= Pteranodon =

Pteranodon (/ t??ræn?d?n / ; from Greek ?????? (" wing ") and ?????? (" toothless ") is a genus of pterosaurs which included some of the largest known flying reptiles , with wingspans over 6 metres (20 ft) . It existed during the late Cretaceous geological period of North America in present day Kansas , Alabama , Nebraska , Wyoming , and South Dakota . More fossil specimens of Pteranodon have been found than any other pterosaur , with about 1 @,@ 200 specimens known to science , many of them well preserved with nearly complete skulls and articulated skeletons . It was an important part of the animal community in the Western Interior Seaway .

Pteranodon was not a dinosaur . By definition , all dinosaurs belong to either order within Dinosauria , either Saurischia or Ornithischia . As such , this excludes pterosaurs . Nonetheless , Pteranodon is frequently featured in dinosaur media and is strongly associated with dinosaurs by the general public .

= = Description = =

Pteranodon species are extremely well represented in the fossil record , allowing for detailed descriptions of their anatomy and analysis of their life history . Over 1 @,@ 000 specimens have been identified , though less than half are complete enough to give researchers good information on the anatomy of the animal . Still , this is more fossil material than is known for any other pterosaur , and it includes both male and female specimens of various age groups and , possibly , species .

= = = Size = = =

Adult Pteranodon specimens from the two major species can be divided into two distinct size classes . The smaller class of specimens have small , rounded head crests and very wide pelvic canals , even wider than those of the much larger size class . The size of the pelvic canal probably allowed the laying of eggs , indicating that these smaller adults are females . The larger size class , representing male individuals , have narrow hips and very large crests , which were probably for display .

Adult male Pteranodon were among the largest pterosaurs , and were the largest flying animals known until the late 20th century , when the giant azhdarchid pterosaurs were discovered . The wingspan of an average adult male Pteranodon was 5 @.@ 6 metres (18 ft) . Adult females were much smaller , averaging 3 @.@ 8 metres (12 ft) in wingspan . The largest specimen of Pteranodon longiceps from the Niobrara Formation measured 6 @.@ 25 metres (20 @.@ 5 ft) from wingtip to wingtip . An even larger specimen is known from the Pierre Shale Formation , with a wingspan of 7 @.@ 25 metres (23 @.@ 8 ft) , though this specimen may belong to the distinct genus and species Geosternbergia maysei . While most specimens are found crushed , enough fossils exist to put together a detailed description of the animal .

Methods used to estimate the mass of large male Pteranodon specimens (those with wingspans of about 7 meters) have been notoriously unreliable , producing a wide range of estimates from as low as 20 kilograms (44 lb) to as high as 93 kilograms (205 lb) . In a review of pterosaur size estimates published in 2010 , researchers Mark Witton and Mike Habib demonstrated that the latter , largest estimates are almost certainly incorrect given the total volume of a Pteranodon body , and could only be correct if the animal " was principally comprised of aluminium . " Witton and Habib considered the methods used by researchers who obtained smaller mass estimates equally flawed . Most have been produced by scaling modern animals such as bats and birds up to Pteranodon size , despite the fact that pterosaurs have vastly different body proportions and soft tissue anatomy from any living animal .

= = = Skull and beak = = =

Unlike earlier pterosaurs such as Rhamphorhynchus and Pterodactylus , Pteranodon had toothless

beaks , similar to those of birds . Pteranodon beaks were made of solid , bony margins that projected from the base of the jaws . The beaks were long , slender , and ended in thin , sharp points . The upper jaw was longer than the lower jaw . The upper jaw was curved upward ; while this normally has been attributed only to the upward @-@ curving beak , one specimen (UALVP 24238) has a curvature corresponding with the beak widening towards the tip . While the tip of the beak is not known in this specimen , the level of curvature suggests it would have been extremely long . The unique form of the beak in this specimen led Alexander Kellner to assign it to a distinct genus , Dawndraco , in 2010 .

The most distinctive characteristic of Pteranodon is its cranial crest . These crests consisted of skull bones (frontals) projecting upward and backward from the skull . The size and shape of these crests varied due to a number of factors , including age , sex , and species . Male Pteranodon sternbergi , the older species of the two described to date (and sometimes placed in the distinct genus Geosternbergia) , had a more vertical crest with a broad forward projection , while their descendants , Pteranodon longiceps , evolved a narrower , more backward @-@ projecting crest . Females of both species were smaller and bore small , rounded crests . The crests were probably mainly display structures , though they may have had other functions as well .

= = = Skeleton = = =

Other distinguishing characteristics that set Pteranodon apart from other pterosaurs include narrow neural spines on the vertebrae , plate @-@ like bony ligaments strengthening the vertebrae above the hip , and a relatively short tail in which the last few vertebrae are fused into a long rod . The entire length of the tail was about 3 @.@ 5 % as long as the wingspan , or up to 25 centimetres (9 @.@ 8 in) in the largest males .

= = Timespan and evolution = =

Pteranodon fossils are known primarily from the Niobrara Formation of the central United States . Broadly defined , Pteranodon existed for more than four million years , during the late Coniacian to early Campanian stages of the Cretaceous period . The genus is present in most layers of the Niobrara Formation except for the upper two ; in 2003 , Kenneth Carpenter surveyed the distribution and dating of fossils in this formation , demonstrating that Pteranodon sternbergi existed there from 88 to 85 million years ago , while P. longiceps existed between 86 and 84 @.@ 5 million years ago . A possible third species , which Kellner named Geosternbergia maysei in 2010 , is known from the Sharon Springs member of the Pierre Shale Formation in Kansas , Wyoming , and South Dakota , dating to between 81 @.@ 5 and 80 @.@ 5 million years ago .

In the early 1990s , Bennett noted that the two major morphs of pteranodont present in the Niobrara Formation were precisely separated in time with little , if any , overlap . Due to this , and to their gross overall similarity , he suggested that they probably represent chronospecies within a single evolutionary lineage lasting about 4 million years . In other words , only one species of Pteranodon would have been present at any one time , and P. sternbergi (or Geosternbergia) in all likelihood was the direct ancestor species of P. longiceps .

= = Biology and ecology = =

= = = Range and environment = = =

Specimens assigned to Pteranodon have been found in both the Smoky Hill Chalk deposits of the Niobrara Formation , and the slightly younger Sharon Springs deposits of the Pierre Shale Formation . When Pteranodon was alive , this area was covered by a large inland sea , known as the Western Interior Seaway . Famous for fossils collected since 1870 , these formations extend from as far south as Kansas in the United States to Manitoba in Canada . However , Pteranodon

specimens (or any pterosaur specimens) have only been found in the southern half of the formation , in Kansas , Wyoming , and South Dakota . Despite the fact that numerous fossils have been found in the contemporary parts of the formation in Canada , no pterosaur specimens have ever been found there . This strongly suggests that the natural geographic range of Pteranodon covered only the southern part of the Niobrara , and that its habitat did not extend farther north than South Dakota .

Some very fragmentary fossils belonging to pteranodontian pterosaurs , and possibly Pteranodon itself , have also been found on the Gulf Coast and East Coast of the United States . For example , some bone fragments from the Mooreville Formation of Alabama and the Merchantville Formation of Delaware may have come from Pteranodon , though they are too incomplete to make a definite identification . Some remains from Japan have also been tentatively attributed to Pteranodon , but their distance from its known Western Interior Seaway habitat makes this identification unlikely .

Pteranodon longiceps would have shared the sky with the giant @-@ crested pterosaur Nyctosaurus . Compared to P. longiceps , which was a very common species , Nyctosaurus was rare , making up only 3 % of pterosaur fossils from the formation . Also less common was the early toothed bird , Ichthyornis .

It is likely that , as in other polygynous animals (in which males compete for association with harems of females) , Pteranodon lived primarily on offshore rookeries , where they could nest away from land @-@ based predators and feed far from shore ; most Pteranodon fossils are found in locations which at the time , were hundreds of kilometres from the coastline .

Below the surface , the sea was populated primarily by invertebrates such as ammonites and squid . Vertebrate life , apart from basal fish , included sea turtles such as Toxochelys , the plesiosaur Styxosaurus , and the flightless diving bird Parahesperornis . Mosasaurs were the most common marine reptiles , with genera including Clidastes and Tylosaurus . At least some of these marine reptiles are known to have fed on Pteranodon . Barnum Brown , in 1904 , reported plesiosaur stomach contents containing " pterodactyl " bones , most likely from Pteranodon .

Fossils from terrestrial dinosaurs also have been found in the Niobrara Chalk , suggesting that animals who died on shore must have been washed out to sea (one specimen of a hadrosaur appears to have been scavenged by a shark) .

= = = Flight = = =

The wing shape of Pteranodon suggests that it would have flown rather like a modern @-@ day albatross . This is based on the fact that Pteranodon had a high aspect ratio (wingspan to chord length) similar to that of the albatross ? 9 : 1 for Pteranodon , compared to 8 : 1 for an albatross . Albatrosses spend long stretches of time at sea fishing , and use a flight pattern called " dynamic soaring " which exploits the vertical gradient of wind speed near the ocean surface to travel long distances without flapping , and without the aid of thermals (which do not occur over the open ocean the same way they do over land) . While most of a Pteranodon flight would have depended on soaring , like long @-@ winged seabirds , it probably required an occasional active , rapid burst of flapping , and studies of Pteranodon wing loading (the strength of the wings vs. the weight of the body) indicate that they were capable of substantial flapping flight , contrary to some earlier suggestions that they were so big they could only glide .

Like other pterosaurs , Pteranodon probably took off from a standing , quadrupedal position . Using their long forelimbs for leverage , they would have vaulted themselves into the air in a rapid leap . Almost all of the energy would have been generated by the forelimbs . The upstroke of the wings would have occurred when the animal cleared the ground followed by a rapid down @-@ stroke to generate additional lift and complete the launch into the air .

= = = Diet = = =

The diet of Pteranodon is known to have included fish ; fossilized fish bones have been found in the stomach area of one Pteranodon , and a fossilized fish bolus has been found between the jaws of

another Pteranodon , specimen AMNH 5098 . Numerous other specimens also preserve fragments of fish scales and vertebrae near the torso , indicating that fish made up a majority of the diet of Pteranodon (though they may also have taken invertebrates) .

Traditionally , most researchers have suggested that Pteranodon would have taken fish by dipping their beaks into the water while in low , soaring flight . However , this was probably based on the assumption that the animals could not take off from the water surface . It is more likely that Pteranodon could take off from the water , and would have dipped for fish while swimming rather than while flying . Even a small , female Pteranodon could have reached a depth of at least 80 centimetres (31 in) with its long bill and neck while floating on the surface , and they may have reached even greater depths by plunge @-@ diving into the water from the air like some modern long @-@ winged seabirds . In 1994 , Bennett noted that the head , neck , and shoulders of Pteranodon were as heavily built as diving birds , and suggested that they could dive by folding back their wings like the modern gannet .

= = = Crest function = = =

Pteranodon was notable for its skull crest , though the function of this crest has been a subject of debate . Most explanations have focused on the blade @-@ like , backward pointed crest of male P. longiceps , however , and ignored the wide range of variation across age and sex . The fact that the crests vary so much rules out most practical functions other than for use in mating displays . Therefore , display was probably the main function of the crest , and any other functions were secondary .

Scientific interpretations of the crest 's function began in 1910 , when George Francis Eaton proposed two possibilities : an aerodynamic counterbalance and a muscle attachment point . He suggested that the crest might have anchored large , long jaw muscles , but admitted that this function alone could not explain the large size of some crests . Bennett (1992) agreed with Eaton 's own assessment that the crest was too large and variable to have been a muscle attachment site . Eaton had suggested that a secondary function of the crest might have been as a counterbalance against the long beak , reducing the need for heavy neck muscles to control the orientation of the head . Wind tunnel tests showed that the crest did function as an effective counterbalance to a degree , but Bennett noted that again , the hypothesis focuses only on the long crests of male P. longiceps , not on the larger crests of P. sternbergi and very small crests that existed among the females . Bennett found that the crests of females had no counterbalancing effect , and that the crests of male P. sternbergi would , by themselves , have a negative effect on the balance of the head . In fact , side to side movement of the crests would have required more , not less , neck musculature to control balance .

In 1943 , Dominik von Kripp suggested that the crest may have served as a rudder , an idea embraced by several later researchers . One researcher , Ross S. Stein , even suggested that the crest may have supported a membrane of skin connecting the backward @-@ pointing crest to the neck and back , increasing its surface area and effectiveness as a rudder . The rudder hypothesis again , does not take into account females nor P. sternbergi , which had an upward @-@ pointing , not backward @-@ pointing crest . Bennett also found that even in its capacity as a rudder , the crest would not provide nearly so much directional force as simply maneuvering the wings . The suggestion that the crest was an air brake , and that the animals would turn their heads to the side in order to slow down , suffers from a similar problem . Additionally , the rudder and air brake hypotheses do not explain why such large variation exists in crest size even among adults .

Alexander Kellner suggested that the large crests of the pterosaur Tapejara , as well as other species , might be used for heat exchange , allowing these pterosaurs to absorb or shed heat and regulate body temperature , which also would account for the correlation between crest size and body size . There is no evidence of extra blood vessels in the crest for this purpose , however , and the large , membranous wings filled with blood vessels would have served that purpose much more effectively .

With these hypotheses ruled out , the best @-@ supported hypothesis for crest function seems to

be as a sexual display . This is consistent with the size variation seen in fossil specimens , where females and juveniles have small crests and males large , elaborate , variable crests .

= = = Sexual variation = = =

Adult Pteranodon specimens may be divided into two distinct size classes , small and large , with the large size class being about one and a half times larger than the small class , and the small class being twice as common as the large class . Both size classes lived alongside each other , and while researchers had previously suggested that they represent different species , Christopher Bennett showed that the differences between them are consistent with the concept that they represent females and males , and that Pteranodon species were sexually dimorphic . Skulls from the larger size class preserve large , upward and backward pointing crests , while the crests of the smaller size class are small and triangular . Some larger skulls also show evidence of a second crest that extended long and low , toward the tip of the beak , which is not seen in smaller specimens .

The sex of the different size classes was determined , not from the skulls , but from the pelvic bones . Contrary to what may be expected , the smaller size class had disproportionately large and wide @-@ set pelvic bones . Bennett interpreted this as indicating a more spacious birth canal , through which eggs would pass . He concluded that the small size class with small , triangular crests represent females , and the larger , large @-@ crested specimens represent males .

Note that the overall size and crest size also corresponds to age . Immature specimens are known from both females and males , and immature males often have small crests similar to adult females . Therefore , it seems that the large crests only developed in males when they reached their large , adult size , making the sex of immature specimens difficult to establish from partial remains .

The fact that females appear to have outnumbered males two to one suggests that , as with modern animals with size @-@ related sexual dimorphism , such as sea lions and other pinnipeds , Pteranodon might have been polygynous , with a few males competing for association with groups consisting of large numbers of females . Similar to modern pinnipeds , Pteranodon may have competed to establish territory on rocky , offshore rookeries , with the largest , and largest @-@ crested , males gaining the most territory and having more success mating with females . The crests of male Pteranodon would not have been used in competition , but rather as " visual dominance @-@ rank symbols " , with display rituals taking the place of physical competition with other males . If this hypothesis is correct , it also is likely that male Pteranodon played little to no part in rearing the young ; such a behavior is not found in the males of modern polygynous animals who father many offspring at the same time .

= = = Terrestrial locomotion = = =

Main article : Pterosaur : Ground movement

Historically , the terrestrial locomotion of Pteranodon , especially whether it was bipedal or quadrupedal , has been the subject of debate . Today , most pterosaur researchers agree that pterosaurs were quadrupedal , thanks largely to the discovery of pterosaur trackways .

The possibility of aquatic locomotion via swimming has been discussed briefly in several papers (Bennett 2001 , 1994 , and Bramwell & Whitfield 1974) .

= = Discovery and history = =

Pteranodon was the first pterosaur found outside of Europe . Its fossils first were found by Othniel Charles Marsh in 1870 , in the Late Cretaceous Smoky Hill Chalk deposits of western Kansas . These chalk beds were deposited at the bottom of what was once the Western Interior Seaway , a large shallow sea over what now is the midsection of the North American continent . These first specimens , YPM 1160 and YPM 1161 , consisted of partial wing bones , as well as a tooth from the prehistoric fish Xiphactinus , which Marsh mistakenly believed to belong to this new pterosaur (all

known pterosaurs up to that point had teeth) . In 1871 , Marsh named the find Pterodactylus Oweni , assigning it to the well @-@ known (but much smaller) European genus Pterodactylus . Marsh also collected more wing bones of the large pterosaur in 1871 . Realizing that the name Pterodactylus oweni already had been used in 1864 for a specimen of the European Pterodactylus , Marsh re @-@ named his North American pterosaur Pterodactylus occidentalis , meaning " Western wing finger , " in his 1872 description of the new specimen . He also named two additional species , based on size differences : Pterodactylus ingens (the largest specimen so far) , and Pterodactylus velox (the smallest) .

Meanwhile , Marsh 's rival Edward Drinker Cope also had unearthed several specimens of the large North American pterosaur . Based on these specimens , Cope named two new species , Ornithochirus umbrosus and Ornithochirus harpyia , in an attempt to assign them to the large European genus Ornithocheirus . As he misspelled the name (forgetting the ' e ') , however , he accidentally created an entirely new genus . Cope 's paper naming his ' ' Ornithochirus species was published in 1872 , just five days after Marsh 's paper . This resulted in a dispute , fought in the published literature , over whose names had priority in what obviously were the same species . Cope conceded in 1875 that Marsh 's names did have priority over his , but maintained that Pterodactylus umbrosus was a distinct species (but not genus) from any that Marsh had named previously . Re @-@ evaluation by later scientists has supported Marsh 's case , and found that Cope 's assertion that P. umbrosus was a larger , distinct species were incorrect .

While the first Pteranodon wing bones were collected by Marsh and Cope in the early 1870s , the first Pteranodon skull was found on May 2 , 1876 , along the Smoky Hill River in Wallace County (now Logan County) , Kansas , USA , by Samuel Wendell Williston , a fossil collector working for Marsh . A second , smaller skull soon was discovered as well . These skulls showed that the North American pterosaurs were different from any European species , in that they lacked teeth . Marsh recognized this major difference , describing the specimens as " distinguished from all previously known genera of the order Pterosauria by the entire absence of teeth . " Marsh recognized that this characteristic warranted a new genus , and he coined the name Pteranodon (" wing without tooth ") in 1876 . Marsh also reclassified all the previously named North American species from Pterodactylus to Pteranodon , with the larger skull , YPM 1117 , referred to the new species Pteranodon longiceps . He also named an additional species , Pteranodon gracilis , based on a wing bone that he mistook for a pelvic bone . He soon realized his mistake , and re @-@ classified that specimen into a separate genus , which he named Nyctosaurus .

Some of the most influential studies of Pteranodon during the 20th century were published by George Francis Eaton , who conducted thorough re @-@ analysis of the known specimens and published some of the first good photographs and illustrations of the best specimens . During the early 1990s , S. Christopher Bennett also published several major papers reviewing the anatomy , taxonomy and life history of Pteranodon .

Fragmentary fossils assigned to Pteranodon have also been discovered in Skåne , Sweden .

= = Classification = =

= = = Valid species = = =

Many researchers consider there to be at least two species of Pteranodon . However , aside from the differences between males and females described above , the post @-@ cranial skeletons of Pteranodon show little to no variation between species or specimens , and the bodies and wings of all pteranodonts were essentially identical .

Two species of Pteranodon are traditionally recognized as valid : Pteranodon longiceps , the type species , and Pteranodon sternbergi . The species differ only in the shape of the crest in adult males (described above) , and possibly in the angle of certain skull bones . Because well @-@ preserved Pteranodon skull fossils are extremely rare , researchers use stratigraphy (i.e. which rock layer of the geologic formation a fossil is found in) to determine species identity in most cases .

Pteranodon sternbergi is the only known species of Pteranodon with an upright crest . The lower jaw of P. sternbergi was 1 @.@ 25 meters (4 @.@ 1 feet) long . It was collected by George F. Sternberg in 1952 and described by John Christian Harksen in 1966 , from the lower portion of the Niobrara Formation . It was older than P. longiceps and is considered by Bennett to be the direct ancestor of the later species .

Because fossils identifiable as P. sternbergi are found exclusively in the lower layers of the Niobrara Formation , and P. longiceps fossils exclusively in the upper layers , a fossil lacking the skull can be identified based on its position in the geologic column (though for many early fossil finds , precise data about its location was not recorded , rendering many fossils unidentifiable) .

Below is a cladogram showing the phylogenetic placement of this genus within Pteranodontia from Andres and Myers (2013) .

= = = Alternate classifications = = =

Due to the subtle variations between specimens of pteranodontid from the Niobrara Formation , most researchers have assigned all of them to the single genus Pteranodon , in at least two species (P. longiceps and P. sternbergi) distinguished mainly by the shape of the crest . However , the classification of these two forms has varied from researcher to researcher . In 1972 , Halsey Wilkinson Miller published a paper arguing that the various forms of Pteranodon were different enough to be placed in distinct subgenera . He named these Pteranodon (Occidentalia) occidentalis (for the now @-@ disused species P. occidentalis) and Pteranodon (Sternbergia) sternbergi . However , the name Sternbergia was preoccupied , and in 1978 Miller re @-@ named the species Pteranodon (Geosternbergia) sternbergi , and named a third subgenus / species combination for P. longiceps , as Pteranodon (Longicepia) longiceps . Most prominent pterosaur researchers of the late 20th century however , including S. Christopher Bennett and Peter Wellnhofer , did not adopt these subgeneric names , and continued to place all pteranodont species into the single genus Pteranodon .

In 2010 , pterosaur researcher Alexander Kellner revisited H.W. Miller 's classification . Kellner followed Miller 's opinion that the differences between the Pteranodon species were great enough to place them into different genera . He placed P. sternbergi into the genus named by Miller , Geosternbergia , along with the Pierre Shale skull specimen which Bennett had previously considered to be a large male P. longiceps . Kellner argued that this specimen 's crest , though incompletely preserved , was most similar to Geosternbergia . Because the specimen was millions of years younger than any known Geosternbergia , he assigned it to the new species Geosternbergia maysei . Numerous other pteranodont specimens are known from the same formation and time period , and Kellner suggested they may belong to the same species as G. maysei , but because they lack skulls , he could not confidently identify them .

= = = Disused species = = =

A number of additional species of Pteranodon have been named since the 1870s , although most now are considered to be junior synonyms of two or three valid species . The best @-@ supported is the type species , P. longiceps , based on the well @-@ preserved specimen including the first @-@ known skull found by S. W. Williston . This individual had a wingspan of 7 m (23 ft) . Other valid species include the possibly larger P. sternbergi , with a wingspan originally estimated at 9 m (30 ft) . P. occidentalis , P. velox , P. umbrosus , P. harpyia , and P. comptus are considered to be nomina dubia by Bennett (1994) and others who question their validity . All probably are synonymous with the more well @-@ known species .

Because the key distinguishing characteristic Marsh noted for Pteranodon was its lack of teeth , any toothless pterosaur jaw fragment , wherever it was found in the world , tended to be attributed to Pteranodon during the late nineteenth and early twentieth centuries . This resulted in a plethora of species and a great deal of confusion . The name became a wastebasket taxon , rather like the dinosaur Megalosaurus , to label any pterosaur remains that could not be distinguished other than

by the absence of teeth . Species (often dubious ones now known to be based on sexual variation or juvenile characters) have been reclassified a number of times , and several subgenera have in the 1970s been erected by Halsey Wilkinson Miller to hold them in various combinations , further confusing the taxonomy (subgenera include Longicepia , Occidentalia , and Geosternbergia) . Notable authors who have discussed the various aspects of Pteranodon include Bennett , Padian , Unwin , Kellner , and Wellnhofer . Two species , P. orogensis and P. orientalis , are not pteranodontids and have been renamed Bennettazhia oregonensis and Bogolubovia orientalis respectively .

= = = List of species and synonyms = = =

Status of names listed below follow a survey by Bennett , 1994 unless otherwise noted .