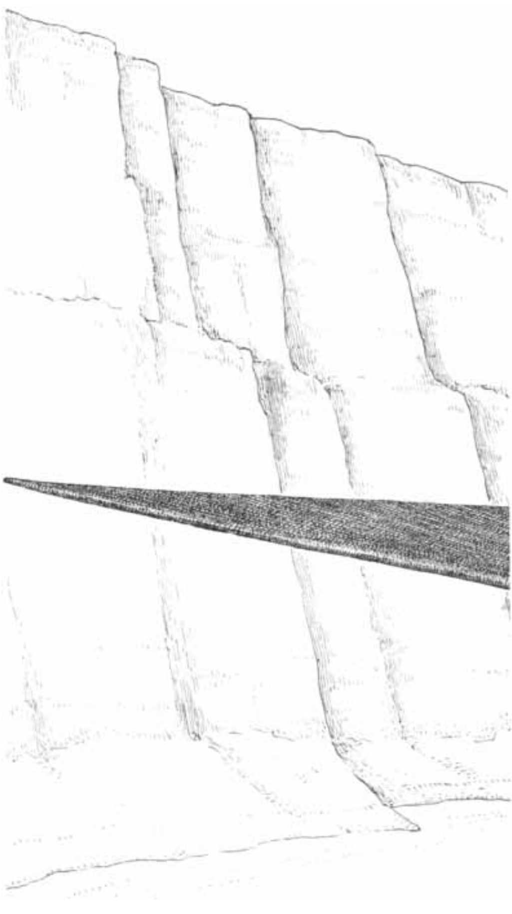
Until recently it was thought that pterosaurs with wingspans as great as eight meters represented the maximum size for flying animals. Nine years ago, however, Douglas A. Lawson, then a student at the University of Texas at Austin, discovered a number of wing bones from an unknown species of pterosaur in the Big Bend National Park in West Texas. The bones were surprisingly large. The radius, a forearm bone, was almost complete. It was nearly three-quarters of a meter long. No additional remains of this animal, named *Quetzalcoatlus northropi* after the Aztec god who took the form of a feathered serpent, have come to light since then, but bones of smaller, quite similar pterosaurs have been found in another part of the park. These further discoveries allow a hypothetical reconstruction of *Quetzalcoatlus* that gives it a wingspan of 11 to 12 meters. *Quetzalcoatlus* may thus have been the largest creature ever to fly. Although the Texas pterosaurs are still imperfectly understood, I shall review here what is known about them today. The subject can best be approached in the context of what is known (or suspected) about the pterosaurs in general.

Perhaps the least controversial assertion about the pterosaurs is that they were reptiles. For one thing, their skull is reptilian, including the shape of the teeth. For another, the pelvis and hind feet are those of a reptile. It seems clear, however, that in their adaptations to flight the pterosaurs departed so far from the reptiles popularly known as the dinosaurs that no investigator would now confuse them with either of the two dinosaurian orders. The pterosaurs and the dinosaurs appear to have evolved on divergent paths from earlier forms of reptilian life.

It also seems clear that the pterosaurs did not evolve into the birds. In this regard the telltale anatomy is that of the wing. In a pterosaur the fourth finger of each forelimb was greatly elongated. It supported the front edge of a membrane that stretched from the flank of the body to the farthest tip of that finger. The other fingers were short and reptilian, with a sharp claw at the end of each one. In a bird it is the second finger that is the principal strut of the wing, and in the bird much of the extent of the wing consists of course of feathers.

Although the fossilized remains of pterosaurs have been found on every continent except Antarctica, most pterosaur fossils come from the chalk deposits of western Kansas, from certain sedimentary strata in England and particularly from the Solnhofen limestone of Bavaria, a fine-grained rock laid down in a quiet lagoon during the Mesozoic era and used by man for lithography throughout the past few hundred years. The first pterosaur fossils were found in a limestone quarry near the Bavarian village of Eichstätt. Their discovery was reported in 1784 by Cosimo Collini, a former secretary to Voltaire. The fossils plainly included a winglike structure. Nevertheless, Collini conceived them to represent an amphibious mammal. Similar misconceptions persisted. Indeed, even after Georges Cuvier, the 19th century master of comparative anatomy, pronounced what he called the "ptero-dactyle" (literally wing-finger) to be a flying reptile, some of his contemporaries continued to regard the pterosaurs as bats, birds or flying marsupials. In 1830 Johann Wagler, a German zoologist, linked the pterosaurs to extinct marine reptiles. He considered them intermediate between mammals and birds. His reconstruction showed a swimming creature with penguinlike wings and rudder-shaped feet.

The modern consensus that the pterosaurs are flying reptiles was established by the turn of the century, and the pterosaurs are now regarded by most investi-



PTERANODON, a pterosaur of the Cretaceous period, which lasted from 135 through 64 million years ago, is depicted in flight. The

gators as making up an order of reptiles: the Pterosauria. Roughly 85 species are known. They are arranged in two suborders. The older suborder, the Rhamphorhynchoidea, appears abruptly in the fossil record in 200-million-year-old Triassic limestone in northern Italy. The distinguishing features of the Rhamphorhynchoidea are many. They had a short face and a short neck. In the wing the wrist was short and the fourth finger was long. The animal had a long tail. The Rhamphorhynchoidea included some of the smallest pterosaurs, which were roughly the size of a sparrow.

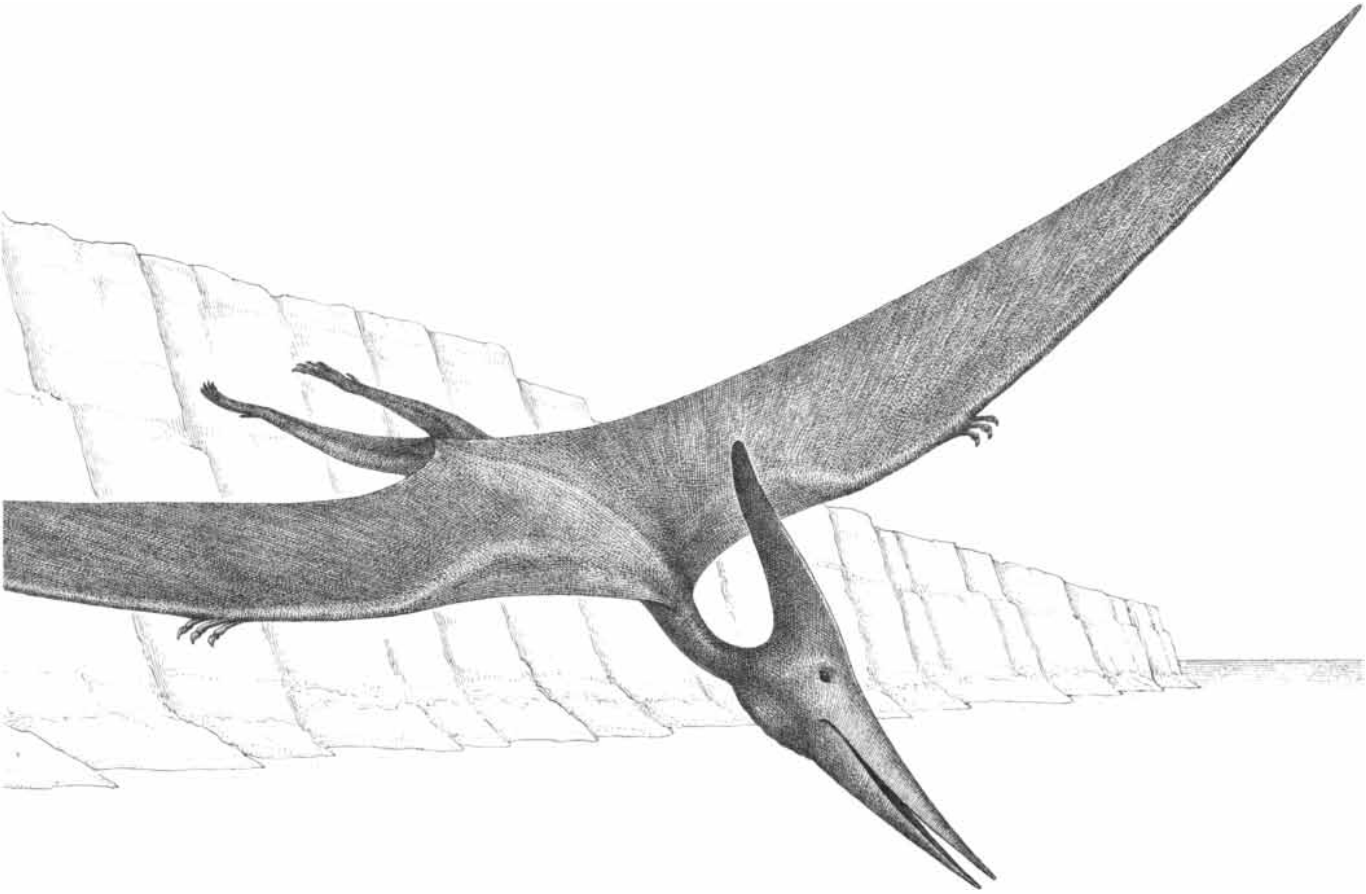
The other suborder, the Pterodactyloidea, appears just as abruptly in the late Jurassic, about 50 million years later. These animals were distinguished by a long face and a long, curved neck. Both the wrist and the fourth finger contributed impressively to the length of the wing, and some of the species were exceptionally big. *Quetzalcoatlus* was a pterodactyloid. The Pterodactyloidea were almost tailless. The sudden appearance of both suborders of the pterosaurs without any obvious antecedents is fairly typical of the fossil record. It emphasizes the random nature of discoveries in paleontology.

The pterosaurs resembled both birds and bats in their overall structure and proportions. In a way this is not surprising. The design of any vertebrate animal that flies is subject to aerodynamic constraints. A more detailed examination reveals both similarities and differences. For one thing the pterosaurs had hollow bones. No doubt this represented a saving in weight. Birds too have hollow bones, but they usually are reinforced more massively by internal struts. In pterosaurs as in birds the fusion of various bones limited the flexibility of the trunk. Movable joints were few, particularly in the wings and the ankles, the places where the stresses on the body were great. The long tail of the rhamphorhynchoids was stiffened by long, overlapping outgrowths of the vertebrae, and other vertebral outgrowths limited the sideward bending and twisting of the neck of the great pterodactyl called *Pteranodon*.

Many pterosaurs had a ridge or crest on their skull. The crest was most extreme in *Pteranodon,* where in some species it doubled the length of the head. The function of the crest is a puzzle. It surely had an effect on the aerodynamics of the animal; experiments with models of the head in a wind tunnel suggest that when it was turned at a right angle to the direction of the animal's flight, it increased the drag. The crest thus may have been an air brake for landing. It also could have served as a front-end rudder to offset the lack of a tail. Further, it may have helped to balance the long beak and in that way allowed a reduction in the mass of the neck muscles.

Other large pterosaurs seem, however, to have managed without a crest. Moreover, the interlocking of the neck vertebrae in *Pteranodon* may have kept the animal from rotating its head to any great degree. Finally, some *Pteranodon* skulls lack a crest. If this is a natural condition and does not merely reflect the imperfect preservation of the fossils, the crest may have been a sexual characteristic. Whether it would then have adorned the male or the female cannot be guessed.

The most remarkable evolutionary adaptation in the structure of the pterosaurs was of course the wing. In its fundamental design it resembled the forelimb of a tetrapod: an animal that goes on all fours. Here, however, the



animal has employed the updraft along a cliff to gain altitude, then turned in a glide toward the sea to search for fish. It is thought to have flapped its wings only slowly and infrequently. The crest on the back of the head could have been an air-control surface; the crest may thus have offset the lack of a tail. The wingspan of a big pteranodon was as much as seven meters, making it large among the pterosaurs.

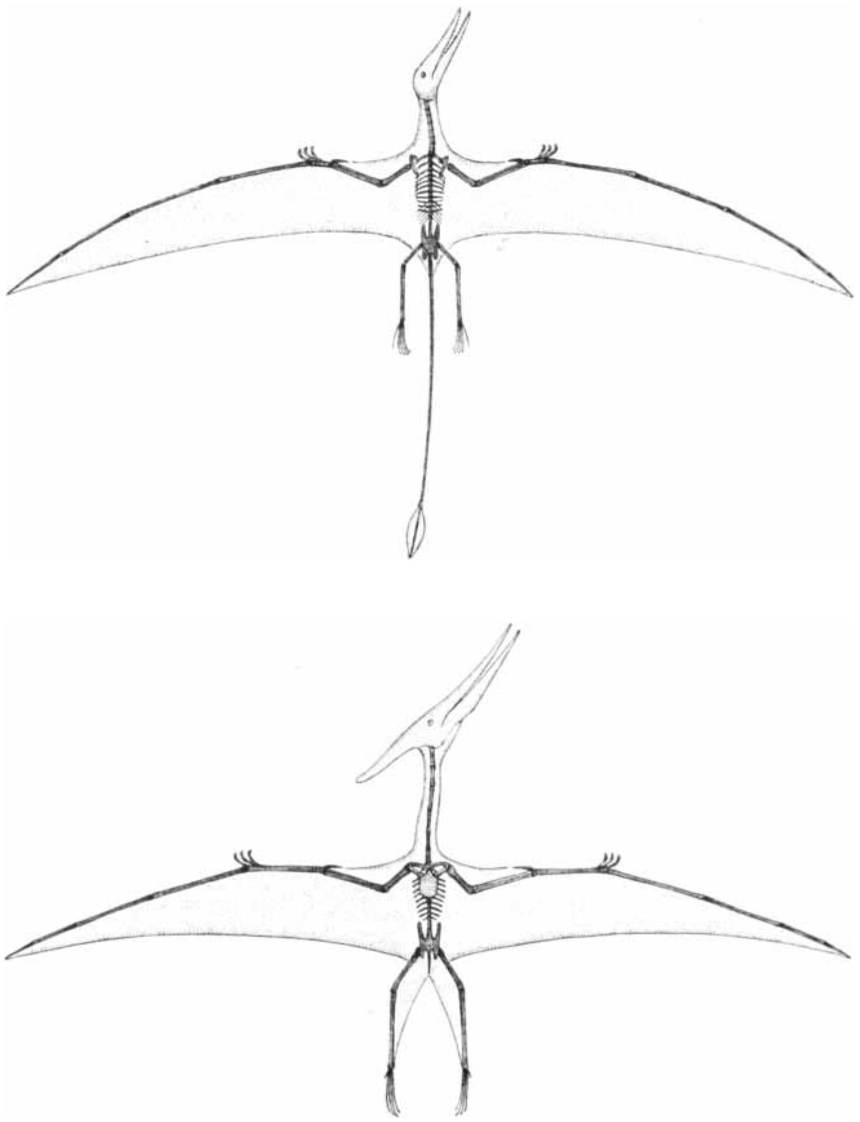
greatly elongated fourth finger had become a long, slender wing spar. The wing was attached to the trunk of the pterosaur by a massive shoulder girdle: a bony ring consisting of the scapula, or shoulder blade, the sternum, or breastbone, and a third bone, the coracoid. In the smaller pterosaurs the girdle roughly resembled the one in a bird. The main difference was the absence of a fourth bone, the wishbone or furcula. Typically, however, the scapula and the coracoid were fused, and in the larger species the scapula no longer lay loosely embedded in the muscles along the flank of the animal, a position typical of the scapula in all the tetrapods except the turtles. Instead the scapula was a massive rod turned inward. At the midplane of the body the top of the scapula was inserted into the notarium, a bony bar unique to the largest pterodactyls. The notarium was formed by the fusion of several of the vertebrae.

Many of the pterosaur fossils that lie in fine-grained sediments include impressions of the wing membrane, which extended from the tip of the fourth finger to the side of the trunk, at least in the rhamphorhynchoids. The membrane was reinforced internally by long, thin, closely spaced collagenous fibers that probably prevented sharp bending of

FOSSIL REMAINS of the sparrow-size pterosaur *Pterodactylus elegans* lie in limestone from Solnhofen in West Germany. The limestone solidified from sediment that lay at the bottom of a lagoon some 150 million years ago, in the late Jurassic period. The attitude of the skeleton is unnatural. For example, both wings extend toward the left and then fold under the rib cage. Apparently the carcass of the animal dried out on a beach before it drifted to the place where it finally sank. In addition to fossilized pterosaurs the Solnhofen limestone has yielded fossils of small dinosaurs and of the first known bird, *Archaeopteryx*. The stone has been used for centuries for lithographic printing. The specimen of *Pterodactylus elegans* shown here is from the collection of the American Museum of Natural History.

the outer part of the wing. Additional fibers were arrayed toward the trailing edge of the wing, where they could decrease the wing membrane's fluttering. The fibers were slightly arched in a fore-and-aft direction, thereby contributing to the camber, or upward-directed convexity, of the pterosaur's airfoil. The fourth finger was stretched out by a long, slender tendon running from a muscle in the inner wing (the homologue of a tetrapod's upper arm) to a bony, elbowlike outgrowth on the first segment of the fourth finger.

Adding to the area of the wing was a triangular membrane that stretched forward from the wrist to the base of the neck. The triangle was supported at the wrist by a uniquely pterosaurian innovation, the pteroid bone, which evidently was a place of attachment for a tendon and a muscle that held the membranous triangle taut and braced the wing in front. It is known from well-preserved specimens that some rhamphorhynchoids had a vertical flap of skin at the end of their tail. This was clearly some kind of rudder that must have enhanced the animal's maneuverability in flight. It could also have served in water if the rhamphorhynchoids were swimmers.



TWO SUBORDERS of the order Pterosauria are compared. The Rhamphorhynchoidea (*top*) had wingspans ranging from .4 to 2.2 meters. The face and neck were short; the tail was long. Each hind limb had five long toes. The Pterodactyloidea (*bottom*) had wingspans as great as 12 meters. The face was long; the neck curved. There was almost no tail. Fifth toe was rudimentary.

Three other aspects of the pterosaur's anatomy deserve separate mention. The first is the pterosaur's hand, or rather the three digits of the hand that projected outward from the wing. If the pterosaurs walked on all four limbs, the hand may have been employed for grasping. Gorillas walk, however, with their fingers folded against the palm of the hand; in other words, they walk on their knuckles. The pterosaur may have done much the same. It may, however, have been a biped. In any case the long fourth finger was folded out of the way by means of a joint at the base of that finger when the pterosaur walked. The joint allowed the fourth finger, and with it the wing, to turn upward along the side of the animal's body.

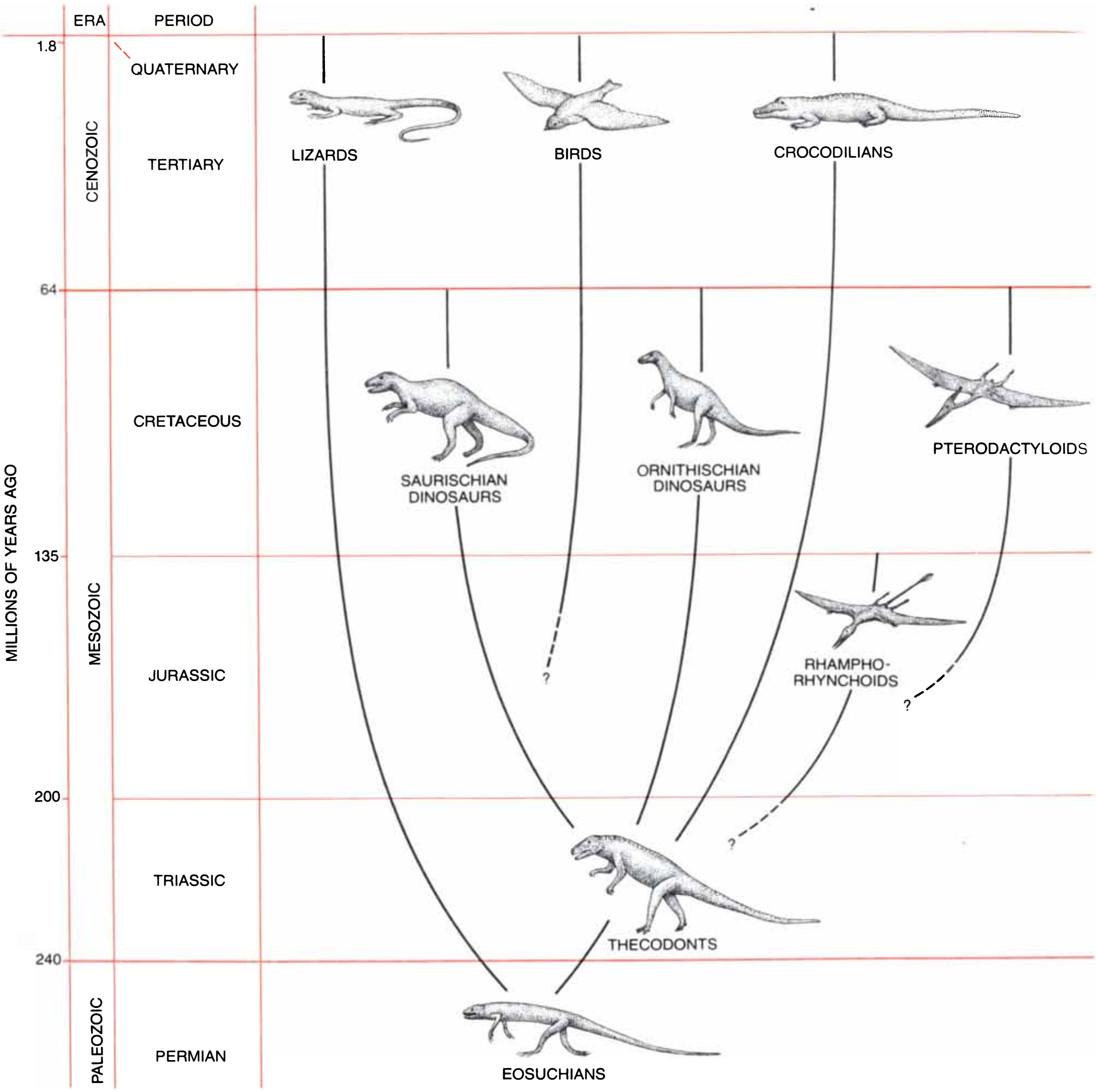
The second notable aspect of the pterosaur's anatomy is the brain of the animal. In this regard an analysis of endocranial casts is illuminating. The casts form when sediment fills the cranial cavity of a skeleton during its fossilization. They therefore suggest the surface features of the brain. Perhaps the best example of a pterosaur endocast was discovered in Jurassic rock in northern England late in the 19th century. The specimen is only 25 millimeters long. It nonetheless shows that the cerebellum was substantially larger in relation to the size of the animal than it is in reptiles that do not fly. Indeed, the floccular lobes of the cerebellum were larger than they are in birds of comparable size today. This suggests a high level of muscular coordination. More specifically, it suggests maneuverability in flight, takeoff and landing.

The olfactory bulbs of the brain were small. This suggests that the animal's sense of smell was poor; thus the pterosaurs did not rely on smell for hunting. In contrast, the optic lobes were well developed. Hence the animal's eyesight was good; doubtless the pterosaurs used vision for hunting and navigation. Moreover, they were probably active in daylight. Overall, the encephalization quotient of the pterosaur—the ratio of the volume or weight of its brain to that of the brain of an earthbound reptile of the same size—was relatively large. It indicates that pterosaur brains were large for the brain of a reptile but had not quite attained the relative size achieved by the brain of a bird.

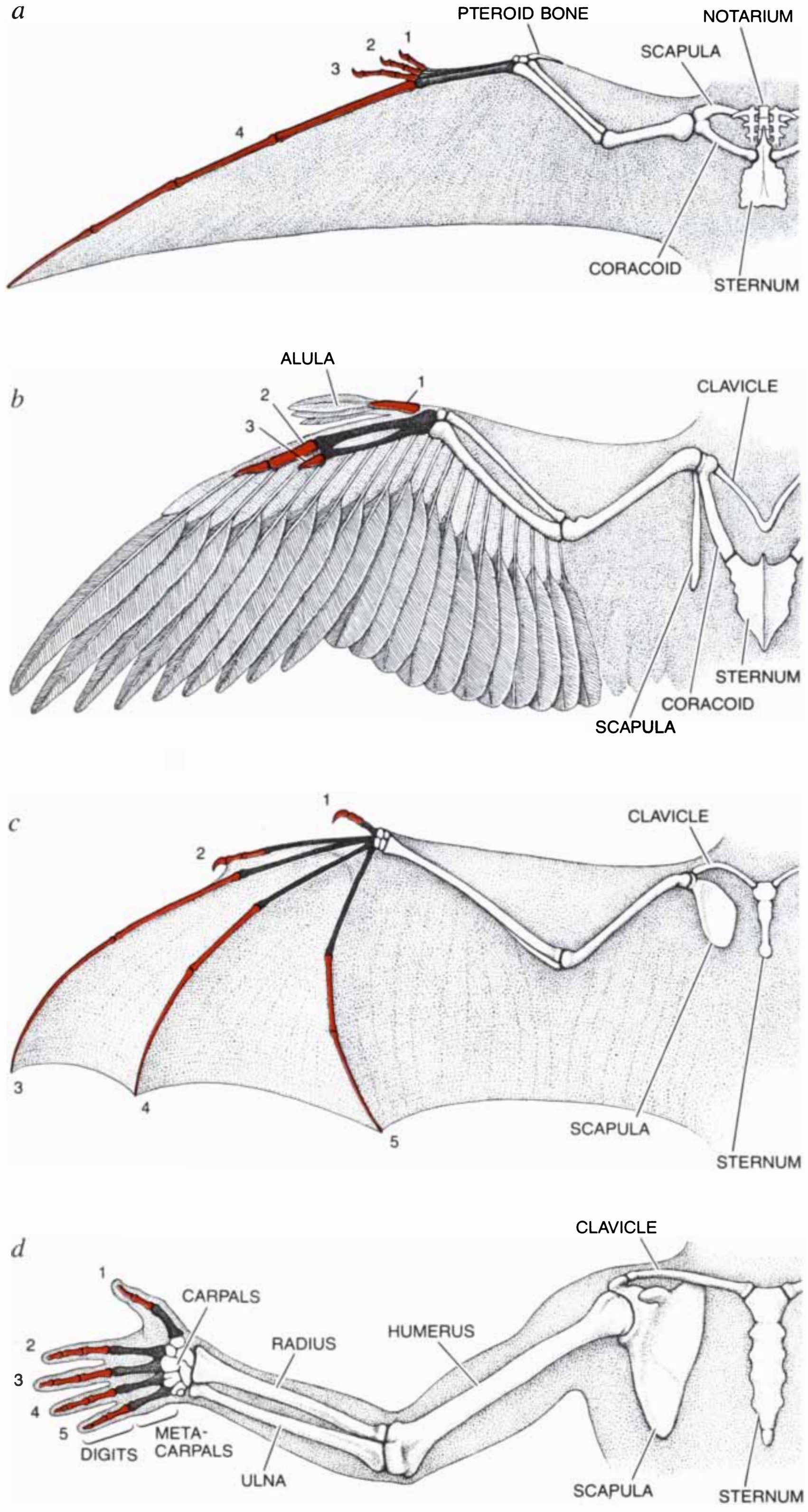
The third notable aspect of the anatomy is the pterosaur's skin. Although reptiles are typically covered by scales and mammals are covered by hair, it has been suggested from time to time that the pterosaurs may have had a hairy coat. The reasoning begins with the hypothesis, offered by T. H. Huxley more than a century ago, that a flying vertebrate such as a pterosaur must have been a warm-blooded animal. After all, flying implies a high rate of metabolism, which in turn implies that the animal must maintain a high internal temperature. A coat of hair would furnish insulation against the loss of body heat. It might also streamline an animal's body to reduce its drag in flight. In 1971 A. G. Sharov, a Russian zoologist, presented the first clear evidence that this reasoning is correct. He had discovered in Kazakhstan the fossil skeleton of a pigeon-size rhamphorhynchoid, *Sordes pilosus.* The fossil was clothed in "long, dense and relatively thick" hairlike fossil material. It appeared to Sharov that the entire body (except for the tail) was indeed covered by hair.

Our knowledge of the giant West Texas pterosaur, *Quetzalcoatlus,* comes mostly from two groups of fossils. The first group consists of fragments from the wing of *Quetzalcoatlus northropi.* The remains of other parts of the body have not been found; evidently the wing of the animal was separated from the body before the burial. The second group of fossils consists of the scattered bones of at least a dozen smaller animals. All of them were found in one area, where it appears that all the animals died over a short span of time, perhaps only a few years.

The sites where the two groups of fossils were found are some 50 kilometers apart, and so it cannot be established that all the fossils represent a single population. Nor can it be shown that all the animals lived at exactly the same time. Nevertheless, the larger and smaller bones would scarcely be distinguishable if it were not for the disparity in size. The smaller bones might therefore be viewed as representing immature specimens of *Quetzalcoatlus northropi.* Pending new discoveries that may settle the issue definitively, the smaller bones are classified in taxonomic shorthand as rep-



PTEROSAURS EVOLVED in the early part of the Mesozoic era. Their appearance preceded that of the earliest birds by about 50 million years and followed that of the earliest dinosaurs by about 20 million years. It is hypothesized that the precursors of the pterosaurs (and of the birds and of both orders of the dinosaurs, the ornithischians and the saurischians) were the reptiles called the thecodonts, which for their part evolved from the early, lizard-shaped reptiles known as eosuchians. Among the pterosaurs the rhamphorhynchoids first appeared some 50 million years before the pterodactyloids. The last pterodactyls died out with the dinosaurs 64 million years ago.



WINGS of a pterosaur (*a*), a bird (*b*) and a bat (*c*) are evolutionary variations on a forelimb that was suitable for an earthbound animal that walked on all fours. The variations are distinctive: in the pterosaur it is the fourth finger that supports the wing; in the bird it is mainly the second, and in the bat it is the second through the fifth. In each animal the wing attaches to the trunk by means of the shoulder girdle, a ring of bones. The girdle of the larger pterodactyls is peculiar in that the scapula, or shoulder blade, turns inward and abuts the notarium, a unique pterosaurian bone, at the midplane of the body. The notarium is several vertebrae fused together. The arrangement provided a base for the action of the wing. The arm of man is shown in *d*.

resenting *Quetzalcoatlus* sp., an undetermined species.

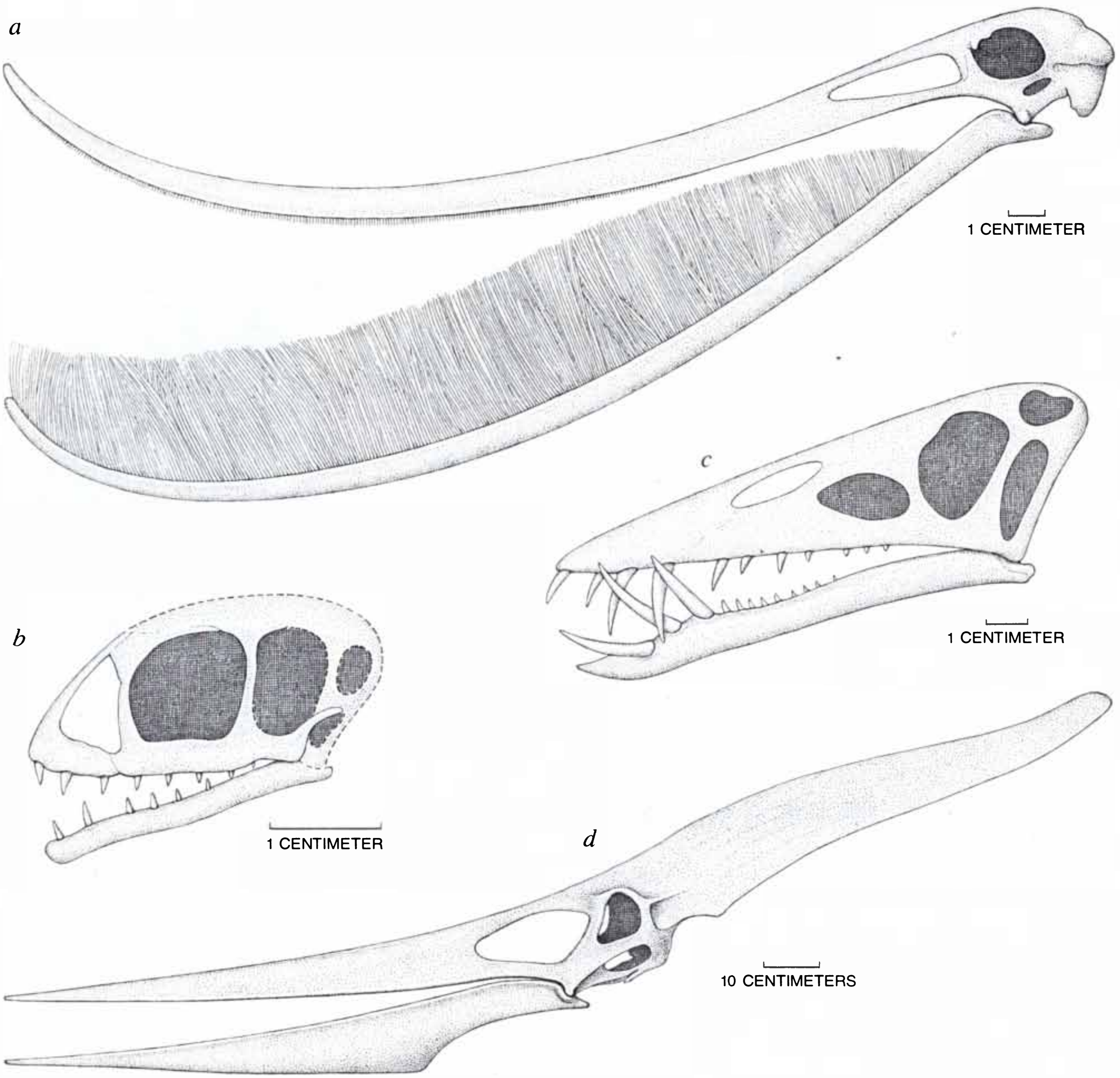
A pterosaur vertebra found in the 1940's in Jordan bears on this problem because it resembles the neck vertebrae of *Quetzalcoatlus* sp. The vertebra was long and slender, and so it was mistaken at first for a wing bone. It clearly represented an animal larger than any pterosaur known at the time. The animal was therefore named *Titanopteryx*. The point is that the vertebra found in Jordan is almost large enough to fit *Q. northropi*. On the other hand, the fossil from Jordan is older than the fossils from Texas. For the present *Titanopteryx* and *Quetzalcoatlus* can be regarded as distinct. If future discoveries demonstrate that they are the same, the International Rules of Zoological Nomenclature stipulate that *Titanopteryx* must replace *Quetzalcoatlus* as the name for the Texas pterosaur.

The preliminary estimates of the size of *Quetzalcoatlus northropi* were based on comparisons between the wing bones of that animal and the wings of some considerably smaller pterosaur species. By this method it was inferred that the wingspan of *Q. northropi* ranged from 11 to 21 meters. Extrapolations from two large pterosaurs, *Quetzalcoatlus* sp. and *Pteranodon*, refined the estimate to 15.5 meters.

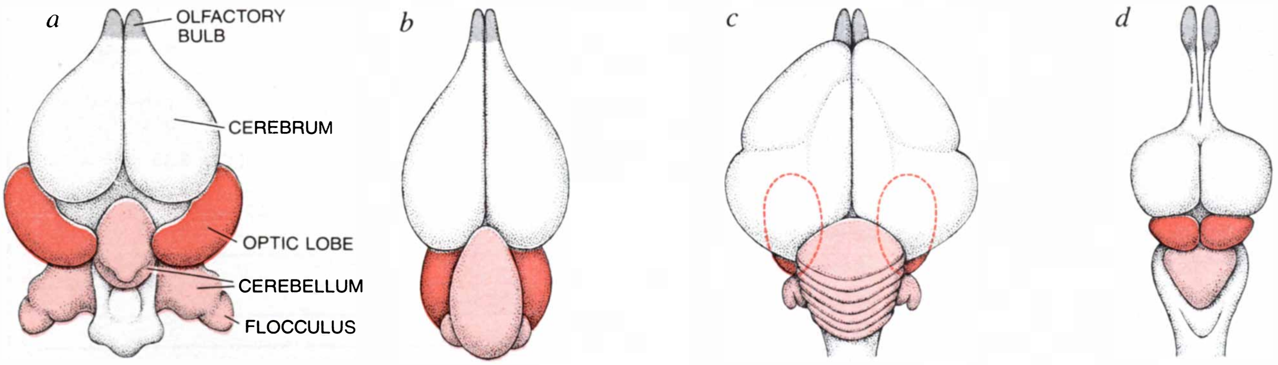
Aeronautical engineers quickly pointed out, however, that a pterosaur with the shape of *Pteranodon* and a wingspan of 15.5 meters might have weighed as much as 136 kilograms. It would then have lacked the muscle power to maintain level flight by flapping its wings. Moreover, the strength of the wing bones would perhaps have been insufficient to bear the stresses the wings would have had to endure. Of course, *Quetzalcoatlus northropi* did not have exactly the proportions of *Pteranodon*. Even so, an animal with a wingspan of 15.5 meters would probably have been at or beyond the engineering limits for a flying machine made of muscles, tendons and delicate hollow bones.

Unfortunately the precise length of the wing of *Quetzalcoatlus northropi* is still uncertain. It is known, however, that the metacarpal bone of the fourth finger was relatively longer in *Quetzalcoatlus* than it was in *Pteranodon* and that some of the other bones of this finger were substantially shorter. These differences suggest an adjusted calculation by which the wingspan of *Quetzalcoatlus* sp. emerges as no less than 5.5 meters, and that of *Q. northropi* as 11 to 12 meters. Such an animal might have weighed 86 kilograms. In spite of the recent discovery in Argentina of an extinct vulture whose wingspan is estimated to have been more than seven meters, *Q. northropi* still would rank as the largest known flying creature.

Few assertions about how the ptero-



SKULLS of four pterosaurs suggest that their diets varied. *Pterodaustro* (*a*) had teeth that resemble the baleen with which some whales strain plankton from seawater. *Anurognathus* (*b*), a tiny pterosaur, had peglike teeth. It may have eaten insects. *Dorygnathus* (*c*) was toothy; *Pteranodon* (*d*) was toothless. It seems that both, however, ate fish, because fossil fish have been found within their rib cage.



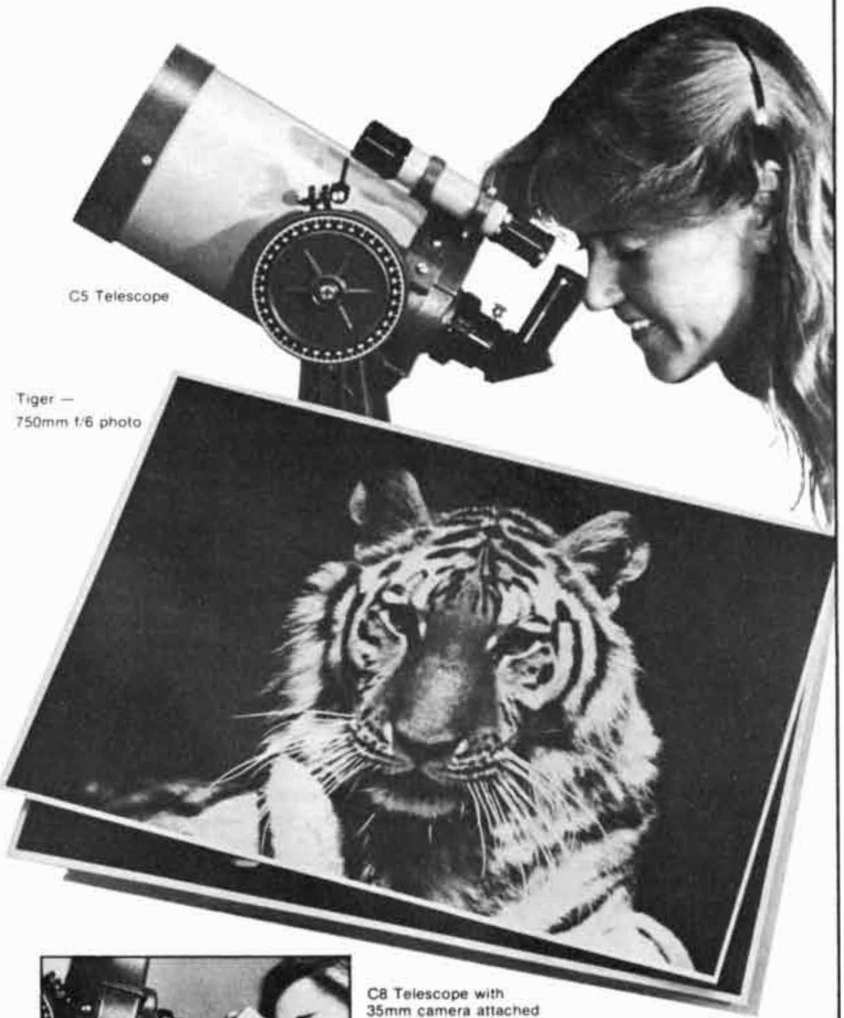
BRAIN of the pterosaur (*a*) is reconstructed from endocasts, which formed from sediment that filled the skull during fossilization. The other brains are of *Archaeopteryx* (*b*), a modern bird (*c*) and a modern reptile, the alligator (*d*). The view is from above. In the pterosaur the optic lobes (indicative of vision) and the cerebellum (indicative of muscular coordination) are well developed for a reptile's brain.

saurs lived are well supported. The difficulty is that vertebrate animals in general are seldom buried immediately in the precise place where they lived. Instead the carcass lies exposed to scavengers, decay, weathering and transport by flowing water. The Kansas pteranodons, for example, are found at sites that were at least 160 kilometers out to sea in the Mesozoic. Almost surely the animals had died in or over water far from home. The Solnhofen pterosaurs are in stone that was laid down as limy sediment in lagoons. The attitudes of many of the skeletons suggest that the carcasses had dried out on a beach and then had floated to where they sank.

Efforts to imagine how the pterosaurs became airborne have led to suggestions that they launched themselves by jumping or falling off a cliff, by dropping from their roosting place in a tree or even by rising into a light wind from the crest of a wave. Each hypothesis has its difficulties. The first one rests in part on the assertion that the hind feet of the pterosaur resembled those of a bat and therefore could serve as hooks by which the animal hung from a cliff in preparation for flight. A recent study by Kevin Padian of the University of California at Berkeley suggests, however, that the hind limbs and the feet of pterosaurs were much more like those of birds and dinosaurs than has generally been assumed. None of these animals is thought to have been much of a cliff-hanger.

As for the second hypothesis, it seems unlikely that large pterosaurs could have landed in trees without damaging their wings. It is conceivable, however, that the pterosaurs climbed the trees. The hooves of the billy goat seem to make the animal suitable only for walking, and yet billy goats can climb into the low branches of trees by clinging to them with other parts of their limbs. The third hypothesis calls for high waves to channel the updrafts the animal would have employed to soar. The wind that made such waves, however, might well have been too strong for the animal to control its flight once it was airborne.

The setting of the Texas pterosaurs presents a special problem for imagining how the animal left the ground. The fossils were found in siltstones and sandstones that were deposited in a broad alluvial fan some 400 kilometers inland from the nearest seacoast of the time. Although highlands extended to the west, there is no indication in the geology of the region that any mountains or cliffs were nearby. It appears, then, that *Quetzalcoatlus* may have lived on fairly flat, low-lying ground. There, as is the habit of a vulture, it may well have had to wait each morning until the sun warmed the ground and strong thermal updrafts developed. In the larger pterosaurs the musculature that animated the wing was not impressively massive, and



the hind limbs were long but weak. All things considered, it seems unlikely that *Quetzalcoatlus* could have run on its hind legs and flapped its wings energetically. Still, if the animal could stand up on its hind legs and catch the appropriate breeze, a single flap of the wings and a kick with the legs may have been all it needed for takeoff.

Landing would have been less problematic. Evidently the air speed at which a flying pterosaur stalled was less for a pterosaur than it is for a bird of the same weight. Hence the pterosaur could touch down gently on its hind limbs. The animal's body would pitch slowly onto its hands as the animal folded its wings. How did it move on the ground? Some investigators suspect that the hindquarters of *Pteranodon,* at least, were too weak to support the body at all. They suggest instead that the animal rested on its breast, which they assume was well padded. The animal would then have dragged and pushed itself in the manner of certain bats. Padian suggests, to the contrary, that the pterosaur had a two-legged stance. Finally, certain fossil tracks from a Jurassic sandstone in Arizona are attributed (perhaps erroneously) to a pterosaur. They were made by an animal that was walking on all fours.

The mechanics of pterosaur flight is a subject also fraught with uncertainties. Yet it too sheds light on how the pterosaurs may have lived. Cherrie D. Bramwell and George R. Whitfield of the University of Reading have made a detailed examination of *Pteranodon* as a flying machine. They conclude that a pteranodon with a wingspan of 6.9 meters and a weight of 16.6 kilograms could have flown only in light to moderate winds. A light wind is one that blows at eight to 12 miles per hour; it will lift loose paper off the ground and make a flag stand out by a third of its length from its staff. The aerodynamic properties of the pterosaur in a glide would give it only a small tendency to sink. Thus it could easily rise in an updraft. All these calculations are based, however, on a model of *Pteranodon* in which the wing membrane stretches from the tip of the fourth finger to the ankle of the hind leg. The fossil record gives no evidence for this. In fact, in some pterosaurs the wing is known to have been narrow at the base.

In general the relation between the area of the wing and the total weight of the pterosaur indicates that the wing bore less weight per unit area than it does in a bird of the same size. Ordinarily this would suggest that the flight of the pterosaur was slow but maneuverable. Pterosaurs, however, lacked many of the control surfaces that are available to the birds. They lacked, for example, an effective horizontal stabilizer. The bird's tail serves such a func-

EVIDENCE OF HAIR on the body of the pterosaurs was provided in 1971, when these fossil impressions of the pigeon-size pterosaur *Sordes pilosus* were found in Kazakhstan in the U.S.S.R. The hairlike marks at the bottom apparently covered the entire body except the tail.

tion. The pterosaurs therefore should have been less able to maneuver in flight than a bird is. The larger pterodactyls probably flapped their wings slowly at takeoff and for restoring level flight when that was necessary. Once airborne, an animal such as *Pteranodon* may have remained aloft for long periods, rising on updrafts near surface features such as cliffs and then riding weak air currents over land or water.

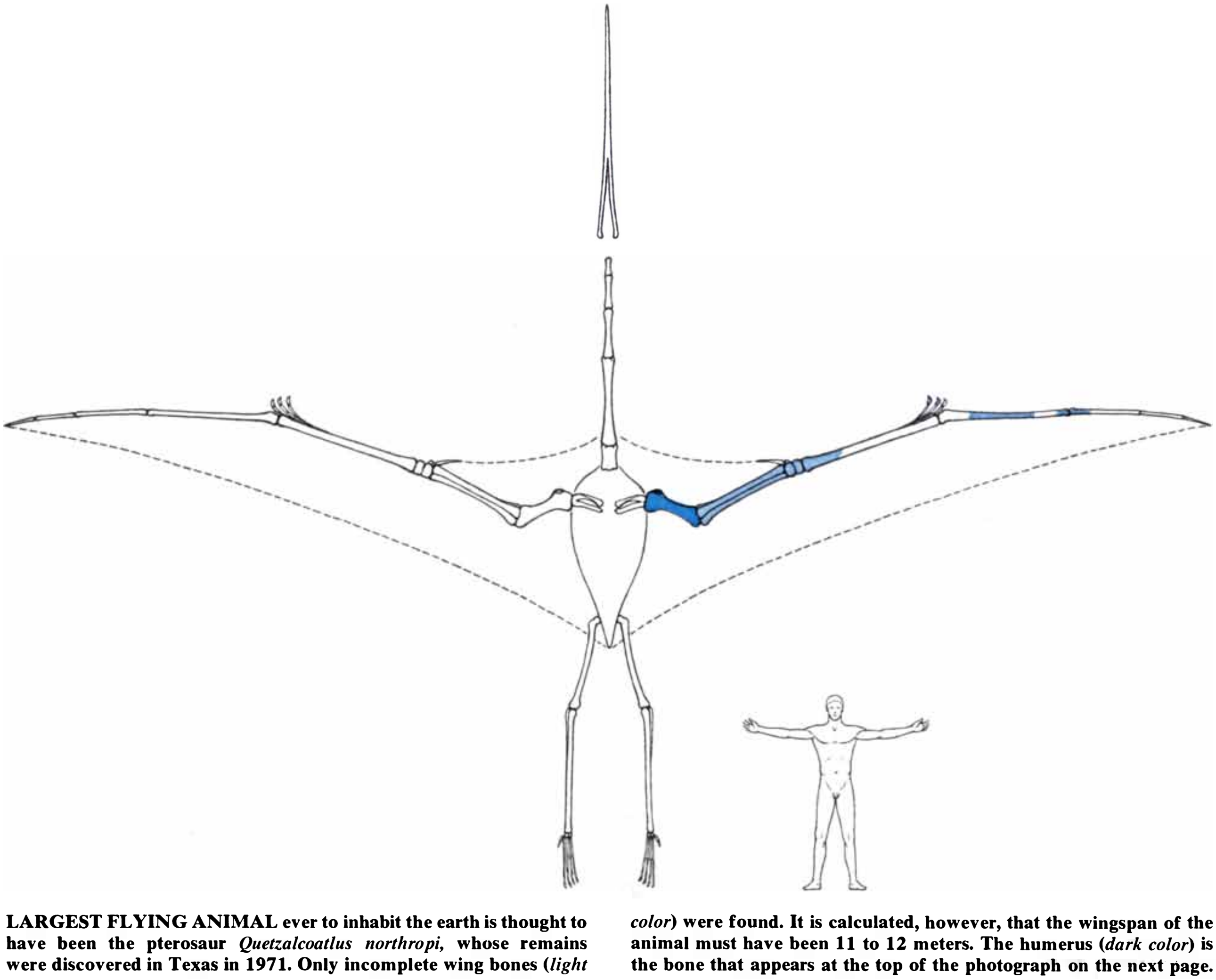
The smaller pterosaurs were probably more active fliers, able to flap their wings more energetically. They nonetheless were probably slower than a bird of similar size. In 1956 Erich von Holst of the Max Planck Institute for Behavioral Physiology at Seewiesen in West Germany constructed a model of a rhamphorhynchoid from rice paper, balsa wood and aluminum. Powered by rubber bands, the model flapped its wings up and down about 40 times with a wingbeat of two to three times per second, then glided to a soft landing. The flight was described as elegant—not at all, for example, like the jerky flight of a bat. The wings of the model were broader, however, than those of a pterosaur, and so it is unlikely that the pterosaur would have flown in the same way. More recent efforts to duplicate pterosaur flight have been disappointing.

The fossilized contents of the stomach of the pterosaur (or at least the fossils found inside the fossilized rib cage) show that several species of pterosaur ate fish. How the fish were caught is not clear. The skeleton of the pterosaur probably could not have withstood the stresses of diving into water, and the body of the pterosaur makes it about as suitable as an unfolded newspaper for motion underwater.

Pteranodon and some other pterodactyls may have fished on the wing. A pteranodon gliding slowly just above the surface of a body of water could have dipped its beak into the water to pluck out a fish. The narrow profile of the beak would meet with little resistance. The fish could then have been gulped down on the spot. Alternatively *Pteranodon* could have carried the fish in its throat sac, a pouch that resembles the pouch of a pelican. The fossil remains of fish have been found in a fossil impression of the sac. Some investigators believe pterosaurs could land on water and thus could fish from a floating platform.

When stomach contents have not been discovered, the best clue to an animal's diet is usually its dentition and the structure of its jaw. On such evidence it has been suggested that *Anurognathus,* a tiny pterosaur with a short face and peglike teeth, ate insects. Whether the animal was maneuverable enough to catch insects on the wing is debatable. Other species clearly had different diets. The lower jaw of *Pterodaustro* has hundreds of teeth that resemble the baleen of a whale. The animal may therefore have fed on plankton. The fish-eating *Pteranodon* was toothless.

Quetzalcoatlus may also have eaten fish, but where it would have caught them is a problem. There is no evidence to suggest that there were large permanent bodies of water near the habitations of *Quetzalcoatlus.* Moreover, the rock in which the fossils of *Quetzalcoatlus* were found are almost devoid of fish remains. The rocks do, however, bear many traces of burrowing animals. In addition the presence of masses of fossilized logs in the area suggests periodic ancient flooding. Perhaps a monsoon was responsible. All of this raises the



LARGEST FLYING ANIMAL ever to inhabit the earth is thought to have been the pterosaur *Quetzalcoatlus northropi,* whose remains were discovered in Texas in 1971. Only incomplete wing bones (*light color*) were found. It is calculated, however, that the wingspan of the animal must have been 11 to 12 meters. The humerus (*dark color*) is the bone that appears at the top of the photograph on the next page.

possibility that *Quetzalcoatlus* employed its slender beak to probe for mollusks or arthropods living in shallow flood basins. That would mean, of course, that *Quetzalcoatlus* foraged on the ground.

Since the pterosaurs were reptiles, it might be surmised that they were oviparous. Indeed, purported pterosaur eggs were discovered in England more than a century ago. On the other hand, the pelvis of a pterosaur is not similar to that of a bird. In particular the passageway for eggs would have been relatively constricted. The problem would have been worsened because a pterosaur egg would no doubt have been large to accommodate the folded wings of the developing animal. It also seems likely that the mother would have had to fly to search for food throughout the gestation, in spite of her additional weight. Perhaps the young were born alive in an immature state of development. Prolonged nurture would then have been necessary. Masses of fossil conifer needles found with the remains of *Quetzalcoatlus* sp. may be the remnants of nests.

From the geographical distribution of the fossils and the age of the rocks in which the fossils are found one may suppose the pterosaurs first appeared in what is now southern Europe. From there they spread into Asia, Africa, India and North America by the end of the Jurassic and reached South America and Australia in the Cretaceous. Their dispersal was facilitated by the relative lack of geographical barriers. In those times the earth's present land masses were all more or less in contact. Later the sea floors spread and the continents moved apart. The pterosaur populations became isolated and evolution accentuated their diversity. Large species evolved on several continents.

As the Mesozoic drew to a close the land masses of the earth approached the positions they have today. It was a time of widespread flooding in the low-lying areas of the continents. The total land surface was temporarily reduced to perhaps half of what it is at present. For example, a wide inland seaway cut North America in two from north to south. Pterosaurs then achieved their greatest distribution: they extended both north and south of the Equator to latitudes of about 70 degrees. Mountain ranges, however, were rising, and when sea-floor spreading subsided at the very end of the Cretaceous, the ocean basins deepened. The sea level therefore fell, and the flooded land reemerged. These changes altered the climates and the habitats to which the pterosaurs were accustomed. Extinction gradually reduced their numbers until only *Quetzalcoatlus* remained. Then it too died out.

The disappearance of the pterosaurs coincided with that of many forms of marine plankton, mollusks and reptiles. On land the dinosaurs disappeared. Indeed, no animal heavier than about 23 kilograms survived the Cretaceous. The reasons for the mass extinction are widely debated. Early ideas have given way to explanations that sometimes invoke such catastrophes as volcanic explosions or the lethal radiation of a supernova near the solar system. The newest hypothesis is that an asteroid struck the earth at the end of the Mesozoic and gave rise to a dust cloud that enveloped the earth for several years, dimming the light of the sun. The forms of life that survived on land were either small or warm-blooded or both. The mammals, it is imagined, survived by eating seeds. It counts in favor of this hypothesis that the end of the Mesozoic in some places is marked in the geological record by a thin layer of clay in which the concentration of exotic chemical elements such as iridium is curiously high.

The consequences of a collision of an asteroid with the earth would surely have disposed of the last of the pterosaurs. But another, less dramatic explanation also seems possible. The fossil record clearly shows that the pterosaurs were in decline during the last few million years of the Cretaceous. Moreover, it is thought the climatic changes at the end of the Cretaceous included decreasing world temperatures and increasing seasonal variation in the weather. The earth thus would have been stormy. The gusty winds of the storms would have been disastrous for creatures such as *Pteranodon,* which were adapted for soaring in light, steady winds. Their only chance would seem to have been to improve their aerodynamic capabilities by reducing their size. The remains of *Quetzalcoatlus* suggest that the pterosaurs evolved in the opposite direction.

COMPARISON OF BONES of *Quetzalcoatlus northropi* with those of smaller, similar pterosaurs found nearby contributed to the reconstruction of *Quetzalcoatlus.* The bone at the top is the left humerus of *Q. northropi.* It is .54 meter long. The bone below it is the right humerus of an animal designated *Quetzalcoatlus* sp. in the absence of proof that it was the young of the species *northropi.* The bone is .24 meter long. The fossils of *Quetzalcoatlus* sp. are sufficiently complete for it to be said that the wingspan of the smaller animal was six meters.