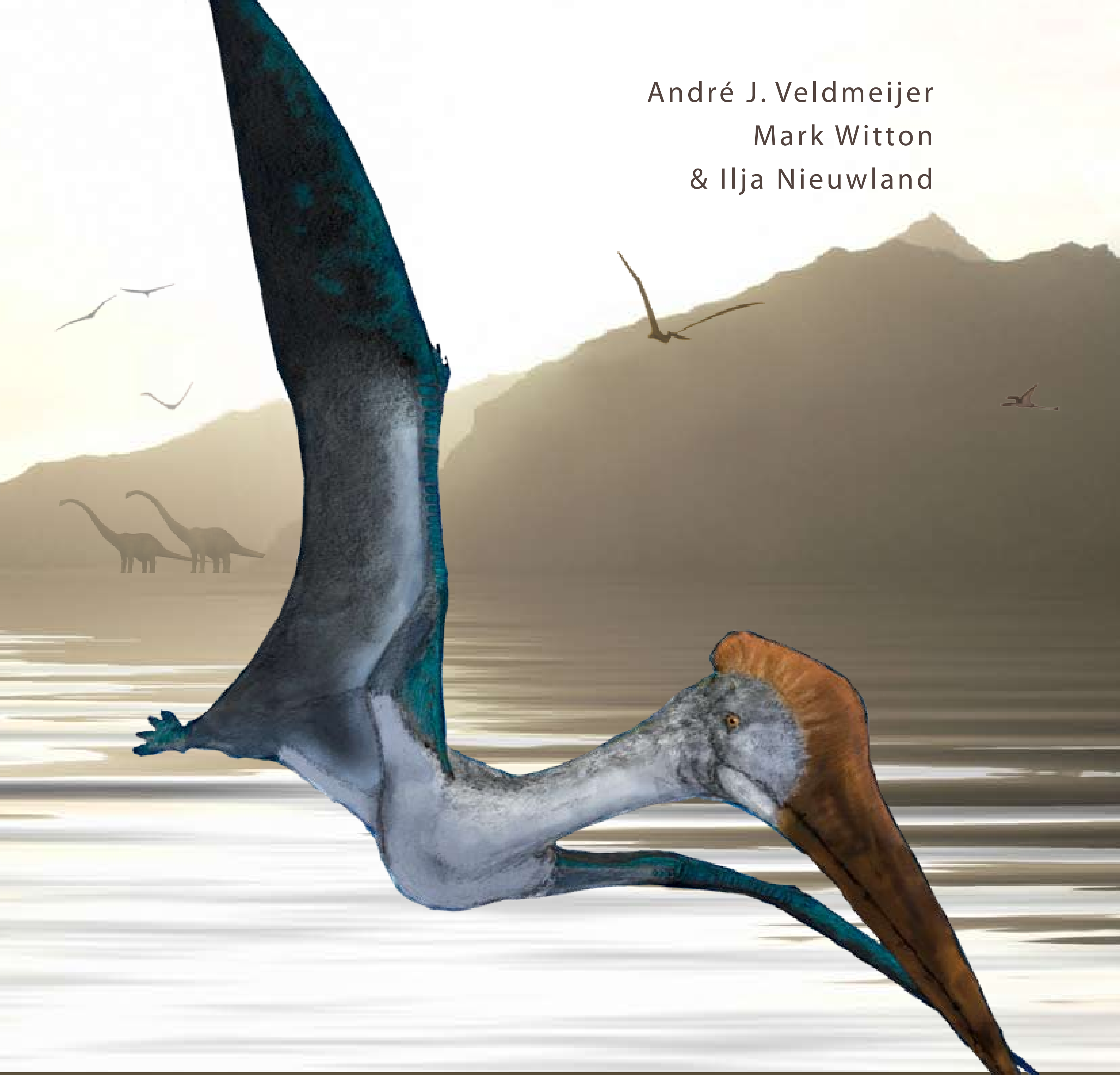
André J. Veldmeijer
Mark Witton
& Ilja Nieuwland



PTEROSAURS

FLYING CONTEMPORARIES OF THE DINOSAURS

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Sidestone Press

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Preface

Many pages in books, magazines and internet sites are filled with plates of prehistoric animals that are brought 'back to life' through a collaboration between artists and palaeontologists. The result, conveniently called 'palaeo-art', offers a glimpse of a long forgotten world, inhabited by creatures that we will never meet in the flesh. But reconstructions on paper, TV or computer screen do not really let us experience prehistory. Images of extinct animals and their habitat do not give a real impression of the incredible size of some of these animals. Moreover, one cannot see the animal in three dimensions and look at them from various angles. That is why the dioramas of decades ago, such as the one at London's Crystal Palace, were so popular and refreshing: they offered a possibility to walk among extinct animals 'in their own world'. This was the only way to appreciate the size and, sometimes bizarre, anatomy of these creatures.

Often, in museums and exhibitions about palaeontology, all attention is focused on the dinosaurs or occasionally some large mammal such as a mammoth. Pterosaurs and other prehistoric animals are rarely seen and so we felt it was time to change this focus. This book aims to refocus attention on these neglected creatures. Not only are these extinct animals illustrated in beautiful drawings, but the last chapter explains how three-dimensional models have been created. Whilst flying reptiles are central to this chapter, the techniques for making such models are fairly universal, save of course for some specific problems related to flight. The inspiration for the models was an exhibition honouring the 350^{th} anniversary of the prestigious British Society in London. After this short exhibition, the models were shipped to the Natural History Museum in Rotterdam in The Netherlands, to become part of an exhibition on pterosaurs (22 September 2010 - 6 March 2011) that included many important fossils from several European collections.

The present book consists of two interlinked parts. After a short explanation of the science of palaeontology and its history, we explain what pterosaurs are, how they looked like and when and where they lived. The chapter about the models at the end of the book shows the results of the latest scientific research. Interlinked are several 'Mark explains' stories. These are reworked from the weblog of Dr. Mark Witton and marked with his self portrait. Mark is a young, English palaeontologist and specialist in Azhdarchid-pterosaurs, but is also a talented artist and narrator. The stories are enhanced with his beautiful art and have a strong focus on how the animals actually must have lived and show how diverse this group of animals was. They take the reader back in time…

Figure 1. The Cretaceous pterosaur Quetzalcoatlus *was one of the real giants with a wingspan of about 10 metres. Here, several animals soar above a river with wading dinosaurs.*

Acknowledgement

First and foremost we thank Paul Nicholson of Cardiff University (U.K), who encouraged us to translate this book from the original Dutch text. Although from the beginning there was the intention to produce an English version of the book, the lack of time prohibited it until Paul offered his invaluable help. The many hours and large efforts to help with the proper translation of the parts of the text that were originally written in Dutch is greatly appreciated. Thanks also to Salima Ikram who proofread the English manuscript.

I (AJV) am indebted to many people for the organisation of the exhibition as well as for contributions to the book. Without good collaboration with my English colleagues at Portsmouth University – particularly Mark Witton, Dave Martill and Bob Loveridge, this project would not have been possible. For this reason I would also like to thank 'Dino' Frey of the Karlsruhe Natural History Museum for allowing the loan of many of the extraordinary fossils under his care for exhibition in The Netherlands. Dino has also helped in the loan of the *Dsungaripterus*-model (with thanks to the *Stiftung Hirsch* Karlsruhe). Erwin Meerman has spent many hours of his spare time to create the superb models and Adri 't Hooft not only made the images but accompanied me to Germany to collect the loans from Karlsruhe and Munich as well as making similar visits himself. George Hall is acknowledged for the translation of parts of the text as well. However, not one of my projects would be complete without the understanding and help of Erno Endenburg, for which I am truly grateful.

Thanks too to Cor Strang, Dave Hone, John de Vos, Kees Moeliker, Linda Oswald, Marjan Scharloo, Mike Everhart, Mikko Kriek, Oliver Rauhut, Reiner van Zelst, Rochus Biesheuvel, Ross Elgin, Larry Witmer for heir help and the American Museum of Natural History (New York), the Bayerische Staatsammlung für Paläontologie und Geologie (München), the Iwaki Museum for Coal Mining and Fossils (Iwaki), the Jura-Museum Eichstätt, the Staatliches Museum für Naturkunde (Karlsruhe), the National Science Museum (Tokyo), the NCB Naturalis (Leiden), the Sedgwick Museum (Cambridge) and Teylers Museum (Haarlem) for permission to publish photographs.

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Loans from: the American Museum of Natural History (New York), the Bayerische Staatsammlung für Paläontologie und Geologie (München), the Staatliches Museum für Naturkunde (Karlsruhe), the NCB Naturalis (Leiden) and Teylers Museum (Haarlem).

Introduction

Pterosaurs (meaning 'winged lizard') were the first vertebrates to fly (figure 1) and are therefore often referred to as 'flying reptiles'. However, like the dinosaurs, they are only remotely related to modern reptiles. For the same reason, it is not correct to refer to pterosaurs as 'flying dinosaurs'.

As far as we know to date, pterosaurs evolved late in the Triassic (over 200 million years ago, figure 2). By the end of the Cretaceous (about 65 million years ago) they became extinct, together with, among other creatures, the dinosaurs. No relatives survived, due to which it became impossible for the palaeontologists to compare them from an anatomical point of view to living relatives as pterosaurs do not look alike any animal that lives nowadays. This makes it even more difficult to understand these prehistoric animals relative to other extinct fauna such as dinosaurs and even living birds. Fortunately, over the last 50 years or so there has been a wealth of new finds and an enormous increase in research. The pace of research is so fast that, even in writing an update, it is already slightly outdated.

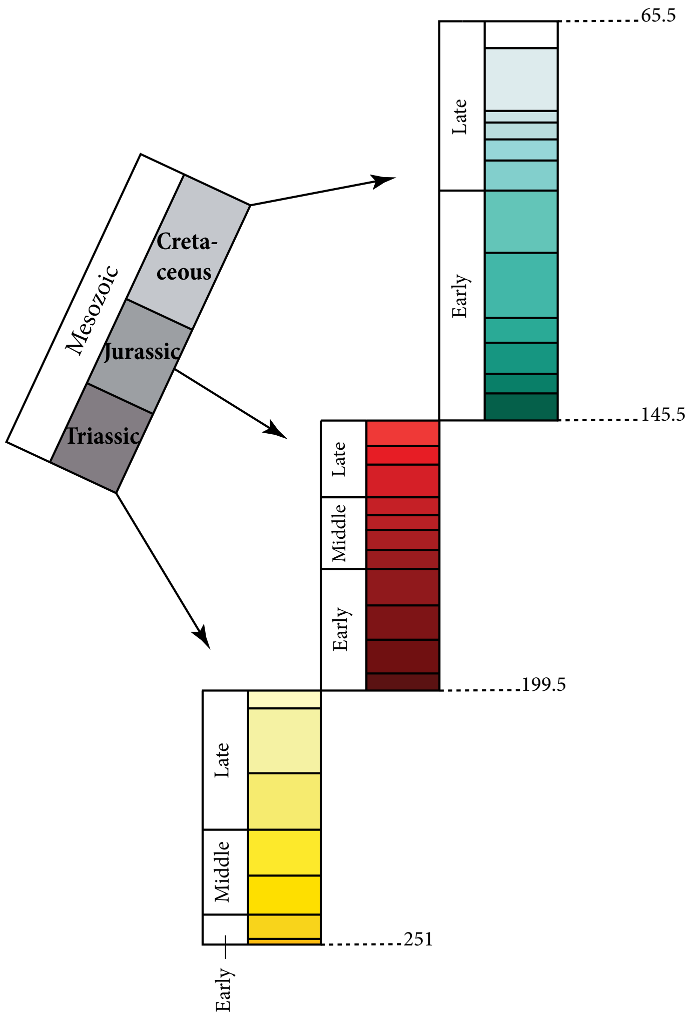
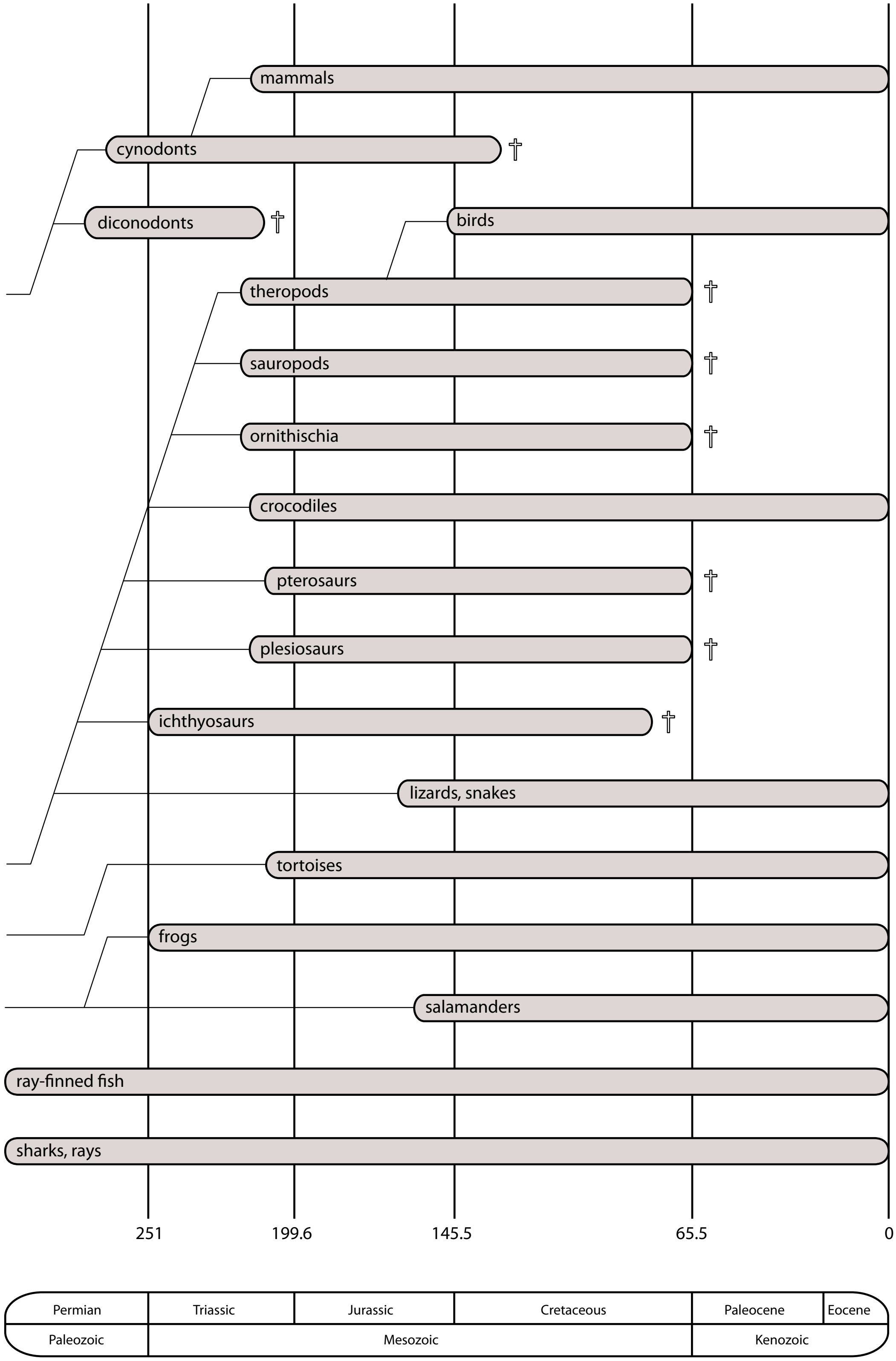


Figure 2. The oldest fossils of pterosaurs are from the Late Triassic, but their evolutionary origin is still further back in time. Pterosaurs became extinct, together with many other groups of animals such as the dinosaurs, at the end of the Cretaceous. Below is an overview of the most important vertebrates that roamed the earth as contemporaries of the pterosaurs.


mammals
cynodonts
diconodonts
birds
theropods
sauropods
ornithischia
crocodiles
pterosaurs
plesiosaurs
ichthyosaurs
lizards, snakes
tortoises
frogs
salamanders
ray-finned fish
sharks, rays
251
199.6
145.5
65.5
0
Permian
Triassic
Jurassic
Cretaceous
Paleocene
Eocene
Paleozoic
Mesozoic
Kenozoic

What are fossils?

Fossilisation is usually simply the replacing or rebuilding of biological parts by minerals (the same building materials that make stone). Thus, palaeontologists do not study real bone. But there are also some fossils, which are produced without replacement by minerals: insects trapped in amber are a good example.

Fossilisation is a very rare process. This is perhaps difficult to understand if you think of all the fossils that are housed in the many museums all over the world. But if you realise that there have been billions and billions of organisms, than perhaps it is a bit easier to understand how rare and unique fossils are.

A prerequisite for fossilisation is burial in a layer of sediment that protects the cadaver from rotting or scavenging. The hard parts of an organism, such as bones and teeth, have the greatest chance of becoming fossilised. The soft parts such as the flight membranes and the intestines are only preserved under exceptional conditions and are therefore even more rare than other fossils. There are fossils of pterosaurs that are so well-preserved that one can study the skin (see figures 63 and 71) and some have a partially intact body covering (a sort of hair). There are even several examples of stomach contents from pterosaurs (see figure 74). Moreover, there are quite a few imprints of the animals, such as the tracks (figure 3) or impressions of the skin. Fossilised pellets and faeces have also been found.

There are between five and six thousand fossils of pterosaurs (but more and more are being found every day) among which are several more or less complete skeletons. Most of the fossils we have are no more than bone fragments a few cen-

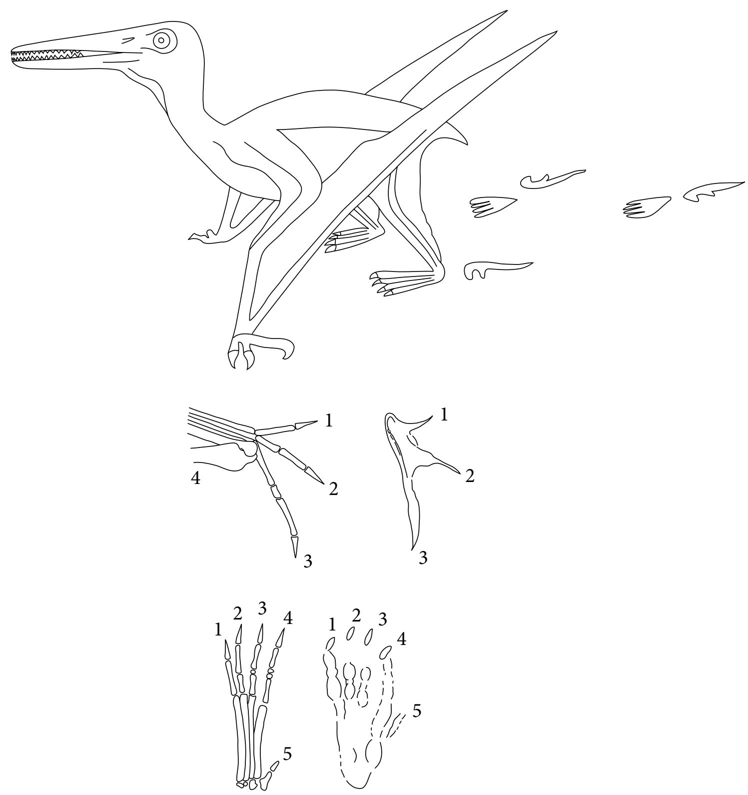


Figure 3. Top: A Pterodactylus *leaves his footprints in the soft, wet sand. Below: The hand and foot of a pterosaur and the imprints left by them.*

Figure 4. Several examples of pterosaur finds from the famous Cambridge Greensands in England. An estimated 2000 small bones were found here, most of which are not more than a few centimetres in size. Fossils from this place were described as early as the mid-19th century, but they remain the subject of heated scientific taxonomic debates to this day.

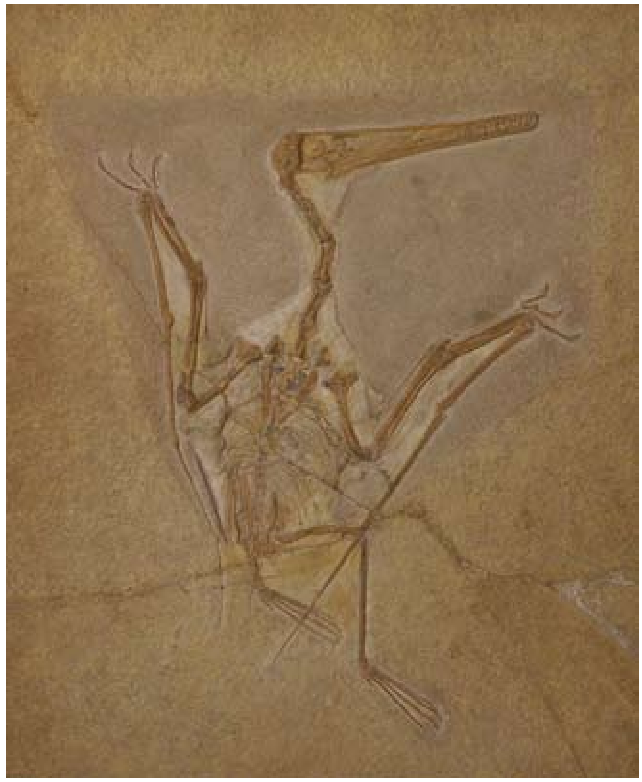
timetres long (figure 4). Moreover, skeletons are often incomplete or jumbled; the head, for example, being relatively heavy compared to the body, is easily broken off after decay of the soft tissue (figure 5).

Palaeontologists distinguish two types of pterosaur fossils. Most sites (you can read more about the most important sites in ‘Where did pterosaurs live?’), among which Solnhofen in Germany (figure 6) and the Crato Formation in Chapada do Araripe in northeast Brazil, produce slabs (figure 7): the animals are as flat as a coin. In the United States (Niobrara Formation, Kansas) fossils are found, mainly of *Pteranodon*, that are not in slabs and sometimes entirely separated from

Figure 5. In rare cases a dead animal is immediately covered by sediment, allowing for undisturbed fossilisation (see figure 6). More often the skeleton is severely disturbed by scavenging or because the carcass has been transported by water. Here you see two examples. Both lack the skull because it is much more prone to becoming detached.

the matrix but are equally flat nonetheless (figure 8). Especially from the Santana Formation, also in Chapado do Araripe in northeast Brazil, are fossils that are preserved in three dimensions: minerals are deposited around the bones after which there is exchange of the biological elements and minerals (figure 9).

1 cm



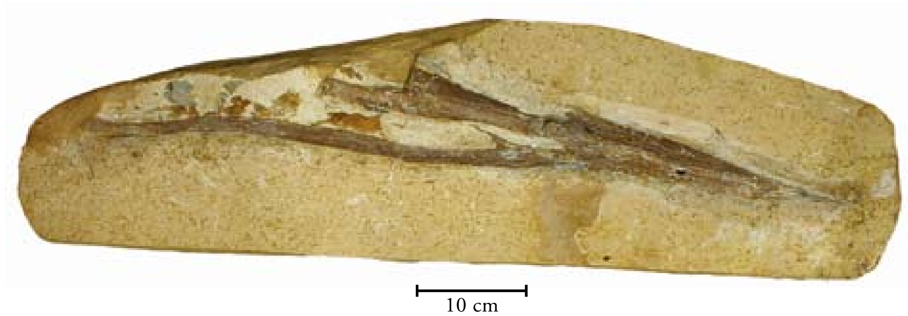
2 cm

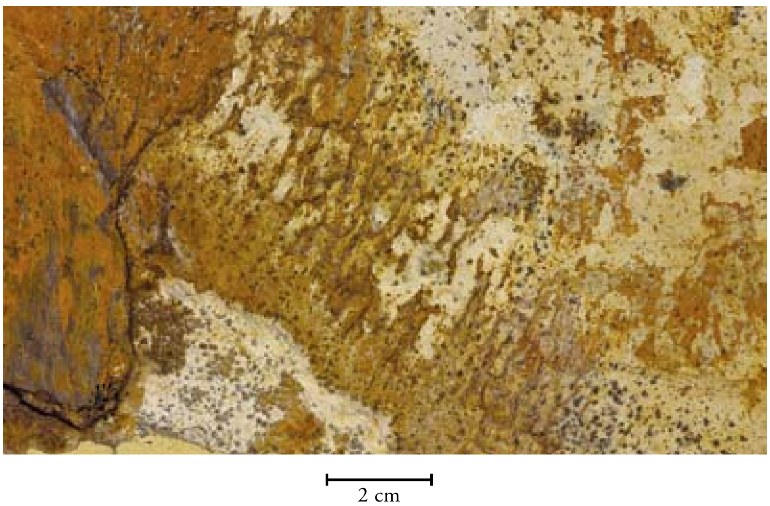
*Figure 6. Two examples of Solnhofen plate fossils, which clearly show how superbly preserved the animals are. Left a baby-*Pterodactylus kochi *and right a fully-grown animal of the same species, including a detail of the skull. Sometimes, even the soft parts of pterosaurs, such as their skin, is preserved, which is clearly visible in the adult animal. Both fossils come from the Jurassic.*

What is palaeontology?

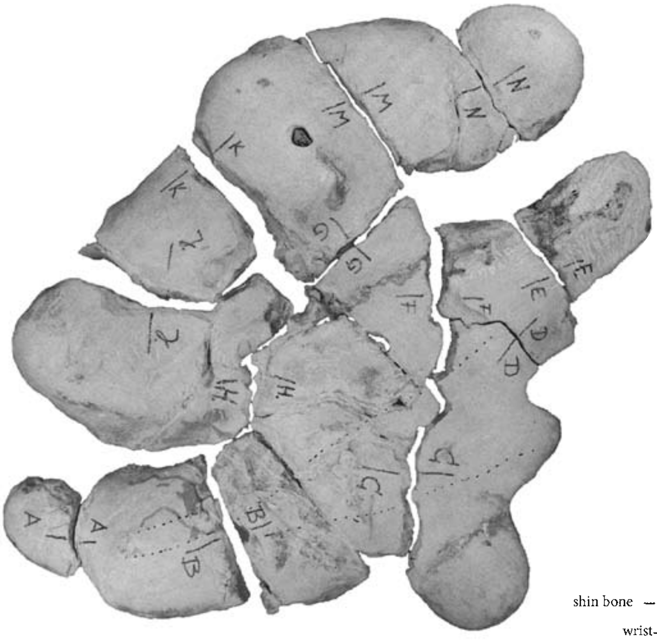
Palaeontology is the study of fossil remains of plants and animals, divided in several sub-disciplines. Often people think that archaeology and palaeontology are the same, but this is not true: archaeology is the science that studies past human activity. An overlap, therefore, might occur with early humans of which the fossil

Figure 7. Two examples of plate fossils from the Crato Formation of Chapada do Araripe, northeast Brazil. Both skulls are of toothless Cretaceous pterosaurs: Lacusovagus magnificens *(previous page and top right) and* Tupandactylus navigans *(centre). The black arrow indicates the crest that largely consists of skin. The white arrow indictates the part from which the detail is taken. Clearly visible are the bundles of fossilised tissues at the edge of the bone, which is an extension of the bones of the skull.*





► *Figure 8. Example of a fossil from the Niobrara Formation, Kansas (United States). This skeleton is put together from real bones but from different animals. Thus, it is not found as it is depicted. See also 'Mark Witton explains:* Pteranodon*', pp. 92-95.*



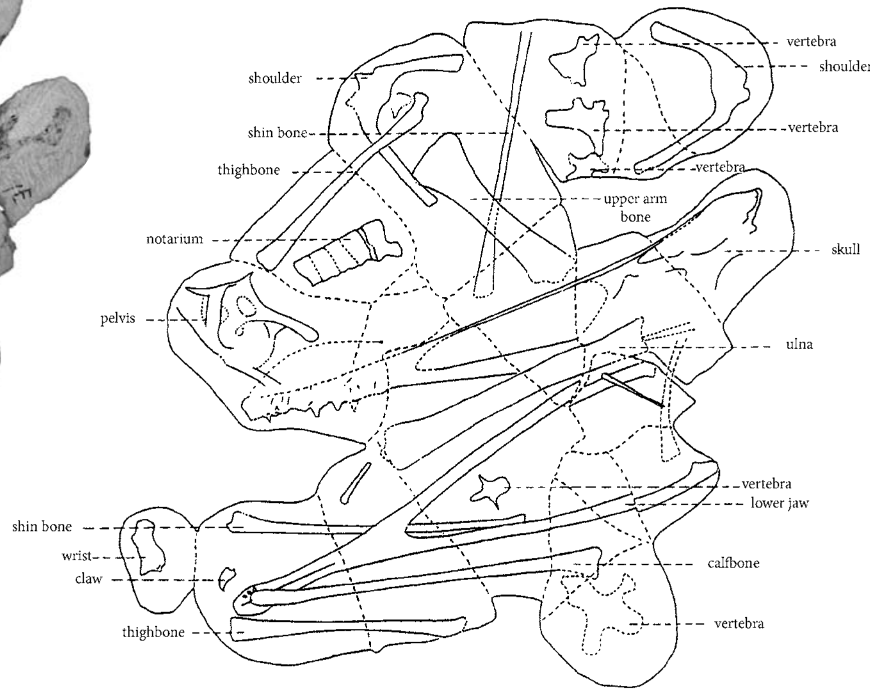


Figure 9. The Santana Formation of Chapada do Araripe, northeast Brazil produces limestone nodules (top left); the bones are preserved within these lumps of stone. Preliminary research with X-rays approximately shows which bones are present (top right). Splitting the nodules shows where the fossils are located (bottom).

Mark explains

Dimorphodon

You know the story … an object has been examined time after time and everyone believes that its structure is obvious. It is forgotten about, and subsequently lies on the shelf gathering dust. Now and again someone with a new idea comes along to have a look, only to allow the object to sink back into oblivion. That was also more or less the case with the drawing of *Dimorphodon*. More than a year after that drawing had seen the light of day, the end product finally arose.

Dimorphodon… the first fossil was found as far back as 1828 by the renowned English fossil collector Mary Anning. Fossil remains of this animal were also described by William Buckland (1829) and Richard Owen (1858). Several new finds have been described since then. In addition, *Dimorphodon* has played an important role in the discussion in the way in which pterosaurs moved about on land. This discussion was primarily conducted by two prominent palaeontologists: Kevin Padian and Peter Wellnhofer. So we now know all the secrets of this primal animal, you might think. Or maybe not …

I have spent a good deal of time investigating the weight of flying reptiles. A new method indicated that previous estimates had been much too low. But the strangest things happened with *Dimorphodon*. It turned out that its weight had been estimated as being twice as large as was usual for an animal with such a wingspan (a little more than one metre). Recalculations produced the same result. In other words, *Dimorphodon* is truly much heavier than it ought to be! I am not the first person to discover this. There is at least one other study that produced an atypical weight.

So, why is *Dimorphodon* so plump? The answer is simple: everything about this pterosaur is out of proportion, but the most striking fact is that its head is gigantic in relation to its wingspan. In addition, the hind legs and torso are much larger than you would expect in a pterosaur of this calibre. As is also the case with chubby people: it's not fat, it's those heavy bones … This, in itself, is not actually a major problem, but if you calculate the consequences for flying it does become much more interesting. A detailed analysis of the shape of the wings of *Dimorphodon* suggests that its flight differed substantially from that of other pterosaurs. In fact, it seems that it only took to the skies with great reluctance!

Isn't that strange … a flying reptile that flies as little as possible? Nevertheless, it is quite logical if my reconstructed wing shape is correct. In my view, *Dimorphodon* had broad but short wings. In itself, this is not so unusual, as many pterosaurs had the same. But the deviant weight means that its wingload (the weight divided by the surface area of the wings) was much greater than normal. Therefore the beast had to work much harder to triumph over gravity. Moreover, its ability to soar and glide was poor due to the ratio between its weight and its size. As a consequence it was forced to flap its wings more frequently, which demanded much more energy than was the case with a similarly-sized pterosaur such as *Rhamphorhynchus*.

Our modern birds also include sorts that are much too heavy for their wingspan: turkeys, pheasants and rails, to name but a few. They can

fly but only do so in short flights when they have to cover a larger distance in a short time or when they are attempting to escape from a predator.

Just as *Dimorphodon* probably was, these birds are good at taking off quickly – occasionally even vertically – but they are not capable of flying long distances because they simply do not have the capacity to do so. Accordingly, if it had to migrate, *Dimorphodon* would be better off seeking a lift from a passing prosauropod than undertaking the journey under its own steam.

Okay … As far as I know, this is a flying style for a pterosaur that has not previously been proposed! Certainly, colleagues have indeed expressed doubt about the flying capabilities of some pterosaurs, but you should see that in the context of the old idea that flying reptiles were clumsy, squawking, archaic gliders that had to depend upon high, steep cliffs and a strong wind to give them lift. What I propose here is completely different: *Dimorphodon* as a small, active fusspot, frantically flapping its wings, with all the nervous energy that you can imagine for a warm-blooded creature with a rich coat or fleece, but one unable to fly long distances without completely exhausting itself.

Of course, this kind of theory on the ecology of *Dimorphodon* leads to discussion. Many pterosaur scholars prefer to regard the beast as a fish or squid-eater. Some of them even go as far as to ascribe puffin colours (including the jaws, as well as a row of newly caught snacks) to the prehistoric animal. Well, this theory should be immediately forgotten, because there is nothing in the anatomy of *Dimorphodon* (or any other pterosaur) that indicates a fishing technique similar to that of the puffin.

I invariably become suspicious when the combination of *Dimorphodon* and fish is articulated. The short neck, the large, coarse skull and strongly varying teeth would seem to be a disadvantage when compared to the features of 'traditional' fish-eaters with their longer necks, slender jaws and teeth that match in form and dovetail together (as shown in figure 40, for example). Moreover, the idea of fishing ignores the development of *Dimorphodon*'s limbs. Its strong limbs, well-developed hands and feet, with long and deep but narrow claws, are advanced features that are important for climbing. The extended middle phalanges indicate that *Dimorphodon* was equipped with genuine 'crampons' and the corresponding 'rigging' to scramble over cliffs and rove around in treetops. Thus, *Dimorphodon* appears to have been much happier with his climbing lifestyle than with any water-based one. And if its prey fled to another tree or if it suddenly fell, the capability for explosive flight would come in very handy.

remains are found together with the objects they made and the traces they left behind. But pterosaurs were already extinct for many million years before the ancestors of modern humans came onto the stage of evolution.

It is a long time ago that a palaeontologist only looked at fossils with a magnifying glass or microscope (figure 10) and comparing the bones of various animals. This way of working is called comparative anatomy and is important to see if the newly discovered fossil belongs to a species that we already know or if it is a new species. And this is of importance for the reconstruction of evolution of animals, but also to understand variation: a large variation means that there were a lot of opportunities for animals to specialise.

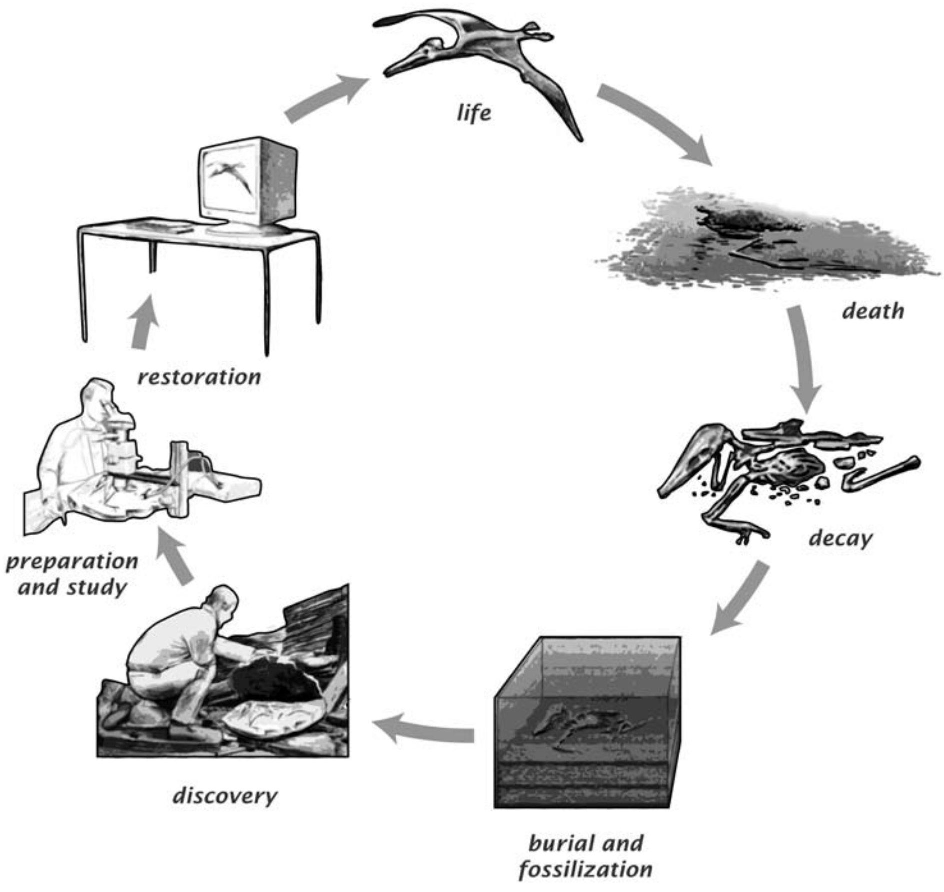
There are many modern research techniques that are an important addition to the basic palaeontological work of comparative anatomy. CT-scanning (Computer Tomography) is similar to X-ray in that it is a radiograph. However, X-ray makes sort of a portrait of the skull – or the unprepared fossil to see which bones there are and where – but the CT-scan makes cross-sections of something (figure 11). The radiation in both techniques is the same but used differently. CT-scanning is done at regular intervals, resulting in a series of images that you can play after each other. Another, fairly recent technique to make details of fossils more visible is to photograph them under UV light: especially the soft parts, like skin, reflect distinctly. This technique reveals details that were not visible before.

The good thing about these techniques is that they do not change the fossil: they are non-destructive. But there are also destructive research techniques. Several scientists from Portsmouth University have sacrificed several teeth that they found

Figure 10. Studying fossils is time-consuming and involves a range of scientific equipment. Here a microscope is seen in use.

in Morocco, to study the internal structure with scanning electronmicroscopy. In order to be able to do this, they had to cut the teeth with a diamond saw, etched them using acids and applied a microscopically thin layer of gold palladium.

The detailed study of fossils (figure 12) enables the palaeontologist to 'rebuild' the animal. But you need to know more than only the bones: namely the rest of the anatomy. You can do this by comparing it with other, living relatives (as explained, difficult for pterosaurs), or to rebuild the animal (as object or digital) and applying muscles and ligaments etc. and see how they were attached and how they functioned. But to get as detailed a picture as possible, the palaeontologists also need to know of the environment the animals lived in, the climate, the flora, the other animals and, which food was available.



▲ *Figue 11. CT-scan images in sequence of the skull of* Coloborhynchus spielbergi, *housed in the NCB Naturalis, Leiden, The Netherlands. The arrow indicates the brain cavity; its shape is clearly visible (see figure 72).*

► *Figure 12. When an animal dies and is rapidly covered by sediment it may become fossilised. Millions of years later, a palaeontologist may find and excavate it. After careful study the animal can be 'brought back to life'.*

Mark explains

Dsungaripterus

The powerful *Dsungaripterus* from the Early Cretaceous period in China. This animal was not at the front of the queue when beauty was handed out. It had a jaw full of large, squat teeth that protruded from its curved jaws, small beady eyes and a greatly oversized skull consisting of thick, inelegant bones. If you compare this to the slender, streamlined skulls of *Pteranodon* or *Tupandactylus* it is truly an ugly duck, but one that does not turn into the beautiful white swan. But it does not need beauty to be cool! With its formidable teeth, this creature could bite through the hardest crustaceans. And the robustness of the rest of its skeleton tells us that this was a real tough guy. *Dsungaripterus* is an example of the victory of functionality over beauty.

The skull of this pterosaur is rather strange due to its diet, which almost certainly consisted of food from the sea, such as bivalve shellfish (our mussel is an example of a modern bivalve marine mollusc). We know this from the structure of its set of teeth. *Dsungaripterus* is the only pterosaur whose teeth increase in size as you go further into its jaws. The teeth themselves are wide, flat and very robust. This is a strong indication of a diet that consists of extremely hard food that you would normally have to treat with a hammer and anvil in order to reduce it to something devourable. Having the largest teeth at the back is undoubtedly an excellent set-up to cope with this kind of work: the biting strength here is much greater because the distance to the jaw muscles is much smaller. However, it is somewhat bizarre that the teeth right at the back of the upper jaw do not have counterparts in the lower jaw. This provokes questions with regard to their presumed role in the crushing of shellfish. The toothless tip of the jaw played no role in this crushing, but it was certainly involved in taking the prey. If you look closely at the jaws, you will see that these beak-like points could not be completely closed because the lower jaw is much more rounded than the upper jaw. This is undoubtedly an adaptation for grabbing and holding round shellfish.

If the skull was formed like the typical pterosaur skull, it would break into thousands of pieces if *Dsungaripterus* were to bite a crustacean. This is the reason why *Dsungaripterus* has densified skull bones that are built in such a way that they can absorb the shocks that arise in the crushing process. The openings in the skull of this pterosaur are very limited in size. One opening, however,

Dsungaripterus weii *in walking stance. This pterosaur from the Early Cretaceous of China had a wingspan of about 3.50 metres. The skeleton is a gift from the* Stiftung Hirsch, Karlsruhe *to the* Staatliches Museum für Naturkunde, Karlsruhe. *Cast.*

has remained rather large: the place where the jaw muscles pass through the bone. This indicates, of course, that these muscles must have been quite substantial, which is not surprising when your diet consists of crustaceans and suchlike. Strong jaw muscles and teeth … not a configuration you would want to explore with your fingers.

But this is not all. The bone structure has a corresponding design. The hollow bones of most pterosaurs have very thin bone walls (often less than one millimetre thick, see figure 66) but – as you already guessed – this is not the case with *Dsungaripterus*. This fellow has substantially thicker bone walls (cortical bone), a feature suited to an animal whose life is largely ground-based. Thicker bone walls suggest a heavier animal, and having more weight is not really a good way of easily remaining in the air. In addition, it had pretty robust hind legs whose shape is such that they are well adapted to absorb the shocks of heavy landing. It has been suggested that *Dsungaripterus* only made short flights, so that natural selection arose on the basis of good landing qualities after brief, powerful, active flying trips. This is difficult to prove, but it sounds reasonable. There are also many bird sorts that only make short flights, and I see no reason why there could not have been pterosaurs that also lived like this. Do not forget that *Dsungaripterus* had wings whose shape indicates active flying rather than long-distance gliding. So they were probably more on the ground than in the air! Oh yes, I forgot to mention it: *Dsungaripterus* fossils have only been found in terrestrial sediments...

FOCUS

Names

How do we know the names of all these animals? If bones are compared with bones that already have been given a name and the palaeontologist recognises enough differences, he or she can create a new name for the animal. But there are strict rules for this procedure, written down in a thick book, called the 'International Code for Zoological Nomenclature'. This contains a detailed explanation as to when a (new) fossil may get a new name. First, the fossil must be housed in a public collection. That is important, because the fossil on which a new species is based is *the* fossil to which all new finds have to be compared (a so-called 'holotype'). It becomes the standard. Recognising different species is important, because it gives us insight in the evolution of the animals, as well as in the diversity of a certain group. Sometimes scholars are vain and bend the rules to make a new species because part of the official name of an animal is the name of the scientist, thus linking them to it forever! The names of species are always in Greek or Latin and, so that everybody in the scientific world can understand them. These names are written in *Italic.* Often the name refers to a known part of the animals or a certain behaviour. *Dimorphodon* for example, means 'two forms of teeth' and refers to the two types of teeth the animal had. *Lacusovagus* means 'lake wanderer' because the animal lived in a water-rich environment. Often animals are named after people, such as the pioneer of pterosaurology Peter Wellnhofer in *Tapejara wellnhoferi,* or someone that has impressed the researcher, such as Steven Spielberg in *Coloborhynchus spielbergi.* But an animal can also be named after the place where it was found (*Anhanguera santana* after the Santana Formation in Brazil) and *Brasileodactylus* (after Brazil), or after indigenous peoples (*Tupuxuara longicristatus* after the Brazilian Tupi indians) or even after gods of ancient cultures (*Quetzalcoatlus* after the Aztec god Quetzalcoatl). The entire name of an animal could then for example be: *Pterodaustro guinazui* Bonaparte, 1970 (the year referring the year the first description was published). See the end of this book for explanation of the names of the animals that are mentioned.

A short history of our relationship with an extraordinary animal

During the largest part of our history, those animals which we nowadays call 'mythical' were an important part of human everyday reality. Unicorns, sphinxes, griffins and all sorts of other animals were revered and feared. That one could not see them did not really matter, because a large part of the world still lay unexplored and could hide any number of these creatures. Indeed, when explorers penetrated the interior of Africa and India, strange creatures such as elephants and giraffes turned out to be real. When first (dead) duck-billed platypuses were shown at the Royal Society meetings in the early years of the 19th century, they were greeted with ridicule – this was a very unlikely creature indeed. But even the platypus, that strange egg-laying mixture of duck, beaver and lizard, really crawled around somewhere on earth. So why could not the same apply to a unicorn?

Much of the base of this myth was created by fossils, the petrified remains of animals and plants. But the discovery of fossils also created curiosity. The Greek historian Herodotus, writing in 500 BCE, already noticed 'bones and spines in innumerable quantities, heaped in mountains, large and small' in Egypt – a possible reference to fossils. As Adrienne Mayor pointed out, fossils were commonly identified as belonging to giants, unicorns and griffins, but also to historical figures and (demi-) gods.

The most-feared creature remained the dragon. Dragons or dragon-like creatures make an appearance in many early cultures, around the world. But nearly everywhere, the image of the dragon is ambivalent: a symbol of darkness, but also often one of wisdom. In Europe the 'evil' dragon usually prevailed, with all the paraphernalia that went with it: black in hue, with razor-sharp teath, breathing fire and shooting through the air in bat-like wings.

When the famous painter and sculptor Benjamin Waterhouse Hawkins toured Britain around 1860 with a lecture about 'dragons', he did not need to introduce his audience to the subject. Hawkins' fame was based on the enormous sculptures of extinct animals he had erected five years earlier in the park surrounding Crystal Palace in Sydenham near London. The sculptures showed the latest insights in the lives of various dinosaurs and other 'antediluvian' (pre-flood) animals. Unfortunately, Hawkins had very little definite information to use for his reconstructions, which meant they were highly speculative. But certain animals were better known: Ichthyosaurs or 'fish-lizards', which had been uncovered on the English south coast, and the 'dragons' which Hawkins used to begin his talk: "*that wondrous animal, the pterodactyl, a combination of fish, reptile, and bird*". In glowing terms he described how he saw the pterodactyl as the original dragon, the basis for the medieval dragon, and also the story of Perseus and Andromeda. But what exactly was a 'pterodactyl'? That was a question, which by this time had troubled many a European scholar.

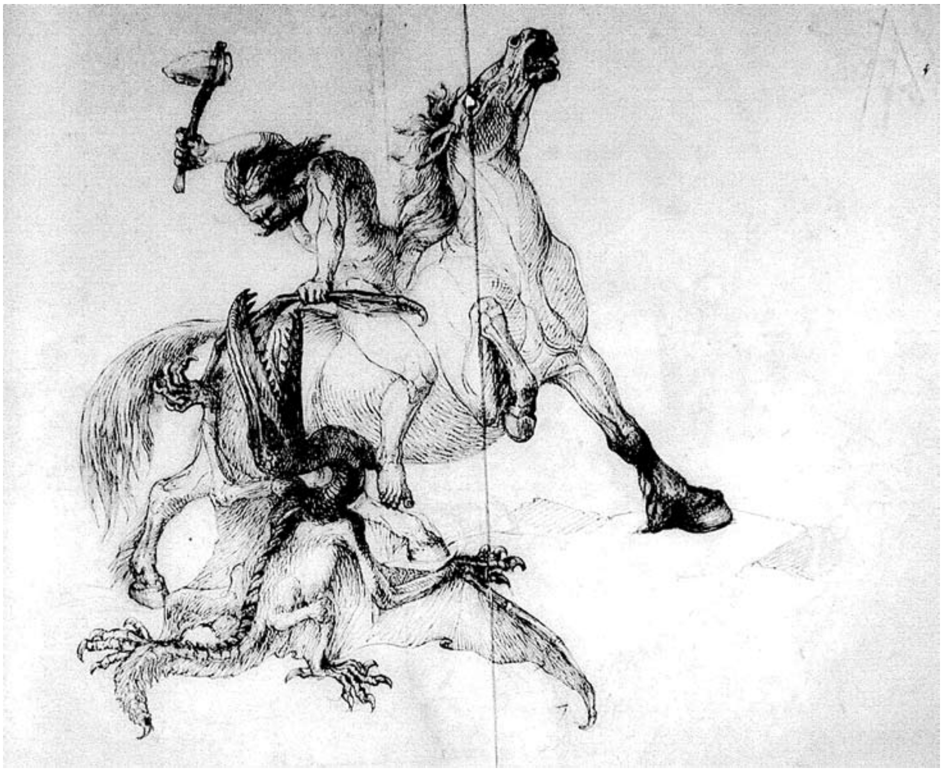


Figure 13. Fantasy sketch of a fight with a 'dragon', by Benjamin Waterhouse Hawkins, ca. 1860.

The animal had shown itself to the modern world for the first time in 1782, in a booklet written by the Italian monk and naturalist Cosimo Collini. Some years earlier, in 1757, he had found a smallish fossil among the collection of the Margrave of the Palatinate, in Marburg, Germany. It had taken him fifteen years to realise what lay before him. Clearly, it looked nothing like anything he had seen before, with a long beak filled with sharp teeth, and something that looked like a very long finger. Because the collection consisted mainly of sea animals, Collini concluded that it must have been a swimming animal, with long flippers. We might scoff at some of these ideas nowadays, but it is important to realise how very little these people had to go on. Dinosaurs had not been discovered yet, and zoological method was still in its infancy.

The German doctor, inventor and naturalist Samuel von Sömmering (1755-1830) inspected the animal as well, and rather doubted Collini's conclusion. He envisioned a flying animal, although he could not say how it should be classified. It clearly was not a bird, and it looked nothing like a mammal. He therefore gave it a name that referred to its wing: *Pterodactylus antiquus*, Latin for 'ancient winged finger'. Eventually, he would classify the animal as a bat. He was not that far off; his definition can, even in hindsight, be seen as a triumph for the methodical application of science. Soemmering was trained as a doctor (among various other trades) and applied his anatomical knowledge to the 'Mannheim riddle'. Not everyone was convinced, though. The famous Lorenz Oken also had a peek, and although he could not make much of it, he did think it was reptilian.

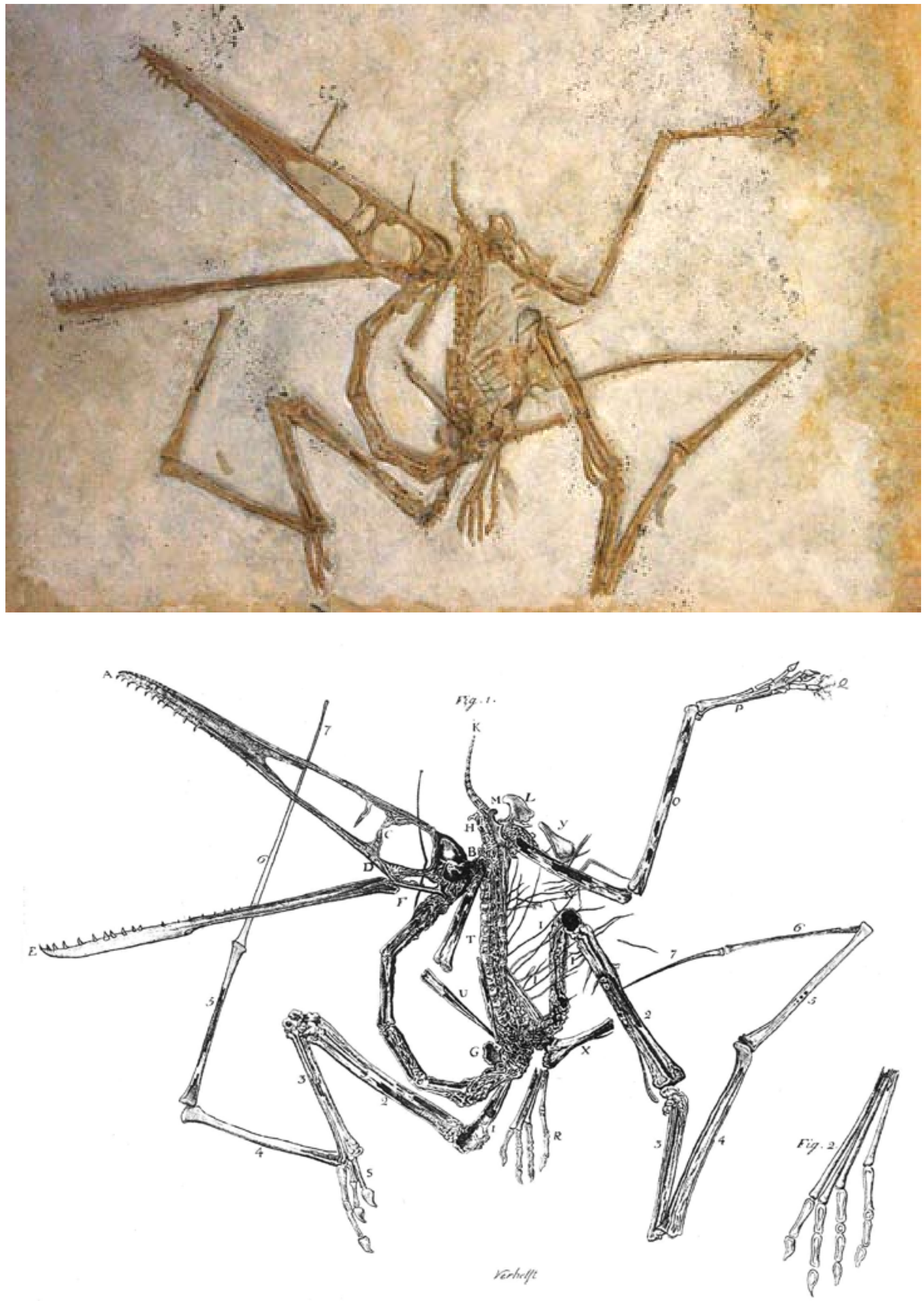


Figure 14. Top: Collini's pterosaur, named Pterodactylus antiquus *by Von Sömmering. Bottom: Drawing by Edig Verhelst jr. (1784).*

But, as usual in the early 19th century, the final say was with the famous French anatomist Georges Cuvier (1769-1832). Baron Cuvier had earned his reputation using the method of compartive anatomy: the systematic comparison of anatomical features to determine kinship between animals. After weighing the alternatives, Cuvier decided that this must have been a flying reptile, thus supporting Sömmering and Oken's earlier observations. But his conclusion went along with a warning:

"These are undoubtedly the strangest of all the creatures that are revealed in [my] book and that, when seen alive, would look like the oddest element of nature" – Georges Cuvier, *Ossemens Fossiles* (1812)

And that was a bit of a revelation. *Pterodactylus* began to show itself as a nail in the coffin of the concept that the entirety of Creation could still be found on earth as it could on the seventh day. That a unicorn might hide itself in some corner of a forest somewhere was, to some degree, plausible. But a *flying* animal?

Cuvier's conclusions were not shared universally: as late as 1830, the German anatomist Johannes Wagler sided with Colloni by condemning *Pterodactylus* to a swimming existence. And its reptilian affiliations were also not undisputed. Alfred Newman wrote in 1843 that he regarded the pterodactyls as flying and hairy marsupials – and took no small pride in his defiance of Cuvier.

However, by this time many more unlikely creatures had revealed themselves to science, and to the public. In 1819, the young country doctor Gideon Mantell (England) described the remains of the dinosaur *Iguanodon* – reconstructed later by Hawkins as a huge and rather overweight iguana. *Megalosaurus*, the horrible animal that had hunted *Iguanodon* was found only a few years later. The fragmentary remains of both animals made reconstruction difficult, but made all sorts of conjec-

Figure 15. Etching prepared for Edward Newman, 'Note on the pterodactyle tribe considered as marsupial bats', from The Zoologist *1 (1843), pp. 129-131.*

ture possible – and attractive. What it made clear, moreover, was that *Pterodactylus* was but one inhabitant of a primeval world that bore little resemblance to the present.

The average 19th-century citizen did not think this something to be ungrateful about because it had been immediately apparent to them that such a world was not one in which good cheer was predominant. The image used as a frontispiece to Thomas Hawkins' *Book of the Great Sea-Dragons, Ichthyosauri and Plesiosauri* (painted by John Martin) gives us some idea of the prevailing image of the ancient earth (figure 16). We see how the night is filled with a writhing mass of infernal creatures making life unpleasant for each other, biting and growling, with a pterodactyl pecking the eye from a mosasaur in the corner. It is an image directly from hell:

> *"the Spirit of Evil, opposed to the existence of all things, not excepting its own Suicidal-self. Its effects upon the first unguarded Sons of Man, gifted as they were with incredible moral and physical energy, must have been awful. To find themselves deposed from Authority as gods, and their falling Empire invaded by frightful Swarms of Venomous Beings, must have torn their hearts with rage and remorse"* – Thomas Hawkins, *Book of the Great Sea-Dragons, Ichthyosauri and Plesiosauri, Gedolim Taninim, of Moses. Extinct Monsters of the Ancient Earth (1840)*

Victorians roughly divided nature into two kinds: the sort that was cultivated and containable, like dogs, gardens and things from Olsen's *Book of British Birds*. On the other side of the equation stood wild nature, untameable and perilous. This view ended in what amounted to the near-extermination of African wildlife and the near-disappearance of the American bison. In which category *Pterodactylus* and its kind belonged was immediately apparent. But this revulsion also created fascination.

Figure 16. Frontispiece to Thomas Hawkins' The Book of the Great Sea-Dragons, Ichthyosauri and Plesiosauri, Gedolim Taninim of Moses, Excinct Monsters of the Earth *by John Martin (London, 1840).*

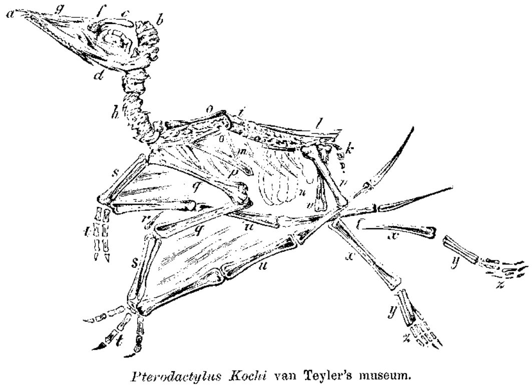
The image of *Pterodactylus* as an over-grown, hellish bat would continue for most of the 19th century, particularly in popular literature. Around 1900, readers were treated to essentially the same images that Hawkins had used, and the era's pulp literature makes frequent use of the 'phantom from hell'. Arthur Conan Doyle's wildly succesfull adventure novel, *The Lost World*, gives us a description of pterodactyls, but they are hardly the heroes of the story:

> *"The place was a rookery of pterodactyls. There were hundreds of them congregated within view. All the bottom area round the water-edge was alive with their young ones, and with hideous mothers brooding upon their leathery, yellowish eggs. From this crawling flapping mass of obscene reptilian life came the shocking clamor which filled the air and the mephitic, horrible, musty odor which turned us sick. But above, perched each upon its own stone, tall, gray, and withered, more like dead and dried specimens than actual living creatures, sat the horrible males, absolutely motionless save for the rolling of their red eyes or an occasional snap of their rat-trap beaks as a dragon-fly went past them. Their huge, membranous wings were closed by folding their fore-arms, so that they sat like gigantic old women, wrapped in hideous web-colored shawls, and with their ferocious heads protruding above them. Large and small, not less than a thousand of these filthy creatures lay in the hollow before us".* – Arthur Conan Doyle, *The Lost World (1912).*

However, professional palaeontologist, insofar as they existed at the time (palaeontology still had some way to go as an established branch of science) had by this time begun to see pterosaurs in a somewhat different light.

An important step had been the final identification of 'pterodactyls' as flying animals. At the Teylers Museum in Haarlem, the Dutch physician Tiberius Cornelis Winkler (1822-1897) stumbled across a fossil bought by the museum from Germany. To his amazement, the fossil of this animal, *Pterodactylus kochi*, seemed to show an imprint of skin running the length of the elongated finger. When Winkler published his observation in 1874, this seemed to take away all doubt about how these animals had lived. But although Winkler reinforced Cuvier's idea about the flight of these animals, he supported Newman's concept as well, by declaring that *'the winged fingers undoubtedly had a life similar to those as the modern bat'*.

By this time, pterosaurs had become treasured – and therefore costly – collector's items. A fossil belonging to *Ramphorhynchus*, a pterosaur with a long tail, was auctioned in 1880 for the considerable sum of 750 Pound Sterling. That might not seem as much by modern standards, but at the time that sum would have bought you a very comfortable home. Much of the cause of this development lay in the rise in 'serious' interest for life from the past. The 1880s in particular were a time of feverish activity. In the United States, Edward D. Cope (1840-1897) and Othniel C. Marsh (1831-1899) were involved in a fanatical competition to outdo one another with more and more sensational fossils. Huge *Brontosauruses*, *Diplodocuses* and *Camarasauruses* were pulled out of the ground by the dozen, it seemed. In Belgium, Louis Dollo (1857-1931) uncovered a complete herd of *Iguanodons*. The fragmentary evidence that had been making life difficult for scholars, was replaced by a much more complete archive. And the horror world that even Doyle still used, was gradually adjusted and replaced by a 'real' ecosystem, one that adhered



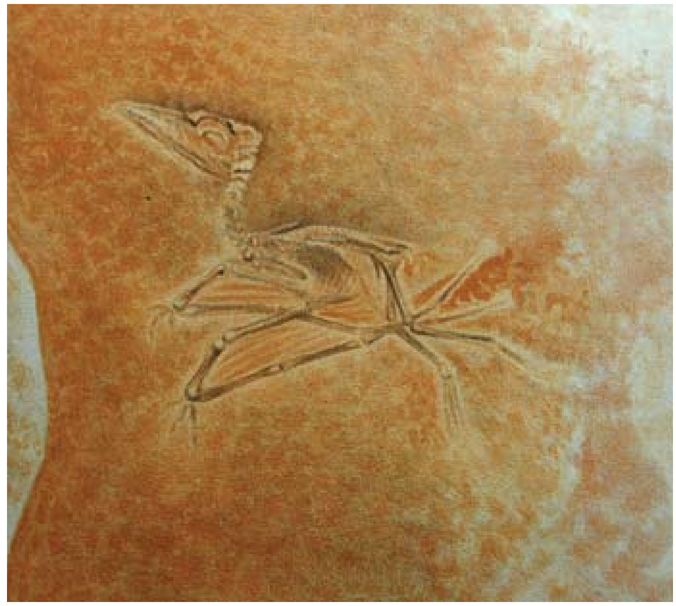


Figure 17. Right: Pterodactylus kochi *drawn in pastel by Tiberius Cornelis Winkler, curator of Teylers Museum in Haarlem, The Netherlands (*Archives du Musée Teyler*, Vol. III, Fasc. 4. Haarlem, 1874). Left: Pen drawing of the same animal.*

to the laws of modern nature, albeit with a dramatically different cast. The 'gentlemen researchers' of the Enlightenment were replaced by professional palaeontologists, who in turn had to make place eventually for professional museums and universities.

Up to this time, most pterosaurs had been found in Europe, mostly in central and southern Germany. Apart from the three genera *Pterodactylus, Ramphorhynchus* and its cousin *Dimorphodon*, not much material was known. That changed when in the summer of 1870, one of Marsh's crews found a number of hollow bones which reminded them of European pterosaurs. These remains were only much, much bigger. Although Marsh was initially convinced to be dealing with a gigantic form of *Pterodactylus*, eventually he decided that this had to be a distinct genus; he named the animal *Pteranodon ingens*, the 'gigantic wing without teeth'. It turned out to be an altogether different animal from *Pterodactylus*. *Pteranodon* was huge, with a wingspan of over seven metres. That was exceptional in it self, but the fact that the animal possessed a large crest on its skull turned it into a truly spectacular animal.

Pteranodon has since become a regular cast member of what can be called the 'dinosaur canon': an exclusive club of the most famous 'dinosaurs' that dominates the museum shop space, and which also contains *Brontosaurus* (nowadys called *Apatosaurus*), *Diplodocus*, *Tyrannosaurus, Dimetrodon* and *Ichtyosaurus.* The trivial fact that the animal is not even a dinosaur does not really seem to matter (it also does not in the case of the pelycosaurian *Dimetrodon* and the 'fish-lizard' *Ichthyosaurus*) (figure 18).

With the participation of Othniel Marsh, and more serious search efforts, the study of pterosaurs gained a different character. The English scholar Harry Govier Seeley (1839-1909) devoted a large part of his life to the study of pterosaurs, culminating in the book *Dragons of the Air* (1901). In this synthesis of knowledge of pterosaurs, Seeley tries to discredit the traditional image of pterosaurs as cold-blooded, slow gliders, and emphasizes their anatomical similarities with birds. Like birds, pterosaurs possessed hollow bones and an air-sac system that played a role in the animal's respiration, a four-chambered heart and various other adaptations for active flight. Nowhere did Seeley uncover any significant indications for a life similar to that of modern reptiles.

Seeley's book, although influential, nonetheless had to compete with the prevailing opinion that had turned dinosaurs – and therefore their cousins, the pterosaurs – into slow, dim-witted and generally uninspiring creatures. The general notion was of a world in which huge chunks of meat moved in slow-motion from one place to the next, supported by water or even 'thick air', not able to deal with changing circumstances. Towards the middle of the 20th century, this view came to totally dominate the image of pterosaurs as well, not only in popular works, but also among the scientific community. There was only marginal interest for palaeontology as a science; the dim-witted dullards that scientists had created out of virtually all extinct creatures were not really 'sexy'. Under these conditions, it was hardly surprising that almost no new discoveries of any great significance were being made in pterosaur palaeontology with the exception of *Sordes*.

It is therefore not entirely coincidental that the renewed interest in pterosaurs only took place after their cousins, the dinosaurs, had become the subject of new study, thereby propelling palaeontology in general again into the public and scientific centre of interest. Over the course of the 1960s, a new generation of palaeontologists put forward a dramatically different image of dinosaurs and pterosaurs as active, warm-blooded, aggressive (sometimes too aggressive) animals that deserved

Figure 18. Pteranodon *as part of the façade of the Berlin Aquarium (Heinrich Harder in co-operation with Gustav Tornier, 1913).*

to be taken seriously. The more long-term consequences included a strong development of vertebrate palaeontology as a science, and a *dinomania* that has never ceased since.

In 1971, Douglas Lawson uncovered an enormous wing in Texas – one that was considerably larger than that of *Pteranodon*. In subsequent years, a number of animals were uncovered that were eventually given the name *Quetzalcoatlus* – a reference to the Aztec god (and flying snake) Quetzalcoatl. The largest animal had a wingspan of about thirty feet – thereby dwarfing *Pteranodon*, who had been described as the largest-possible flying animal.

Giant forms such as *Quetzalcoatlus* and *Pteranodon* appear to have developed as a consequence of the selective pressure caused by birds. After the early Cretaceous smaller forms such as *Pterodactylus* vanished, whereas the largest pterosaurs would last as long as the dinosaurs. As small pterosaurs were out-competed by birds, the route of least resistance lay in gigantism, where pterosaurs had an advantage because of their build. A study from 1974 demonstrated how a seven-meter-wingspan *Pteranodon* did not need to weigh much more than sixteen kilograms and could fly at a minimum speed of around 25 kilometers per hour (the minimum airspeed of an albatross is around 45 kilometers per hour). That allowed for a very soft and controlled landing (compare that to the albatross's mode of landing, which basically involves a not-so-controlled crash into the earth). *Pteranodon* needed a soft landing, because with all the weight saving features, such as hollow bones, it had become a fragile animal. What this made clear was that pterosaurs represented some of the most extremely adapted creatures that had ever lived.

That conclusion has been confirmed since the 1970s by a veritable explosion of finds in North America, Russia, China and most of all, Brazil. The unique formations in that country have yielded a very rich harvest, both in numbers and diversity: from small to huge, from relatively simple forms to bizarre, complex creatures with sailed crests. One of the strangest creatures is the 'ur-flamingo' *Pterodaustro*. Each year, it seems as though the history and taxomony of pterosaurs requires a re-write.

Pterosaurs: a short introduction

Pterosaurs were the first animals with a spine that could fly. They are related to modern reptiles. One of the many groups of reptiles to which pterosaurs belong have an additional hole in the skull – between the orbit and nasal opening – which is a characteristic of 'Archosaurs', a group of animals that includes crocodiles (figure 19), dinosaurs and birds. But pterosaurs nonetheless differ distinctly from the other groups within the Archosaurs.

But with which reptiles are pterosaurs most closely related? The rather old-fashioned and rigid system of classifying plants and animals, which has been developed in the 18th century by Carolus Linnaeus, does not really work because of the diagnostic features used and also because Linnaeus never thought animals would evolve through time. Therefore, it might be better to classify pterosaurs in a separate group rather than within the reptiles.

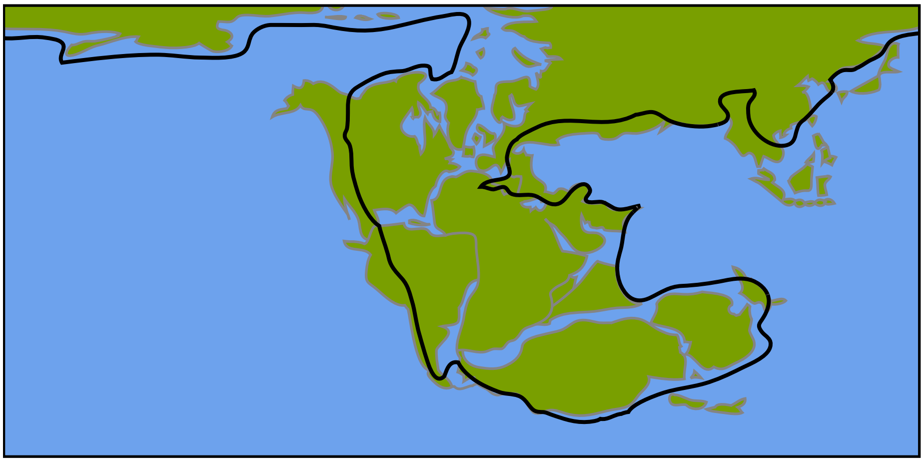
When did pterosaurs live?

Pterosaurs evolved in the Triassic, over 200 million years ago (see figure 2), but the exact origin of the pioneers of the skies and how the start of this evolution took place is not exactly known. The oldest finds show animals that were entirely adapted to their flying existence and ancestors are either not yet found or not recognised.

Triassic (figure 20)

During the Triassic, the big landmass known as Pangaea started to divide. Big parts of northern Europe were deserts with big, very salty lakes. But southern Europe was a big, shallow sea with enormous reefs. A new ocean, named Tethys, evolved

Figure 19. Crocodiles are archosaurs, just like pterosaurs, because they have an additional opening in the skull between the orbit and nasal opening.



Figue 20. The Triassic world (251 - 199.5 million years ago).

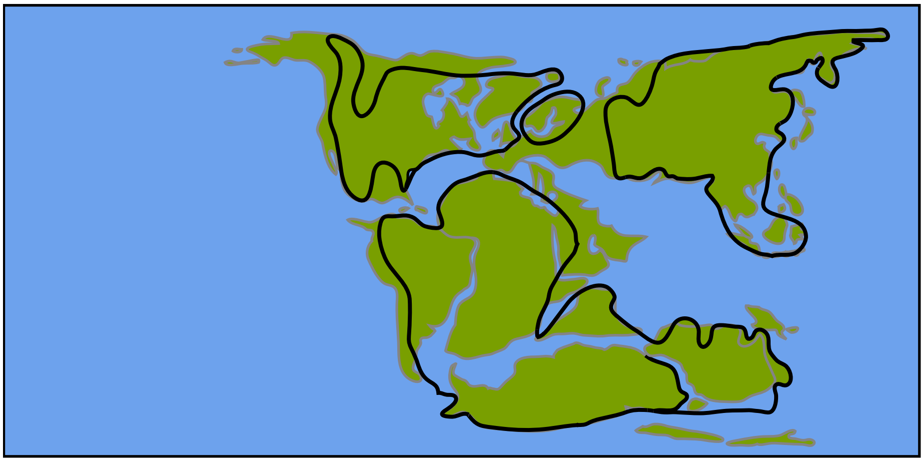


Figure 21. The Jurassic world (199.5 - 145.5 million years ago).

between Africa and Europe. The biggest extinction earth has ever seen marked the end of the Permian and the beginning of the Triassic (more on extinctions below). Life started to recover from the devastating effects of this extinction, which offered enormous opportunities for evolution due to which new, big groups of animals evolved. Enormous sea creatures evolved in the oceans, whereas on land the first dinosaurs and mammals appeared and also the first flying vertebrates came onto the stage. By the end of the Triassic the diversity of dinosaurs increased distinctly and one group of bipedal, meat-eating dinosaurs became the dominant predators. Although some of these animals gained incredible sizes, most, however, were very lightly built and rather small.

Jurassic (figure 21)

The worldwide rising of water levels and adaptive radiation of about everything that had survived the mass extinction at the end of the Triassic mark the beginning of the Jurassic. Adaptive radiation is the evolution of new species from a common ancestor in order to adapt to and be able to survive new environments. The Jurassic is famous for dinosaurs such as *Stegosaurus* and the large variation of ammonites (related to octopuses, squid, and cuttlefish). It is also the time of the dramatic increase in bio-diversity. Some fishes, such as *Leedsichthys* grew to sizes comparable to our whales, and monstrous big marine reptiles, such as the pliosaur *Liopleurodon,* were the top predators of the seas. During the Jurassic the Atlantic Ocean started to form. There are almost no signs of ice caps and the tropical climate was far more north than nowadays. The first birds (such as *Archaeopteryx*; figure 22) and feathered dinosaurs (among which *Anchiornis*) evolved.

Cretaceous (figure 23)

The Cretaceous period was a time of rising sea levels that, at the beginning of the Late Cretaceous, had submerged most of the big continents of the world. Europe was almost entirely submerged and there were big inland seas in Africa and North America. The big rise in sea levels was due to the rapid development of the Atlantic and other oceans, which created more, high mountain riches at the bottom of the oceans. Another possible reason was rise of global temperatures, which melted the icecaps.

But life flourished as never before on land. Dinosaurs continued in their spectacular diversity, resulting among others in enormous sizes: *Spinosaurus* was a north African fish eater 18 metres in length, whereas *Giganotosaurus* and *Tyrannosaurus* hunted in North and South America. The oceans were inhabited by the longneck-necked plesiosaurs and the predatory pliosaurs, that grew bigger and bigger. They were accompanied by mosasaurs, yet another fierce predator, and giant turtles. Mammals also saw a marked increase in diversity, with some feasting on small dinosaurs and possibly also on our flying friends. Pterosaurs were still master of the skies and they too grew to monstrous sizes, with *Quetzalcoatlus* being one of the largest with a wingspan of 10 metres! Birds were rather rare in the Jurassic, but diversity increased distinctly in the Cretaceous. Still, pterosaurs and birds were not real competitors, because they occupied entirely different niches. At the end of the Cretaceous, pterosaurs became extinct.

Figure 22. Archaeopteryx *is a theropod-dinosaur with feathers. Moreover, it has a large number of small, curved teeth and fingers with claws to its wings. However, it does not have a bird-like pelvis and shoulder and without his feathers would not have gained much attention when it was discovered in 1860.* Archaeopteryx *is a classical example of the 'missing link' with features that are seen in meat-eating dinosaurs but also has feathers like those of a bird.*

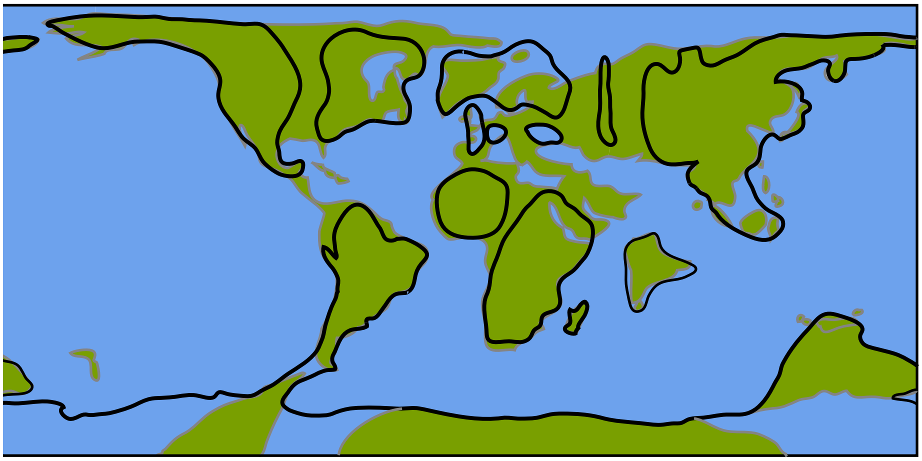


Figure 23. The Late Cretaceous world (145.5 - 65.5 million years ago).

Where did pterosaurs live?

The relatively newly discovered Crato and Santana Formations in the Araripe Basin in northeast Brazil produces abundant remains of pterosaurs. Comparably rich formations are also to be found in China, where three formations (the Daohugou layer, part of the Tiaojishan Formation) and the Yixian and Jiufotang Formations all produce the most spectacular finds. But pterosaurs are found elsewhere too: not least in Morocco, Argentina and Mongolia. Indeed fossils of these pioneers of the air have been found everywhere in the world. Recently an entirely new species has been discovered at Solnhofen, Germany, the same site that yielded the first pterosaur fossil in 1784, over 200 years before this newer find.

FOCUS

Extinction

Extinction is just as much a part of evolution as the evolution of new species and frequently happens in a series of waves. The earth has witnessed several major and minor extinctions, the most devastating being the one at the end of the Permian period when some 90 to 95 percent of all life in the seas and over 70 percent of all life on land perished. The main cause was a series of prolonged and severe volcanic eruptions in Siberia. Another major mass extinction occurred at the end of the Cretaceous period when the dinosaurs, a highly successful group, along with other animals, were wiped from the face of the earth by a huge meteorite. Its diameter is estimated at between 10 and 30 km and the impact took place at Chicxulub on the Yucatan peninsula of Mexico. This impact also marked the end of the pterosaurs, but not for birds nor for another group of relatively small, insect-eating mammals which took the opportunity to take to the air and who would come to dominate the night sky: the bats.

Mark explains

Quetzalcoatlus

The Azhdarchids comprises a group of pterosaurs with very long, narrow skulls, even longer necks and long hind legs, but with relatively small wings. Some pterosaurs, such as *Quetzalcoatlus* and *Hazegopteryx*, were as tall as a giraffe and large enough to swallow the average pterosaur researcher whole … They probably had the longest jaws of all non-marine prehistoric animals. Those long, stiff necks … not very dynamic as the creature could do little more than move its head up and down. Its neck allowed only a minimum amount of sideways motion. So what could it do under these circumstances? Well, it could walk 'on stilts'. For this kind of life it was not necessary to have a flexible neck! Even their wings corresponded to those of modern storks and ibises. Literature confirms this, but none of these publications was based on real research. The first theory was that they were specialist scavengers that, as a kind of overgrown vulture, circled high in the sky seeking food in the form of dinosaur carcasses for example. Others came to the conclusion that they sought buried molluscs along muddy coasts, or sought other small, tasty meals in the shallows of the coastal waters. Yet others saw them as swimming fishers or as creatures that dived down from the sky to snatch fish out of the water (see: 'Mark explains: *Anhanguera*', pp. 81-83) or ploughed through the water with their lower jaw, as skimmers do.

Well ... just a fleeting glance at our modern animals suggests that these gigantic pterosaurs could not perform any of these actions. Modern animals that gather food by similar means are very specialized creatures with millions of years of fine-tuning behind them. Most adaptations have led to a different lifestyle.

With the extremely sleek jaws of the skimmer, for example, tearing off pieces of flesh from a carcass would be impossible, whereas the jaws of a true scavenger are not suitable for seeking out worms and suchlike in the soil. It is not easy to uncover how these gigantic pterosaurs satisfied their hunger but it must be possible to find the

Quetzalcoatlus *is sometimes referred to as the prehistoric stork. Here you see the beautiful saddle-billed stork (*Ephippiorhynchus senegalensis*).*

answer on the basis of enough fossil material and by approaching things in a straightforward and logical manner with regard to the places where the fossils were found. To begin with the latter: by simply examining the geological circumstances at the places where the fossils were found – and also the fossils that were found in the same sedimentary layers – it became evident that more than half of the fossils (including the most complete, articulated skeletons, and the locations where various individuals were found together) were discovered inland. Only a handful of discoveries came from an environment abundant in water. And these finds are the most fragmentary of all. In other words, the animals at the inland discovery points died where the palaeontologist found the fossils or at least very close by. The longer and the more a carcass is transported through water, for example, the quicker it falls apart and the longer it is exposed to external factors, such as scavengers. And that is exactly what we see in watery environments.

The complete animals were interred very rapidly, whereas the isolated bones have probably drifted around for quite some time. This indicates that the animals spent their days on flood plains and in woods rather than on the beach or next to the sea. However, the idea that these giant creatures actually lived by the water is still championed by some people. According to their theory, the animals found land inwards were those that died on their way from one coast to another. But this is approximately the same as suggesting that *Tyrannosaurus rex* was in fact a beach dweller and that the numerous finds in inland sediments are the result of death during migration: isn't this a bit far-fetched? A much less complicated explanation, one supported by the data, is that these animals simply lived inland!

But what if we now compare the skeleton to that of modern animals that inhabit the same niches as the large pterosaurs allegedly also inhabited? A 'niche' is described by NCB Naturalis on the website www.natuurinformatie.nl as: '*Every organism fulfils a certain function within the community within which it lives. We know the functions of herbivore and carnivore, for example. This type of functional position is called a "niche". In different continents, the same niches were often occupied by very different organisms. For instance, in North America the niche of the "large grazers" was occupied by bison, in Africa by zebras and antelopes, and in Australia by kangaroos.*"

So: could these largest pterosaurs have ever lived as vultures? The wings, relatively short and wide, were extremely well suited to flying in an inland environment, because they effortlessly generate upward force when taking off in surroundings with varying wind conditions. In addition, the creatures would incur fewer injuries to their smaller wings in the presence of much vegetation. It is possible that *Quetzalcoatlus* and its relatives made use of thermal air currents, as many present-day birds of prey do. Thus, there can be little discussion on whether or not these large pterosaurs were capable of soaring and seeking carrion; but how would they eat it once they had found it? This was less straightforward than might seem. Although the size of the pterosaurs must have frightened off most other scavengers, enabling them to have first pick of the available food, but their long stiff neck and large skull prevented them from penetrating deep into the carcass, so that much food remained out of reach. The jaws were not equipped with a 'meat hook' as many of the modern scavengers are, so it is improbable that they were specifically adapted to tearing carcasses apart. Of course, this does not mean that they were not opportunistic and gnawed at carrion now and again.

So, why shouldn't they have meandered around in swamps and ponds, rooting for food? Actually, it would have been rather difficult for them to discover where something edible is hiding, as there are no indications that they had sensors. These densely packed 'bumps' or receptors form a sensitive instrument that gives modern birds information about the underground situation so that they know where they might find food. Moreover, it is much simpler to stick your snout in the sand and mud if it is narrow and streamlined, instead of having deep, high jaws like *Quetzalcoatlus*. And how can you grab a bite to eat if, like the pterosaurs, you only have a hinge with the skull at the back of the jaw? Modern birds that seek food in the soil have a second joint more to the front, which gives them the opportunity to open the tip of their beak without having to open the jaw itself. This is very handy if your beak is in the mud! There, we can conclude that our giants did not follow this way of gathering food.

What about swimming? Well, of all the pterosaurs, Azhdarchids are approximately the least adapted to water. Their long, slender limbs and narrow hands and feet were of little use in moving through water. The structure of their skeleton also precludes the notion that they could snatch their prey out of the water with their hands. Both the hands and the feet were embedded in the wing membrane so they would be completely dependent on their snout for gathering food. The long neck and skull are not what you might expect of a hunter that can fly. Modern birds of prey rely on their beaks to seize their prey. They have large, wide beaks and short necks, and combine these with great manoeuvrability. *Quetzalcoatlus* and its fellows have none of these adaptations.

Palaeontologists are fond of the idea of catching fish in the air as a method of gathering food (see 'Mark explains: *Anhanguera*', pp. 81-83), but this is rather far-fetched for the Azhdarchids. That

Catching fish in flight is a popular theory with palaeontologists but the evidence suggests that only a small group of pterosaurs were anatomically well equipped for such methods.

unusually long, stiff neck simply cannot bend adequately to grab prey out of the water. In relation to the flying danger above it, a fish is suspended motionlessly in the water. So you need a very flexible neck to grab it, and these large pterosaurs just do not have that. The importance of having a flexible neck is even greater than among birds that cut through the water with their lower jaw, as skimmers do: on impact with a prey (or accidently with a twig, stone or ground, for example), the head is suddenly folded under the body with great force. The neck functions as a buffefor these intentional or unintentional collisions.

In the case of *Quetzalcoatlus* this would have led to serious neck complaints. In addition, this method of gathering food – cutting through the water with your lower jaw – is an extreme specialization and only occurs in a few bird species that have had to overcome all kinds of evolutionary obstacles in order to become effective enough to be able to feed on fish. One of the most important adaptations is the streamlining of the lower jaw to a thickness comparable to that of a knife so that the resistance of the water is reduced to a minimum (see figure on page 82). At the same time, the jaw is high and relatively robust in order to withstand any impact during skimming. For the same reason, the hinge of the jaw is hugely reinforced and the muscles are sufficiently developed to absorb the major forces involved. Absolutely none of the Azhdarchids has features such as those described. On the contrary, they have slender jaws with flattened masticating surfaces, relatively small muscles and a rather fragile jaw joint. In combination with the stiff neck, these characteristics ensure that this method of fishing would not work for them.

Wading in water is a lifestyle that demands much less energy and adaptation. *Quetzalcoatlus* and its fellows belonged to a group of pterosaurs that were very well equipped to live on land.

▲ ► *Skimmers gather food by ploughing through the water with their lower jaw (see also 'Mark explains:* Anhanguer*', pp. 81-83).*

Pedestrian activity must have been no problem. The long legs were extremely convenient for wading through shallow waters, and their necks – the great snag in the other theories – is now no longer a problem. They only had to bend it a little to seize the food that was abundantly available on the ground. The enormous jaws were of great value, because they ensured that the neck did not need to bend too far to allow their snouts to reach the ground. So, that appears to be clear. But the traces that have recently been found in Korea have tarnished that theory. In a nutshell, the hands and feet are pretty small for the size of their body. If you want to wade through shallows with soft ground underfoot, it is best to have large feet with toes you can spread out wide, so that you have as large a surface area as possible to distribute your weight and avoid sinking deep into the mud. This is a problem, of course, with the largest of these critters, which are estimated to have weighed 250 kg!

Hmm…, we have probably held on too tightly to the idea that all pterosaurs lived in and around water. What would happen if we, as a matter of speaking, would tie them to a post on a very long rope in an environment far distant from rivers, ponds and swamps? What would they do then when they became hungry? Well, having small hands and feet has a great advantage when walking on dry ground and even requires less energy than walking around with large hands and feet! In addition, their heels and toes were furnished with small cushions (see figure 71), which makes walking and standing much more comfortable while also providing protection. Long limbs are also a bonus because you cover more distance with each step, and you thus increase your walking efficiency. One of the tracks found – with seven metres one of the longest ever found! – revealed another interesting fact. Most advanced pterosaurs had limbs that stretched slightly diagonally outwards, but these giants had their limbs right under their bodies and they combined this with the efficient, vertical posture of mammals and birds. Having limbs directly under the body has enormous benefits, forming a most efficient and stable platform for supporting their massive bodies. This means that *Quetzalcoatlus* was a perfectly adapted land animal, more adapted than most other pterosaurs.

You may expect that *Quetzalcoatlus* picked up everything that was edible, from insects to fruit to baby dinosaurs ... After all, 'ready-to-eat' can be a pretty large category if you have a skull that is more than two metres in length! There are quite a number of modern birds that lead a similar existence. Storks and ground hornbills, for example, terrorize the African grasslands in their search for ready-to-eat creatures. The figure shows the monstrously large *Quetzalcoatlus* on a foray across the Cretaceous prairies. The animal on the right has seized a baby *Titanosaur*, of which fossils have been found in the same sediment layers as the pterosaur fossils.

The Solnhofen Limestones: the rocks that gave us pterosaurs (figure 24)

Man has a long history with the laminated limestones of the Solnhofen *Plattenkalk* (lithographic limestone). These rocks outcrop at numerous sites around southern Germany and have been quarried since the Stone Age, first for use in construction, and later for carving reliefs and most recently for use in printing. The perfectly-flat, millimetre-thick limestone sheets are still actively quarried today for use in construction and lithography, a printing technique that uses polished Solnhofen limestone as a printing plate. The quarrying methods for the rocks remain distinctly low-tech, with great slabs of rock split manually with hammers and chisels as they

Figure 24. Around Solnhofen, southern Germany. Many pterosaur species as well as numerous other animals have been found here together with the famous prehistoric bird Archaeopteryx *(figure 22).*

have been for generations. While this makes obtaining the stone a laborious process, it ensures that the eyes of thousands of quarrymen have, over the centuries, kept a keen look out for the fossils that riddle the stone. Fossils may have been of significance even to our Palaeolithic forebears but have been studied scientifically only since the early 1700s. Three centuries on, we now appreciate Solnhofen as an almost unique window into the Mesozoic. Thought to represent a shallow, reef-ridden lagoon, the limestone of Solnhofen is so fine that even jellyfish – animals comprised of 90 per cent water – have been fossilised. Such preservation is quite astonishing and allows us to study the diversity of the ecosystem in much greater depth than normally would be possible.

With such detailed preservation it is not surprising to learn that much is known of the Solnhofen fauna. Plants, insects, molluscs, echinoderms, fishes, marine reptiles, lizards, crocodiles, dinosaurs, pterosaurs and birds are all known from the Solnhofen lagoon. Perhaps the most famous fossil remains are that of *Archaeopteryx*, the earliest known bird, and a fossil that has been at the core of various controversies since its discovery in 1861 (figure 22). Pterosaurologists have a particular affection for Solnhofen since it was in these deposits that the first pterosaur fossils were discovered sometime before 1757. The first pterosaur specimen was a complete skeleton of an animal that would later be named *Pterodactylus*. As explained previously, its discovery caused a stir over its habits and taxonomic affinities: some experts thought it was amphibious, others saw it as a flier. Several scholars claimed that it was of mammalian origin, but others argued for reptilian affinities. Such

Figure 25. An example of the fossil of Rhamphorhynchus muensteri. *Note the preserved flight membrane and tail vane. See also figure 34.*

confusion, possibly appearing a little strange in the modern day when the concept of pterosaurs is very well established, originated because of the bizarreness of pterosaur anatomy: no one had ever seen anything like it before. Furthermore, the idea that different animals existed before man was not generally accepted at all by the predominantly Christian scientific community of that time; the discovery of an animal as clearly alien as a pterosaur was an important piece of evidence for the concept of life before man.

Over two centuries later, the Solnhofen deposits continue to provide pterosaur fossils and, to date, at least 12 Solnhofen pterosaur species are known including the seagull-like *Rhamphorhynchus*, the insect-chasing *Anurognathus* and the spoonbill-

Figure 26. One of the early pterosaurs, Anurognathus, *was insectivorous. This is one of the smallest pterosaurs known with a wingspan of about 40 cm.*

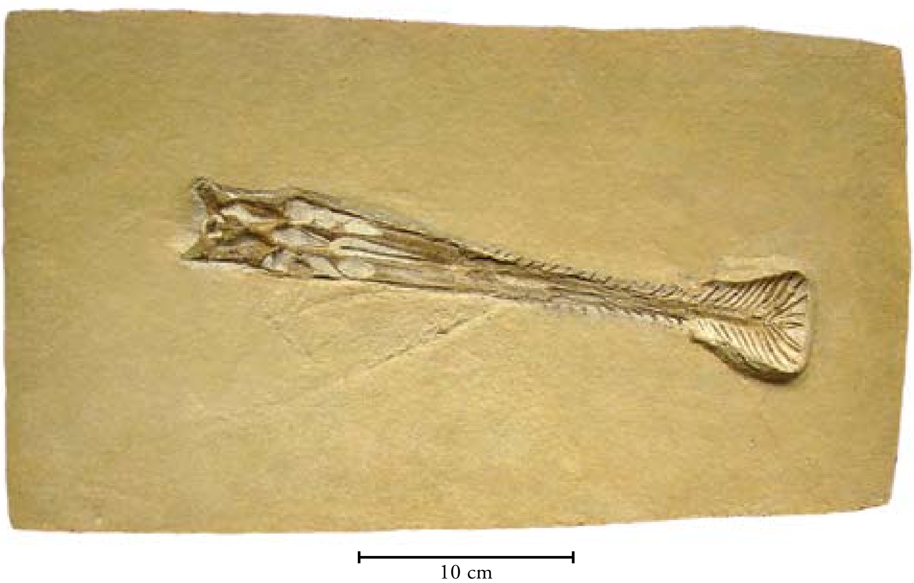


Figure 27. Gnathosaur *was probably a filter feeder - its dentition consists of many long, slender teeth. The skull is seen from below.*

mimic *Gnathosaurus*. Some, like *Anurognathus*, are extremely rare with only one or two specimens known, but others are preserved in enough abundance that we can trace their development from hatchlings to fully grown adults. Moreover, new techniques of looking at specimens recovered as early as the 1700s mean that new discoveries are still being made. Analysis of pterosaur specimens with ultraviolet light, for instance, developed by Helmut Tischlinger, has revealed previously unseen soft tissues such as cornified crests, 'fuzz' (*pycnofibres*) and entirely preserved muscles. Despite having the longest history of a pterosaur-bearing deposit in the world, there is clearly still much which can be learned from Solnhofen.

Where Pterandon roams: the Niobrara Formation (figure 28)

For much of the Upper Cretaceous, North America was split by a shallow seaway that, at its greatest extent, covered much of central America, the entire region between what would become the Rocky and Appalachian mountain chains and much

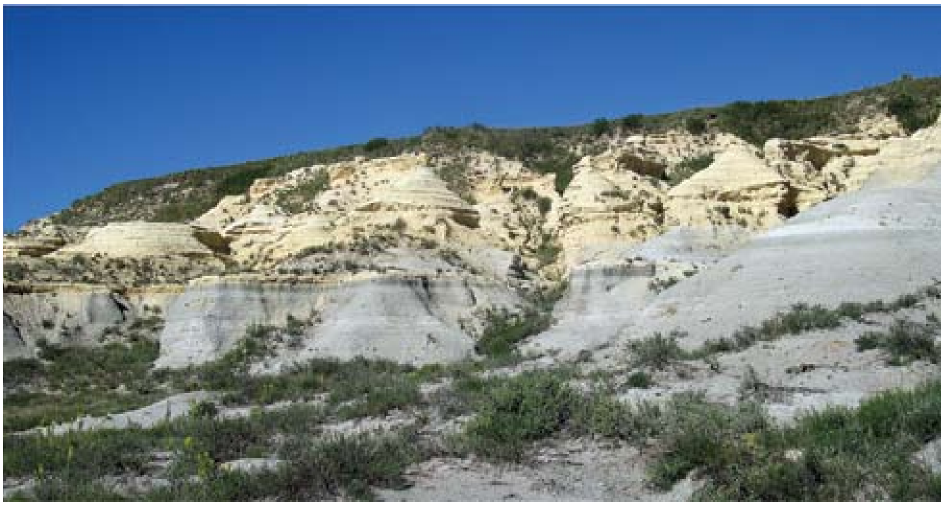


Figure 28. The Smoky Hills are in Cove County, Kansas (United States). Pteranodon *and* Nyctosaur *are the only known pterosaur-taxa from this location.*

of Canada. The innumerable skeletons of calcareous algae that lived in this sea accumulated in chalky deposits that provide an excellent record of an entire ancient marine ecosystem. A wealth of giant oysters, enormous marine reptiles, sharks, bony fish, swimming birds and some of the most spectacular pterosaurs known are just some of the fossils which also exist in these deposits. Although the remains of these creatures can be found across North America, the most complete record of their existence is found in the Smoky Hill Member of the Niobrara Formation of Kansas. This productive fossil site has been explored since the late 1860s and many famous North American fossil collectors and palaeontologists (including several members of the Sternberg family, Othniel Marsh and Edward Drinker Cope) – have played a part in uncovering its secrets. With over 150 years of research and collecting, the Smoky Hill Member is now recognised as one of the most comprehensively known Mesozoic marine ecosystems.

The Smoky Hill Member is significant to pterosaur researchers for a number of reasons. First, the discovery of pterosaurs in these deposits in 1870 was the first indication that pterosaurs existed in the New World. Secondly, save for a few scraps from southern England, the Smoky Hill pterosaurs provided the first indication that some of these creatures were *huge*. The discoverer of a pterosaur in Kansas, O.C. Marsh, wrote in his first report of these finds in 1871 that their wingspans were predicted to be "*not less than twenty feet!"* Complete remains of these giants were quickly unearthed and, over a hundred years on, the Niobrara provides us

Figue 29. Othniel Marsh and 'his' Pteranodon.

with the most comprehensive record of giant pterosaurs. In addition, the Smoky Hill pterosaurs were the first to be clearly toothless, a find that contrasted with the entirely toothed pterosaur record known from Europe at that time.

However, compared to the other fossil deposits (known as *lagerstätte*) discussed here, the Smoky Hill Member has a relatively impoverished pterosaur fauna. In fact, there are only three species currently recognised from this deposit, and they all belong in the same group, the pteranodontians. This group is best known for the giant pterosaur *Pteranodon* (wingspan seven metres), but the smaller *Nyctosaurus* (two metre span) is a minor fossil celebrity thanks to its oversize, antler-like head crest. Both are specialised pterosaurs that were well adapted for soaring long distances over the Western Interior Seaway. *Nyctosaurus* is the rarer of the two, but *Pteranodon* is known from over 1100 individual specimens, some of which are relatively complete skeletons (and others of which are isolated bones) so that we have evidence of every bone in their bodies. Such abundance means that *Pteranodon* is one of the best studied and understood pterosaurs: we have enough data to perform statistical analyses on its growth and sexual dimorphism, for instance, as well as to develop a catalogue of is pathologies. There is also fossil evidence of the creatures that they ate and of those that ate them. The Smoky Hill Member, then, is not so important for the diversity of the pterosaurs but for the depth of information it reveals about those few types of pterosaur that existed there; few other fossil sites come close.

Giving pterosaurs more depth: the Araripe Group lagerstätte *(figure 30)*

Prior to the 1970s, there was little evidence that Brazil could harbour pterosaur remains, and still less that it would, arguably, yield some of the finest in the world. Only one isolated pterosaur bone had ever been reported from the entire country, a record hardly suggestive of the exquisite fossils that would follow. In 1971, however, pterosaur fossils from the Araripe Group, an extensive outcrop of Lower Cretaceous deposits in northeast Brazil, put this forgotten corner of South America firmly on the pterosaur map. Finds from these rocks have become an indispensible component of modern pterosaur research.

The first pterosaurs from the Araripe stemmed from deposits known as the Santana Formation, a site with unusual depositional conditions that makes its pterosaur fossils unique. Rather than being squashed flat, these fossils were undistorted and three-dimensionally preserved in amazing detail, right down to the millimetre-thick trabeculae, which criss-cross the shafts of limb bones. Though initial remains were scanty, further discoveries made throughout the 1970s, 1980s and 1990s revealed that almost entire skeletons of Santana pterosaurs could be found and, occasionally, would be associated with exquisitely preserved soft tissues. The secret to this three-dimensionality lay with the limestone nodules that grew around the skeletons of fossils buried within the ancient Santana lagoon. Whilst the sediments around them were vulnerable to compression as more sediment accumulated, the nodules were strong enough to resist compaction and prevented their bony cargo

Figure 30. The Araripe basin in northeast Brazil: the small villages of Nova Olinda and Timorante.

from being squashed to the pancake-like state typical of most pterosaur fossils. The importance of these fossils to pterosaur research cannot be overstated: as well as revealing hitherto unseen details of pterosaur wing membrane structure, the undistorted nature of the Santana pterosaur bones makes them the 'go-to' fossils for

Figure 31. Thalassodromeus sethi*, with its enormous head, is known only from Brazil. See also figure 77.*

research into their skeletal mechanics. These details, coupled with the fact that the Santana Formation holds the thalassodromids, a group of sail-crested pterosaurs not definitively known from anywhere else in the world, makes it a particularly special pterosaur fossil site.

The bounty from the Araripe Group does not stop here, however. Remains published in 1994 revealed another Araripe deposit with excellent pterosaur fossils – known as the Crato Formation. These rocks, slightly older than those of the Santana Formation, are not only known for their pterosaurs; plants, insects, fish and a number of other fossil types have been extracted from the limestone slabs that represent the Crato lagoon in the modern day. Once, this lagoon was a large body of water that slowly cycled between fresh- and saltwater conditions, apparently with anoxic bottom waters that prevented disruption to potential fossil material. Although the fossils are not three-dimensional like those of the neighbouring Santana Formation, the Crato layers preserve soft tissue far more readily and, in two cases, provided the first evidence that some pterosaurs significantly extended their famous head crests beyond their bony limits. Apparently comprised of a keratin-like material, some Crato crests occupy over 80 per cent of the lateral skull area and are, proportionally speaking, the largest cranial crests of any animal known. Pterosaur wing membranes, soft tissue components of their beaks, claw sheaths and scaly foot pads have also been recovered from Crato slabs. Unfortunately, this exquisite detail appears to come at the expense of completeness: to date, not one Crato pterosaur has been found in its entirety. In fact, not one Crato pterosaur skull has been found with associated body remains and, paradoxically, the only complete Crato pterosaur body skeleton has no head! Nonetheless, there is no reason to assume that associated skull and body material would not turn up one day and, in the meantime, the amount of detail observable from Crato soft tissue discoveries alone more than makes up for the bizarre selective preservation of this deposit.

Figure 32. Tugulu and (next page) a young man that looks suspiciously like a well known pterosaurologist standing in front of the Yixian Formation in China.

The ancient lake deposits of Liaoning Province (figure 32)

Few fossil localities have revolutionised our understanding of the Mesozoic like those of Liaoning Province, China. First recognised in the 1920s by American geologist Amadeus W. Grabau, it took over 60 years for the uniqueness of the Liaoning sites to be appreciated but they are now recognised as the most comprehensive window into inland Mesozoic ecosystems yet known. Yielding insights into the Middle Jurassic and Lower Cretaceous, there are plants, molluscs, insects, fish, amphibians, lizards, mammals and, most famously, feathered dinosaurs. All are known in abundance from these localities, often in more complete and detailed states than can be found anywhere else in the world. Furthermore, Liaoning has not only yielded many of the best examples of previously known animals but has also shed light into otherwise totally unknown groups of Mesozoic forms. It is no exaggeration to say that as the 21st century progresses, the eyes of most vertebrate palaeontologists will be focussed on Liaoning.

The reason for Liaoning's astonishingly high calibre preservation stems from its ultra-fine, sometimes paper-thin, layers of mud and siltstone. These layered deposits can, quite literally, resemble the pages of a book, and were deposited at the bottom of a series of deep lakes. They are interbedded between conglomerates, sandstones and volcanic tuffs, recording rivers crossing the lake plains and the fallout from local volcanic eruptions. The bottom of these ancient lakes appear quite inhospitable to life and any live organisms or carcasses that fell into them were safe from scavengers and other forms of decay, leaving their remains perfectly primed for fossilisation. The fact that they survive for Chinese fossil collectors to discover today is all the more remarkable considering the turbulent tectonic history of Liaoning in more recent times.

Perhaps unsurprisingly, few deposits reveal such a complete Mesozoic biota; pterosaurs are very well represented in Liaoning with, presently, over 20 species of pterosaur named from this region. In time many of these will almost certainly be recognised as variants of the same form but, crucially, many of the pterosaur species from Liaoning represent entirely new, exciting groups like the primitive (basal) monofenestratans, chaoyangopterids and boreopterids.

Groups previously only known from scanty remains are also known in their entirety from Liaoning, so that we finally can grasp the anatomy of tapejarids and istiodactylids with more certainty. Perhaps the most celebrated pterosaur from this region is *Darwinopterus*, a form that not only provides the bridge between the long-recognised basal pterosaur/pterodactyloid split (see below) but also reveals insights into some fundamental processes of evolution itself. Other finds provide incredibly detailed soft-tissue preservation that show the internal structure of pterosaur wing membranes, their 'fuzz' and colour patterning. Furthermore, if some recent work on dinosaur fossils from these deposits is transferred to pterosaur fossils, we may soon have a handle on actual pterosaur *colouration*. As if this were not enough, Liaoning has provided two of the three pterosaur eggs currently known, an essential contribution to our understanding of pterosaur reproductive biology. With plenty of unexplored quarries and exposures, there is no reason to think that

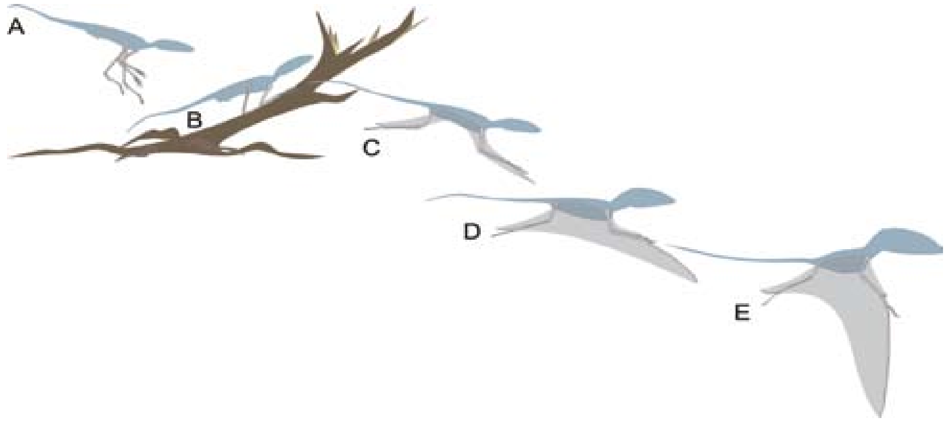


Figure 33. The hypothetical evolution of flight in pterosaurs.

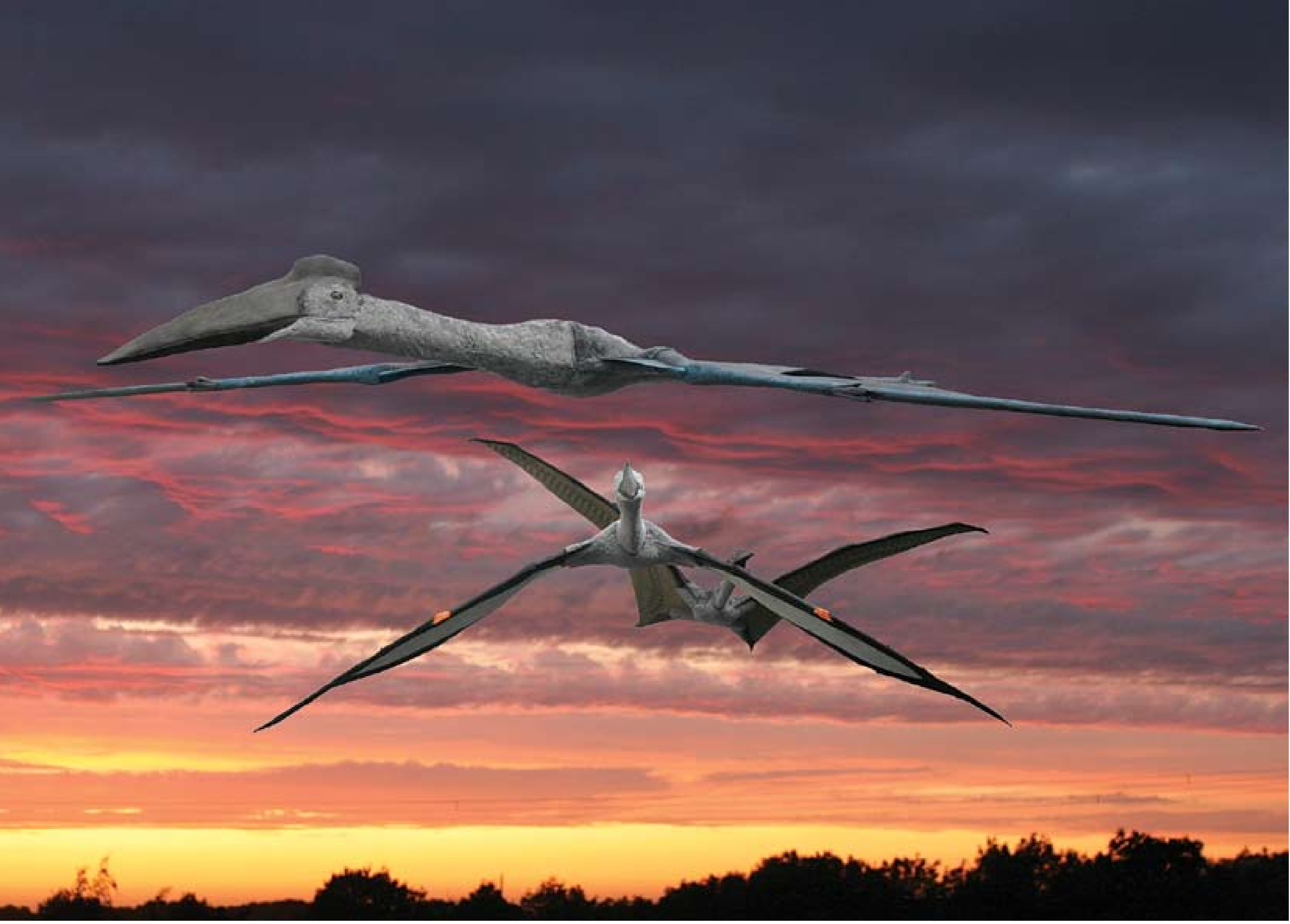
Liaoning will cease to provide still further surprises and, undoubtedly, the importance of these deposits to pterosaurologists and other fossil vertebrate workers is only going to increase.

Evolution

It seems that the transition from a non-flying, possibly soaring animal to flying pterosaurs happened in the forests of the Middle Triassic (figure 33). Unfortunately, such an environment is not conducive to fossilisation, which means that our quest for these pterosaur ancestors may be in vain.

The first flying reptiles were rather basal, which differed distinctly from the later, more advanced pterosaurs. They had a long, rigid tail (figure 34) with a vane at the end (see figure 50), had a comparatively small, short and relatively wide head (which with the evolution of *Eudimorphodon* in the Jurassic period became considerably longer), short wings and a foot with a outwards extending toe. This toe was used to span the membrane between the hind legs (*cruropatagium*). The metacarpals were short rather than long as seen in the later species (see figure 34). All early

▼ *Figure 34. The basal pterosaur* Rhamphorhychus *differed from the later, more advanced pterosaurs. For example, they had a long, rigid tail. Both fossils are among the best examples known and are housed in the famous Teylers Museum in Haarlem, The Netherlands.*



pterosaurs had teeth: the loss of teeth (edentulous) is a fairly late development that is seen first in the Cretaceous in *Pteranodon*. The early pterosaurs were also quite small, but sizes increased in the Cretaceous, resulting in spectacular giants such as *Quetzalcoatlus* (figure 35).

Figure 35. The biggest flying animal to date: Quetzalcoatlus.

For many years, palaeontologists classified pterosaurs into two groups: the oldest animals, so-called Rhamphorhynchoidea-pterosaurs (see figures 25 and 34) and the geologically younger, more advanced Pterodactyloidea-pterosaurs (figure 36, but see also figure 6). We now know that this classification is far too simplistic and does not show the evolutionary relationship between the groups. For example, some *Rhamphorhynchus*- species did not have a long tail and recently a new pterosaur, *Darwinopterus,* has been recovered, with a neck like that seen in the younger short-tail pterosaurs but combined with the long tail characteristic of the early group.

Figure 36. The traditional classification in 'long-tail pterosaurs' (see figure 34) and 'short-tail pterosaurs' is no longer adequate for visualising the relationship between the two groups.

The skeleton

Pterosaurs are differentiated from other vertebrates such as dinosaurs and mammals by their ability to fly. Although most birds as well as bats can fly, still there are differences between their morphology and that of pterosaurs (figure 37). No creature, living or extinct, resembles the pterosaurs. What then makes the skeleton of these animals so special?

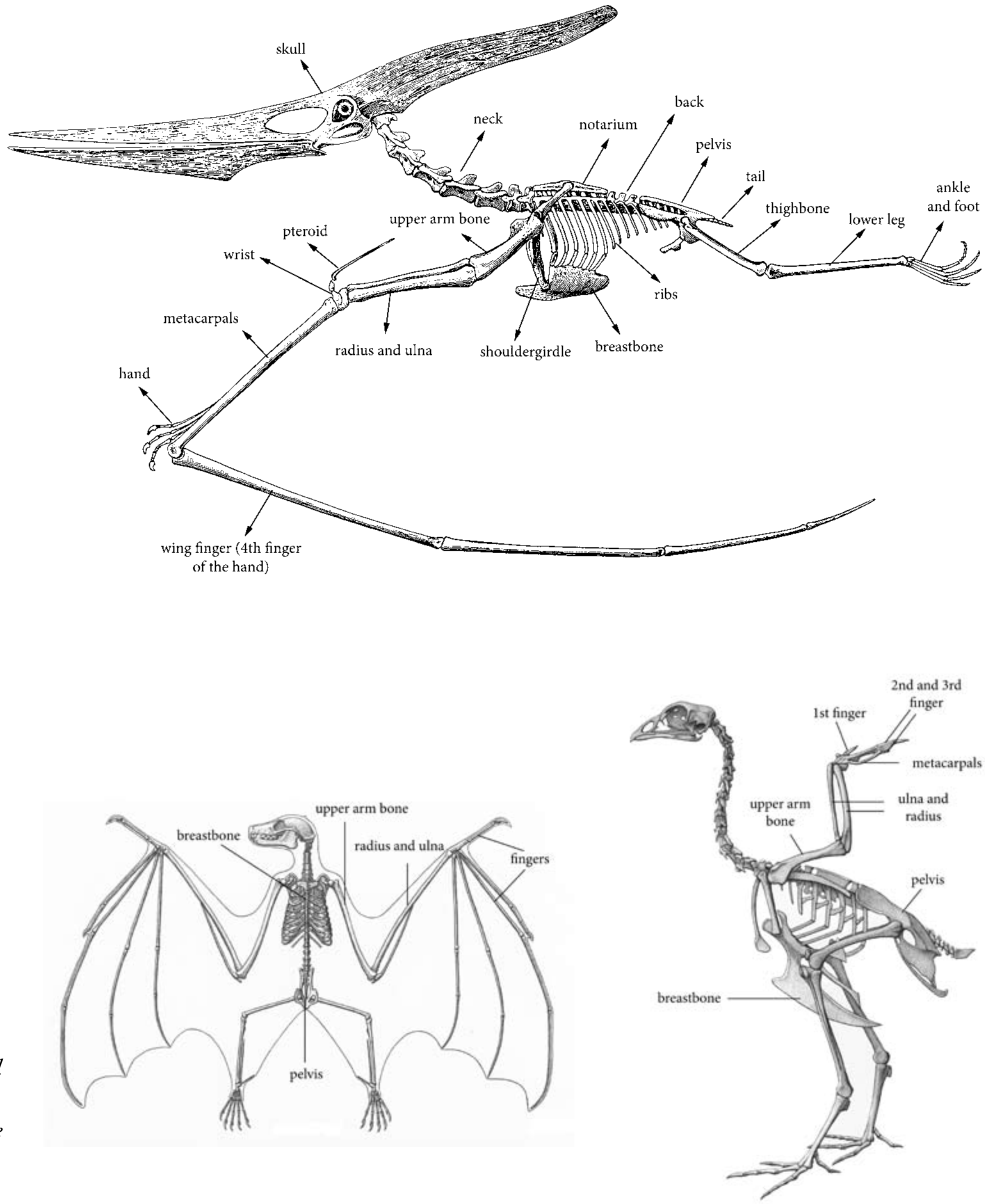


Figure 37. The skeleton of Pteranodon. *For comparison the skeletons of a modern bird and a bat are depicted. The most important differences are indicated.*

The skull

It is not possible to give a generalised description of a pterosaur skeleton because there is so much variation. However, if we concentrate on the animals that lived in the Cretaceous period we see a relatively big skull with a lot of openings (so-called *fenestrae*; figure 38). The reason of the openings is that it makes the skull much lighter and thus easier to fly. The ratio between skull and body was well balanced in the earliest pterosaurs. The cross-section of the skull of the more advance pterosaurs is triangular, due to which the orbits are orientated more towards the front and upwards than in the earlier and less advanced forms. This means that the animals looked forwards rather than sideways and therefore were better at depth perception and thus better able to grasp prey. The eyeball was protected by small, partially overlapping bony plates (figure 39). In the advanced pterosaurs, in front of the orbits, were large openings that, together with the nasal opening, formed one massive cavity (the so-called nasopreorbital fenestra; compare figure 38 with 39). The skull makes an angle with the neck, but it is smaller in the older, less advanced species in which it is roughly in line with the spinal column.

Figure 38. Several examples of skulls of Cretaceous pterosaurs from Brazil. Top to bottom: Criorhynchus mesembrinus, Coloborhynchus spielbergi, *the skull of an* Anhanguera-*species (see also figure 64) and the toothless* Tupuxuara.

Figure 39. The eye-ball is protected with a ring of tiny bony plates which partially overlap, their impressions are visible in this Rhamphorhynchus *fossil.*

FOCUS

Teeth

Many pterosaurs had teeth, a characteristic seemingly inherited from their pre-flight ancestors. There is a huge difference in shape, size, number and the way they were set into the jaws. Detailed mapping of the teeth (figure 42) allows the palaeontologist to recognise species: some had only teeth in the front of the jaws, in others the teeth ware facing markedly outwards. For example, the teeth in *Coloborhynhus piscator* were long and robust (see figure 40), whereas *Anhanguera* had much shorter and thinner teeth. Those in *Rhamphorhynchus* incline outwards and towards the front (see figure 34) and those of *Eudimorphodon* had three or five cusps. This diversity is related to the diet and the way their owners obtained it (see 'Mark explains: *Dsungaripterus*', pp. 24-25 and *Pterodaustro*'; pp. 66-68).

Like crocodiles, pterosaurs developed more teeth with age. At least twice during their evolution pterosaurs became edentulous but this was a rather late development. Why, when and how teeth in some species disappeared is not well understood, but it seems that these species later had an advantage and could better respond to changes in ecosystems (about 90 million years ago). It is notable that these edentulous species were able to grow to gigantic proportions, although also smaller edentulous species are known with a wingspan of only about 1.5 metres.

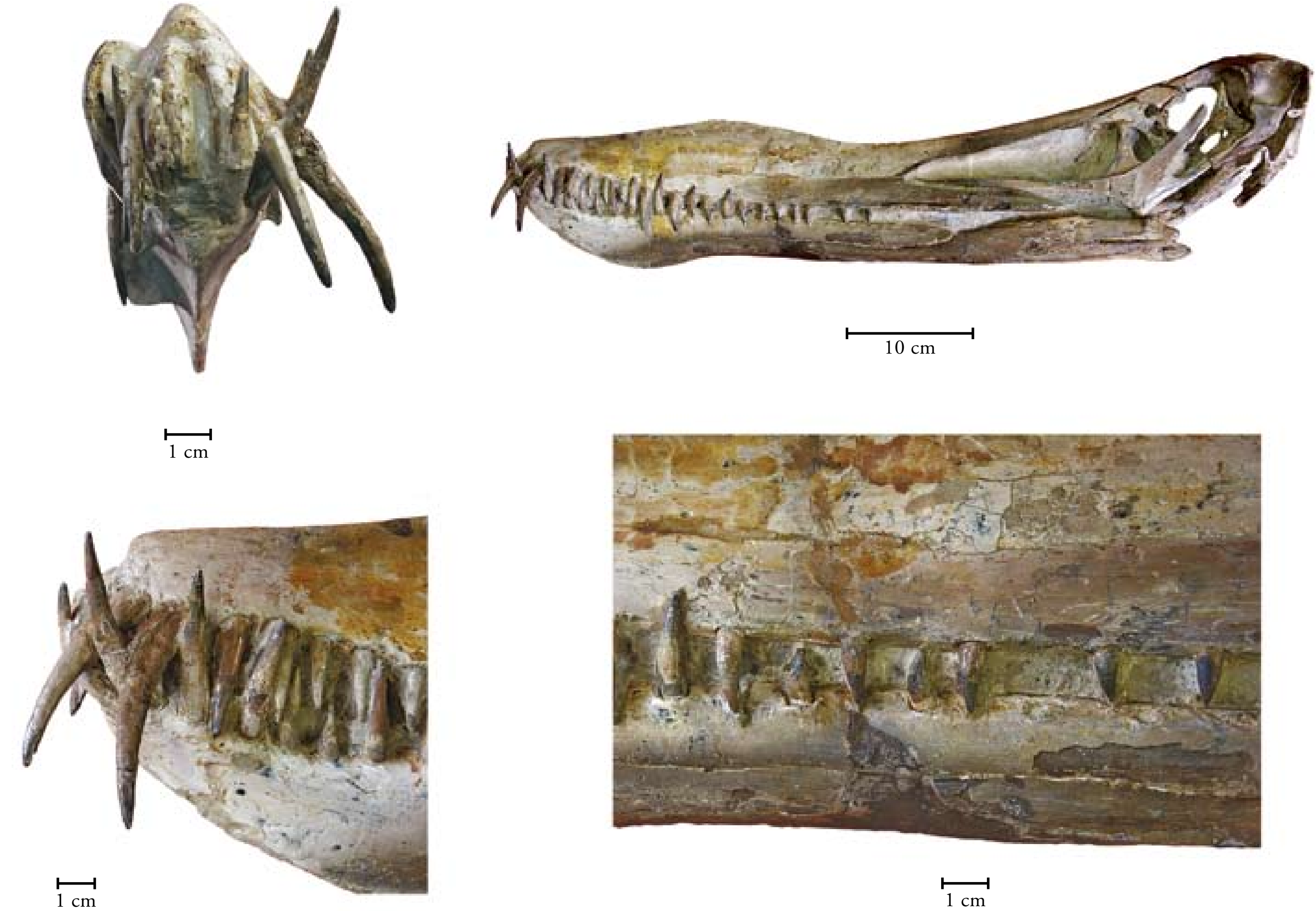
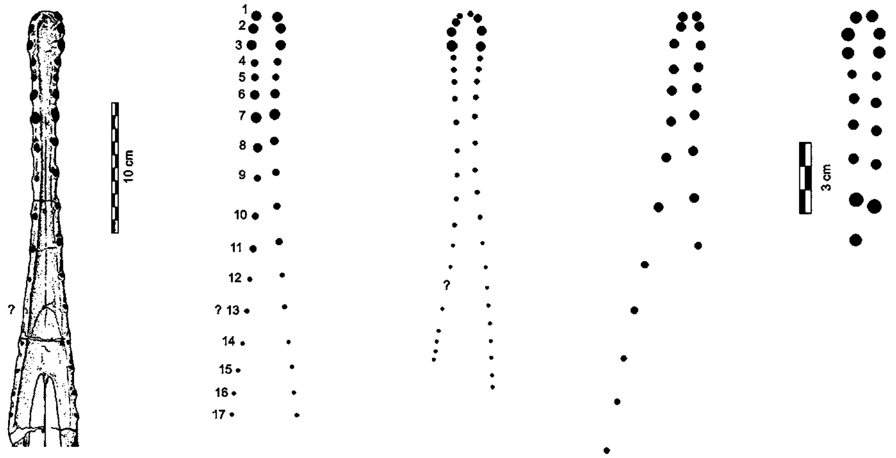


Figure 40. The skull of Coloborhynchu piscator *is one of the best fossils we have and also the biggest of this species, despite the fact that it was not a fully grown animal. The large, curved teeth are excellent for grasping slippery fish. Note the teeth at the back, which are distinctly smaller and more widely spaced. The bottom series of photographs are of an* Anhanguera-*species. The teeth are substantially smaller and thinner.*



► *Figure 42. Mapping the dentition in detail allows the palaeontologist to differentiate between species.*

▲ *Figue 41. The cross-section of the lower jaw of* Coloborhynchus spielbergi *clearly shows how the teeth are anchored in the jaw. Note the bony struts in the hollow bones that reinforce them.*

From the beginning onwards, pterosaurs had teeth, but there is great variation in their number, size and shape. Some species had teeth only in the front of the jaws, whereas others had them along the whole length of the jaw (figure 40, but see also figure 34).

Many pterosaurs had head crests. As early as the Triassic species developed a crest, such as *Austriadactylus*, but the diversity increased enormously in the Jurassic and especially in the Cretaceous (figure 43). Crests could be situated at the back of the skull but also at the front; some animals had crests at the front *and* back.

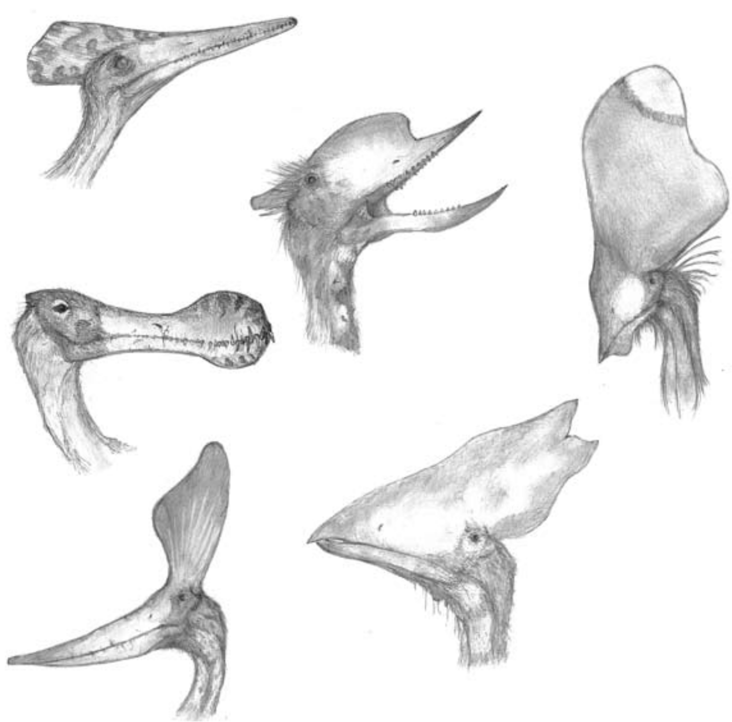


Figure 43. A few examples of the great variety of crests.

The lower jaw could have a crest but this is relatively rare. There is also a big variation in size and construction. Some crests are made of bone, others consist of skin with internal reinforcement consisting of tough, fibre-like network or a combination of bone and reinforced skin (see figures 7 and 44). There are small, low and very thin crests as seen in several *Anhanguera* skulls or big antler-like constructions as seen in *Nyctosaurus* (see 'Mark explains: Nyctosaurus', pp. 72-73). Seemingly, the species without head 'decoration' were a minority: of these, the badly known *Brasileodactylus* might be an example, as well as *Pterodaustro* (see 'Mark explains: Pterodaustro', pp. 66-68).

Figure 44. The fossil of Tupandactylus imperator *with a well preserved crest, including parts that are made of soft tissue. See also figure 85.*

FOCUS

Crests

Much speculation has developed over the function of the crests in pterosaurs (see ‘Mark explains: *Tapejara*’, pp. 114-115 and ‘Mark explains: *Anhanguera*’, pp. 81-83). For a long time, scientists have tried to prove that some crests played an important part in collecting food. For example in *Coloborhynchus* (see figure 38) the crest had an important role in stabilising the animal when, in full flight, they dipped their head in the water to catch fish. So, a mechanical explanation is proposed, just as in the past the crests at the back of the head were explained as aerodynamic adaptations for flight. However, it is becoming increasingly clear that an aerodynamic explanation is unlikely. Most palaeontologists currently agree that the crests were primarily communication devices enabling species recognition, distinguishing between males and females (sexual dimorphism) and providing a display mechanism during mating – a way to discourage rival males whilst attracting females. This has been convincingly proven for *Pteranodon* (figure 45); those with a crest were males (see ‘Mark explains: *Pteranodon*,’ pp. 92-95). A supporting argument for their function in communication is the fact that pterosaurs had good sight (see ‘Soft parts: brains’) so that a large crested animal, possibly further enhanced by colouration, could not go unnoticed by rivals or potential mates and members of the flock.

Figure 45. Models of a female and male Pteranodon.

Mark explains

Pterodaustro

All right, with its wingspan of around 2.5 metres it is not the world's largest pterosaur, neither does it have a striking crest like some other pterosaurs do. No, indeed these are not the things that make *Pterodaustro* so remarkable. So why is it worthy of attention? It is because it looks like it has flown into the broom cupboard with its mouth wide open! Its lower jaw is packed full of rows of improbably large, vertical teeth, similar to the baleens of a whale. But in contrast to these, *Pterodaustro*'s mouth contains hundreds of real teeth with enamel, dentin and a pulpa cavity. Each tooth is approximately a third of a millimetre thick! There are so many teeth that they are arranged together in grooves – parallel to the edges of the jaw – rather than independently, in alveoli (tooth sockets). But … there are also loads of teeth in the upper jaw: small, more or less spatula-shaped teeth that are not embedded in the jaw itself but are held in place by supporting ligaments. And, as if this weren't strange enough, there are also ranges of miniscule 'bones' – small tooth pads that are entrenched in the skin – above each of the teeth. Fascinating, uh? The function of the teeth in the lower jaw could not be clearer: *Pterodaustro* filtered the water in its quest for food. You can imagine this process: straining out seeds, small invertebrates, and suchlike. But, as far as I know, it has never been comprehensively investigated how *Pterodaustro* actually did this.

Besides teeth there are another two details of the jaws that need attention. One is that the extension behind the lower jaw is very robust and curves downward, away from the skull. This suggests that the muscles that were attached to it (the

same muscles that you can so clearly see behind the jaws of modern crocodiles) were probably rather large. This means that *Pterodaustro* had a very strong bite at the moment its jaws were almost closed. And this is quite rare inasmuch as, in terms of jaw muscles, pterosaurs in general were much better equipped for quick snapping actions rather than for relatively slow biting techniques.

In addition, the animals have unbelievably long jaws that curve upward. Curved jaws are fine if you intend to close the whole jaw in one action. What this could mean is that *Pterodaustro* did not simply wade through water with its mouth open in the hope of catching food. Instead, this pterosaur probably pumped water between its teeth with the aid of the muscles at the back of the jaw. The curved jaw ensured that the water did not directly spray out of its mouth but ran along the teeth at the edges of the jaws.

We do not yet know enough about *Pterodaustro's* physique to explain how they removed the filtered food from their teeth and transported it to their throat, but probably they had a large tongue by means of which they could press filtered elements against their palates. The small, spatula-shaped teeth, as well as the tooth pads, could have helped in holding the food in position. Just as with our modern geese and ducks, the food could have been transported backward during successive straining sessions and subsequently swallowed when it arrived in the throat itself. Well, it's possible …

It is clear that *Pterodaustro* was kind of a wading animal with big, wide feet, which were nearly as large as the lower leg. This also seems to indicate that they fed when standing still. Remarkable is also the long neck, similar to other pterosaurs that possibly found their food on land. Does this mean that all pterosaurs with such a long neck did this? Something to look into more closely in the future.

But there is more to the story: *Pterodaustro* was very numerous! There are hundreds of fossils of this animal and most originate from a site where they were so numerous that this place was named after them: *Loma del Pterodaustro* in Argentina. Probably, if one would be able to time travel to the beginning of the Cretaceous and would stroll to this prehistoric sweet water basin, one would see huge flocks feeding in the water, not unlike present-day flamingo's.

The *Pterodaustro* fossils represent animals of various stages of life, from embryo's to old individuals. Recent research of this flock with all the diversity in ages gave a good insight in the speed of growing of these pterosaurs. *Pterodaustro* grew very fast the first two years, just like dinosaurs, and probably also other pterosaurs, reaching about half of their final size. From here onwards, growth decreased, lasting for another three to four years before they reached the final size. In contrast to some modern reptiles, such as crocodiles and tortoises who continue growing their entire life, *Pterodaustro* seems to have had a 'predetermined' size. In other words, they reached a certain size, after which growth stopped, just like with us humans. But, and that is the same as for the recent reptiles just mentioned, they were able to reproduce before fully grown. And this seems to occur at the age of two, when growth slowed down, because from this moment onwards a change in bone structure can be seen. This suggests that energy partially went to reproduction, hence less energy for fast growing.

The post-cranial skeleton

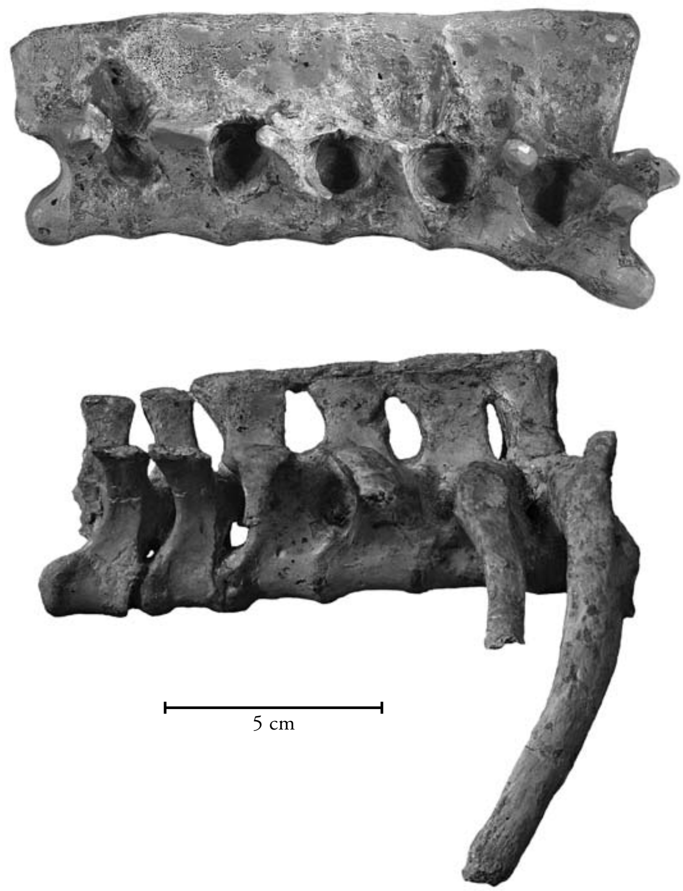
The post-cranial skeleton (the part behind the skull) of pterosaurs is fully adapted to flying. The torso is relatively small and tapers toward the rear. The front is broad and is shaped by the massive shoulder girdle.

Spine

The spine is divided by anatomists into several parts: cervical, dorsal and sacral vertebrae (including the tail). The neck consists of seven vertebrae. The last one is sometimes fused with the first dorsals into a *notarium* (see below). In general, the neck in the advanced short-tail pterosaurs is long and always much longer than in the earlier, basal pterosaurs. Elongation of the neck did not happen through developing additional cervicals but by the elongation of these seven vertebrae (figure 46). Sometimes this is so extreme that one cervical vertebra could reach one metre in length.

In some large species, the first dorsals are fused with the last cervical into a notarium (figure 47). This solid construction serves to cope with the forces that originate from flying. In order to develop an even more powerful construction, the

▲ *Figure 46. Elongation of the neck is obtained by elongation of each cervical rather than by adding more. Here are two examples of cervical vertebrae. Left is of* Arambourgiania *and right of* Coloborhynchus piscator.



► *Figure 47. Bottom: Notarium of a juvenile* Tapejara wellnhoferi*: the last vertebrae (left) or still not entirely fused. The notarium of* Coloborhynchus *(top) is fully fused: even the dorsal protrusions are fused together.*

dorsal protrusions of the individual vertebrae are sometimes fused into a strong ridge, the so-called *supraneural spine.* Here are situated the articular facets of the shoulder (*scapula*). A reduction in size is noticeable towards the back of the spine: the sacral vertebrae are substantially smaller. All cervical vertebrae have openings at their sides, *pneumatic foramina*, to reduce weight. Despite the lesser size of the dorsals (figure 48), they too have comparable openings, but the vertebrae towards the rear are more solid. Despite the fact that in the more advanced pterosaurs the tail is shorter than that to the earlier animals, it can still consist of many vertebrae (figure 49).

Shoulder girdle

In the large species of the Cretaceous, the shoulder blade (*scapula*) and the collarbone (*coracoid*) are fused into a single construction, the *scapulocoracoid*, which is a semi-circular construction designed to withstand the great forces that develop from flight (figure 51). The coracoid articulates with the breastbone (*sternum*;

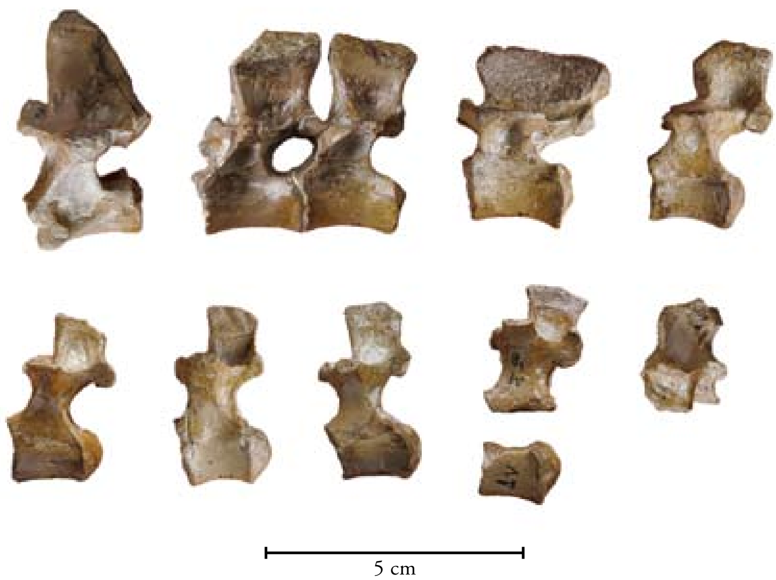


Figure 48. The first ten dorsal vertebrae (left lateral view, seen from left to right). The first dorsal is sometimes identified as last cervical. The next two dorsals show the beginning of fusion. The last ones, however, show incomplete fusion indicating that the animal was still young when it died.

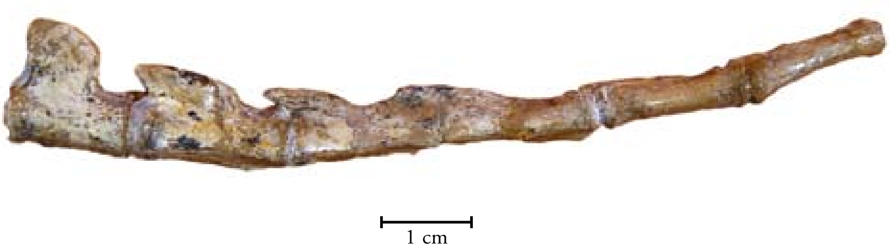


Figure 49. Although the tail in the advanced Pterodactyloidea-pterosaurs was short, it nonetheless consisted of a large number of vertebrae.

FOCUS

Tail

The first pterosaurs had a long tail that consisted of many vertebrae. These were reinforced with long extensions that ran parallel to its length (figure 34). The tail, therefore, could not bend. The reinforcement was to support a vane at the end of the tail, a feature that is a peculiarity of these early Triassic pterosaurs. These differed in shape between species and were made of skin with internal reinforcement, resulting in a permanently spread vane. It stood vertical relative to the body and served as rudder in flying. In the later, advanced, pterosaurs the number of tail vertebrae are greatly reduced, resulting in a short tail (see figure 49). Moreover, the long extensions lack and the tail was, therefore, flexible.

Figure 50. The tail in Rhamphorhynchus *was long and could not bend because of the long rod-like protrusions along the vertebrae (see figure 34). At the end, they have a sort of vane of skin that was orientated at right angle to the tail proper. The shape of this vane differed between species and acted as rudder.*

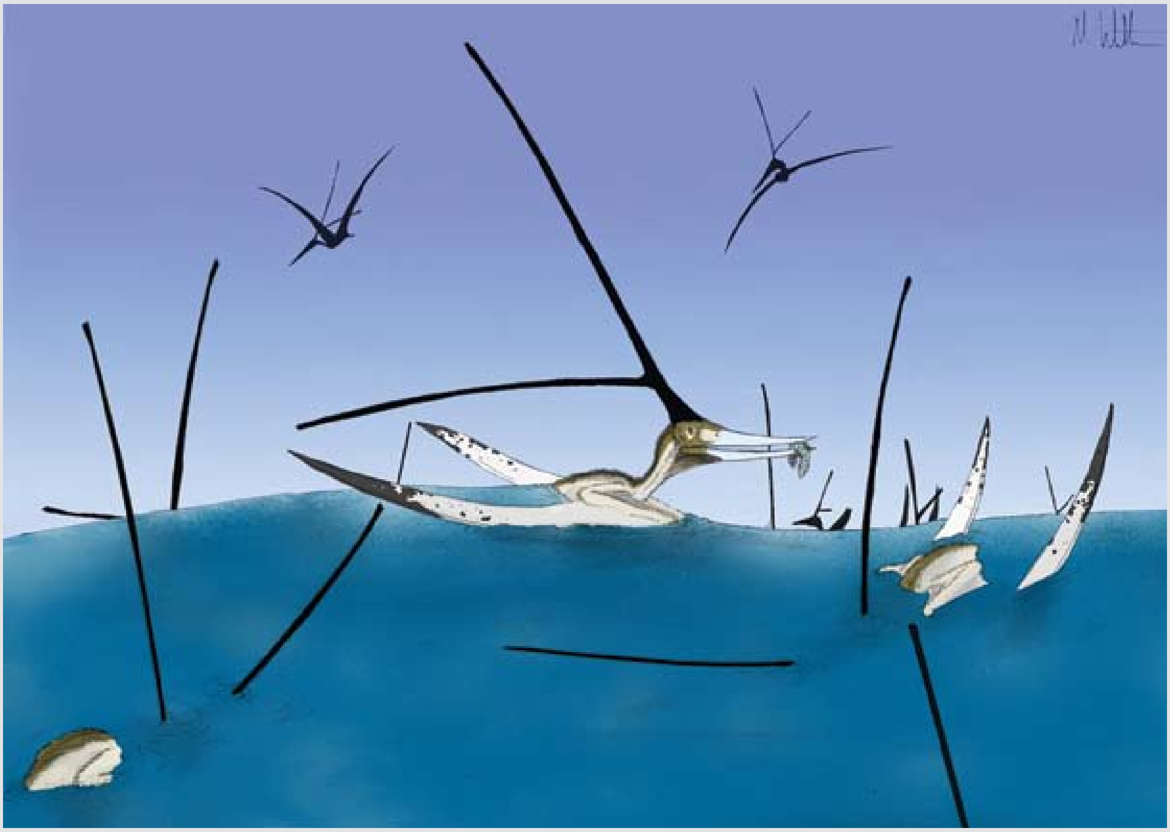
Mark explains

Nyctosaurus

Nyctosaurus is one of the oddest pterosaurs we know. In which way? Well, first of all it lacks the first three fingers. Although there was originally doubt about this, there are now enough fossils to be certain that this was not the result of incomplete fossilization. Second, the wings do not consist of the usual four phalanges, but three. However, this development is not unique to *Nyctosaurus*, but also occurs among another group of pterosaurs.

No, the most striking feature is the gigantic crest on its head, which can rightly be called 'bizarre' even in comparison to *Tapejara* and *Tupandactylus*. In most reconstructions, the crest is depicted far too modestly, with the backward-reaching horizontal branch being around one third of the length of the front vertical one. In reality, the backward branch was just as long as the front one! Some people claim that there was a membrane between the branches, making the pterosaur a windsurfer. However, no indications of the existence of such a membrane have been discovered in the fossils themselves. Crests made of membrane and soft tissue are normally anchored in coarse bone with a powerful structure (see figure 7). But the bone of the crest in *Nyctosaurus* is smooth and is therefore not a good surface for the attachment of soft tissue.

It is difficult to believe, but this crest was unknown to palaeontologists for many years. The first skulls of this animal completely lacked any crest: no protruding parts, no broken crest edges … nothing! Ultimately, in 2003, two new fossils were described with crests, but the rest was wholly identical to the skulls already known. What could be the explanation for this? The 2003 animals were mature animals, whereas the other known skulls belonged to young animals that were not yet fully grown. This means that the crest only began to grow at the moment the pterosaurs became adult. There are very few *Nyctosaurus* fossils, so we cannot state whether or not there was a difference between male and female examples,



as is also the case with *Pteranodon* (see 'Mark explains: *Pteranodon*', pp. 92-95. The fact that the crest only began to grow when the animals reached adulthood suggests that it was not functional but was instead linked to the behaviour of the animals.

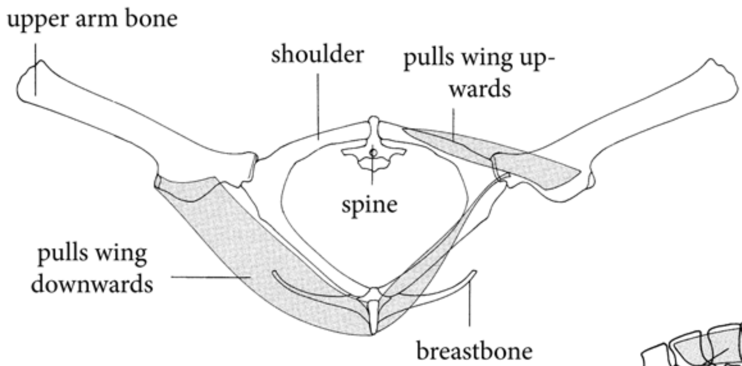
When I created the figure, I thought of an interesting point. Many modern seabirds obtain food by 'surface feeding'. In other words, they float on the water and dip their heads into the water now and again to grab a fish or something else that is edible. It would not surprise me – in view of the variation in food-gathering among seabirds and also of the crests that do not allow many other alternatives – if *Nyctosaurus* also behaved like this. In such cases, the crest would stick out of the water. If a whole flock did that, this would be one of the most absurd scenes in nature.

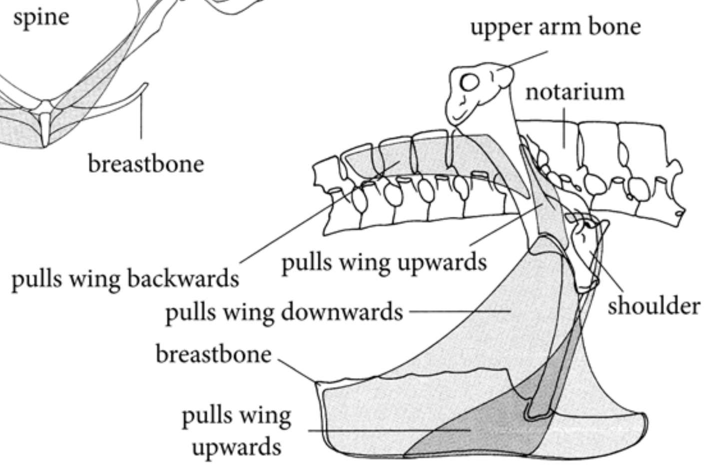
This gets you thinking … Perhaps, just as is the case with gannets feeding, these crests are 'signals' to inform others: 'Look, you should be here, here is food!' And with the rear part of the crest always visible, even if the animal has its head under water, you do not need to do more to pass on the info to your fellow creatures. Of course, only adult animals could give these signals but, with gannets, it is also only the adult birds that have snow-white plumage. So? It is no more than speculation and cannot be verified … but it is an interesting idea, isn't it?

figure 52). This bone differs markedly between various groups of pterosaurs, but in most species covers the thorax. The sternum articulates through a special joint with the shoulder girdle. Moreover, it has special ribs that articulate with the common ribs: they are a kind of intermediate rib.

Pelvis

Compared to the shoulder girdle the pelvis is far less robust and strong (figure 53). At either side of the sacral vertebrae are the illia: these articulate with the ischium and pubis. In pterosaurs from the Late Cretaceous the ischium and pubis are fused





▲ *Figure 51. The shoulder in Cretaceous pterosaurs was a closed ring: above the notarium, at the sides the fused scapula and coracoid (scapulocoracoid) and below the breastbone (sternum). There are big attachment areas for the well-developed flight muscles.*

◀ *Figure 52. The breastbone (sternum) differed in shape but always covered the body nearly entirely. Both breastbones are here seen from below.*

Figue 53. Below: The fully grown pelvis of Coloborhynchus spielbergi *(Cretaceous, Brazil) seen from behind and from the side. Top: The pelvis and the hind leg of a* Pterodactylus*-species (Jura, Germany) seen from above.*

Figure 54. The thighbone seen from the front and from the side. Note the angle of the head. The hind legs are less strongly developed than the front limbs (compare with figure 58).

into one plate, the ischiopubis, as is clearly visible in the 'Leiden' specimen of *Coloborhynchus spielbergi* (see figure 53). In some cases, the fusing is so great that a more or less massive construction exists. The pre-pubes, small bones that support the intestines, point diagonally forward and downwards. These small bones are often lost during fossilisation because they are not fused to the pubis but are attached with ligaments. The pelvis is an important part of the skeleton in identifying the sex of the animal: because females have to lay eggs, the pelvis is constructed differently than in male animals.

Hind legs

The hind legs in Triassic and early Jurassic pterosaurs are much more strongly developed than in more advanced Cretaceous animals. The socket for the thighbone (*femur*) (figure 54) is directed slightly upwards (see figure 53) and because the head of the thighbone makes an angle relative to the shaft, the legs in most pterosaurs are not straight under the body but are inclined slightly outwards (see 'Mark explains:

Dsungaripterus', pp. 24-25). This position is stronger among the basal pterosaurs; with the advanced Cretaceous examples, such as *Quetzalcoatlus*, the legs are situated under the body. The thighbone itself is rather straight and slim, especially when compared with the front limbs. The shin- and calfbone (*tibia* and *fibula*) are longer than the thighbone. Often in the Cretaceous pterosaurs, the fibula is lacking. The ankle is a simple hinge joint (figure 55) and is built in such a way that pterosaurs walked with their feet flat on the ground – a plantigrade gait (figure 56). The toes have claws (figure 57).

Figure 55. The ankle is a simple joint, the fifth toe in the later 'short-tail pterosaurs' is reduced to a little stub. In the earlier 'long-tail pterosaurs' this toe is elongated to support the skin between the legs (which is split in the later pterosaurs).

Wing

The most characteristic part of a pterosaur skeleton – and also the most unique – is the development of the front limbs into wings. As previously explained, the shoulder girdle articulates with the notarium and the coracoid to the downwards and forwards projecting part of the breastbone (see figure 51). At the side of the articulation of the scapula and the coracoid is an articular surface for the strongly developed upper arm bone (*humerus*; figure 58). This bone is relatively short and thick and has a large, downwards and forwards projecting process for the attachment of strong flight muscles (see figure 51). The bones of the lower arm, the ulna and the radius, are always longer than the upper arm bone. The ulna is the strongest of the two; the radius lies close to the ulna (figure 59). The articulation of the lower arm with the upper arm is such that the lower arm could only move in one

Figure 56. Pterosaurs were plantigrade, which means that they walked on their soles rather than on their toes. Here a Pterodactylus antiquus*, an abundant species from the Jura of Solnhofen, Germany is shown.*

Figure 57. The claws of the feet are clearly visible in this beautiful fossil. For a photograph of the hand see figure 63.

direction, due to which, when the wing is folded, the metacarpals, and consequently the wingfinger, point backwards and upwards (see also below). In other words, the wings of a pterosaur were, as in birds, automatically folded.

The so-called *pteroïd* is a bone, which is unique to pterosaurs (figure 60). This flat, tapering bone articulates with the wrist and points forward and toward the body. It supported the front wing membrane that ran from the wrist to the neck. The wrist bones in pterosaurs differ markedly from those in humans (figure 61) in that they had only one carpal bone that articulated with the ulna as well as the radius, followed by another bone that articulated with all the metacarpals.

► *Left to right::*

Figure 58. The upper arm bone (humerus), seen from the back, was a strong bone with a large protruding part for the attachment of the powerful flight muscles (see figure 51). Left a humerus of a Coloborhynchus*-species; right the humerus of a toothless species. Note the different shape of the protrusions.*

Figure 59. The ulna is the strongest of the two bones of the lower arm: the radius lay close to the ulna.

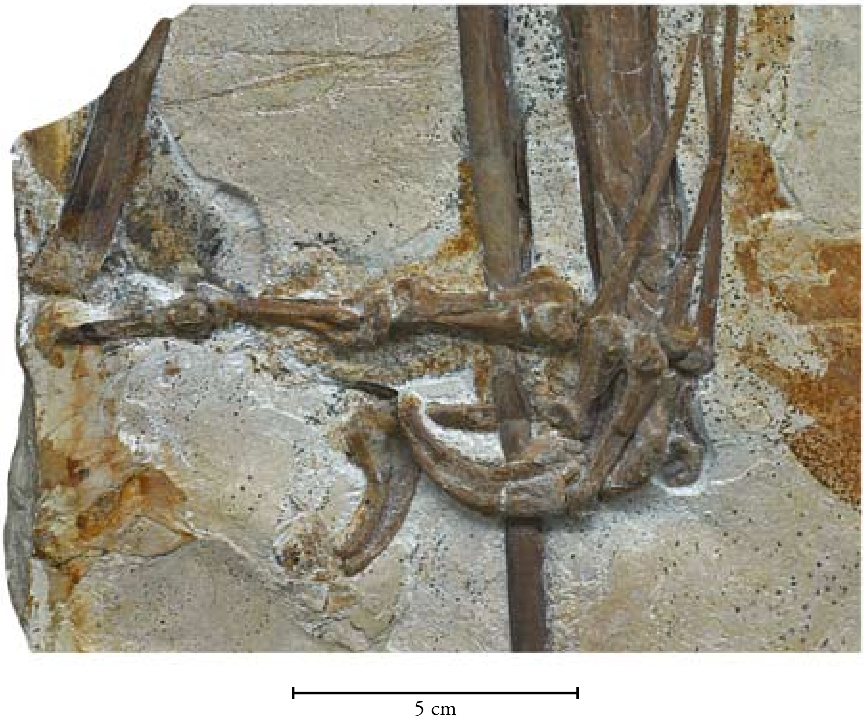
Figure 60. The pteroïd is a bone that only occurs in the pterosaur skeleton. It served to support the membrane to the front of the wing. Top: The pteroïd of a Coloborhynchus*-species. Bottom: Arrow points to the pteroïd of a* Pterodactylus*-species.*

There are only four metacarpals of which three are thin and fragile and supported the short fingers with claws (figure 63); the bone that supports the wingfinger is the most strongly developed (figure 64). The metacarpals in the early basal pterosaurs are short (see figure 50) whereas they are long in the advanced pterosaurs. The wingfinger is a specific adjustment for flight and is nothing else than the extremely elongated and strongly developed phalanges of the fourth finger of the hand (see figure 37 and the skeleton in 'Mark explains: *Dsungaripterus*', pp. 24-25). The wingfinger largely determined the wingspan of the animal. The wing, when folded, ran along the body upwards and towards the back (see above and figure 64&65).

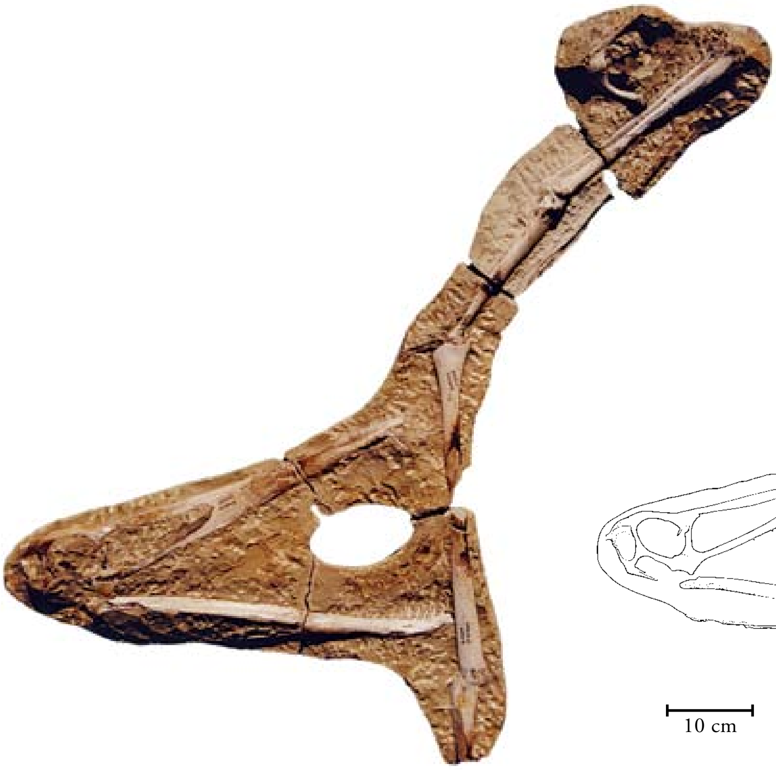
Fossils of bones are rare, but fossilisation of the soft parts of an organism almost never occurs. There are only a few examples of pterosaur fossils that can tell us anything about skin or intestines and by far the majority of these are of the skin and flight membranes. There are, however, examples of fossilised impressions left by the intestines of dinosaurs (most famously *Scipionyx*) but not of pterosaurs.

Figure 61. The wrist of an Ornithocheirid pterosaur.

▲ *Figure 62. The metacarpal that articulates with the wingfinger was much more strongly developed than the other metacarpals.*



◄ *Figue 63. The claws of the hand were much smaller than those of the feet (compare with figure 57).*



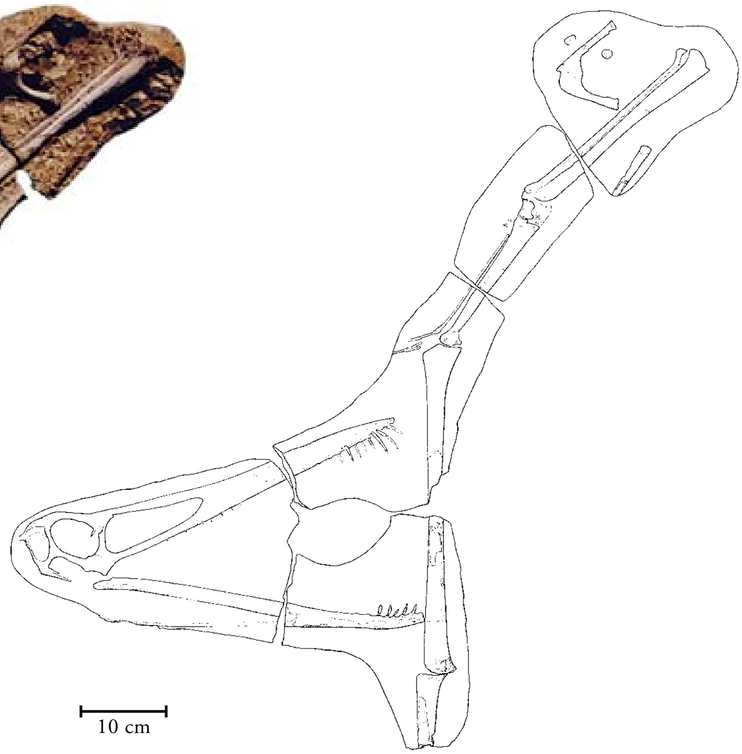


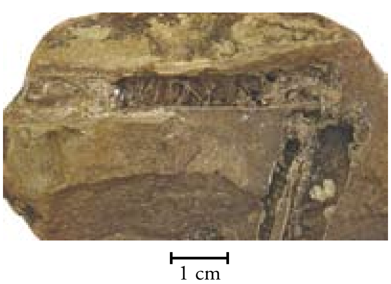
Figure 64. An un-prepared fossil. The fossil was brought to The Netherlands by the Natural History Museum Rotterdam for preparation of the bones, which was professionally done by Cor Strang. A preliminary scientific description was published in 2003. See also figure 38. The life-size model was made by Erwin Meerman.

Figure 65. In rest the wing-finger was directed upwards along the body.

FOCUS

Adaptations of the skeleton for flight

The pterosaur skeleton is unique and many of its peculiarities correlate with its ability to fly (see figure 37). One is the light construction of the skeleton. Not only are the walls of the bones extremely thin (sometimes less than 1 mm; figure 66, see also figure 41), but they are also punctuated with holes (so-called *pneumatic foramina*) which are linked with a system of airsacks in the bones. This construction is much comparable to that in birds, which also have similar airsacks in their bones. Airsacks not only make the skeleton lighter but they also point to a specialised breathing apparatus. The presence of a honeycomb structure or thin struts in the bones gives them the necessary strength. This construction did not necessarily reduce the weight of the skeleton, but did permit it to stand up to the forces that result from flight and the carrying of the relatively large skull.



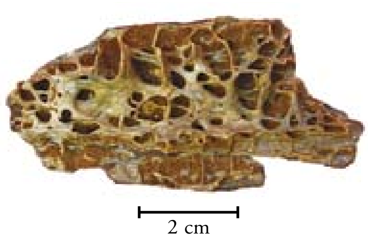


Figure 66. Pterosaur-bones were hollow and had thin walls. Inside, they were reinforced with bony struts or a honeycomb structure.

Mark explains

Anhanguera

As mentioned, the idea that pterosaurs were something like Cretaceous seabirds is a stubborn picture that arose due to the fact that pterosaur fossils were originally found in marine sediments (see 'Where did pterosaurs live?'). The consequence was that people believed that there was very little diversity. In addition, it was commonly accepted that the animals were unable to do anything at all on the ground. Generations of palaeontologists concluded that pterosaurs lived on fish that they caught by ploughing through the water with their lower jaw, like present-day skimmers (see 'Mark explains: *Quetzalcoatlus*', pp. 41-45), or that they seized fish from the water while in flight, an idea that dominated popular and scientific literature for years. Fortunately, the general picture is now beginning to change a little.

But even if pterosaurs are imagined much too often as flying fishers, this does not mean that there were no animals whatsoever that lived this way. Take *Anhanguera*, for example, a pterosaur from the Early Cretaceous of Brazil (see figures 40 and 64). There is much taxonomic debate about this taxon and a few others including *Coloborhynchus* and *Criorhynchus*, but nevertheless there are clear differences (figure 67). They are all closely related to one another. The group to which they belong spread across the whole world: *Anhanguera* fossils have even been found on Antarctica! *Anhanguera* and its fellows are an invariable feature of every Early to Middle Cretaceous collection of fossils of vertebrate flying animals, and occur in living environments that vary from deep inland to close by the sea.

Thus, this group of pterosaurs is a muddle in terms of classification, and attempts are repeatedly made to create more clarity. However, new results are not accepted by everyone – this is almost always the case in all fields of science. Their anatomy is known from very small fragments (see figure 4), as well as from the most surprisingly well-preserved, three-dimensional, nearly complete skeletons (of which only the skull is depicted in

Figure 67. Anhanguera*,* Coloborhynchus *and* Criorhynchus*, three closely related species.*

figure 40). Because these pterosaurs were, supposedly, among the best-known prehistoric animals, it seems as if they possess the 'standard' (if such a thing exists at all) pterosaur skeleton. But if you compare it to other large groups of pterosaurs, you can see that they deviated considerably. They had high shoulder joints, strange, angular upper arms with an oddly curved protrusion for the attachment of the flight muscles, robust wrists, abnormally long wing phalanges, short hind legs, flexible, strong necks and small bodies. In other words, if we hadn't known these animals so well due to the many fossils available, we would have taken them to be the most remarkable pterosaurs! All these anatomical features were not present just for the show, of course, but were adaptations to a lifestyle more airborne than that of all other pterosaurs.

The entire skeleton design is no more than two long, narrow wings with a large head at the front. The small bodies and pretty feeble hind legs indicate that they were exceptionally lightweight in comparison to their size, and that their efficient wing shape probably made them very good flyers. Long, narrow wings are extremely suitable for soaring (compare to long-distance gliding birds such as the albatross); these chaps could probably travel long distances without too many efforts. Their high shoulders were very useful for this, as they helped to obtain stability in the air. In contrast, they would have been rather awkward on the ground, because their hind legs were much shorter than their front limbs. Nevertheless, the image of clumsy gawks seems somewhat exaggerated. Moreover, their long wings would have made taking off rather troublesome because they would have needed speed for this – and, of course, enough space to beat their extended wings. In other words, the wings suggest that these pterosaurs were more at home

A young skimmer. Note the thin, sharp edge of the lower jaw.

flying in free space, where they could make full use of the wind and other airflows. However, they could probably not make much use of thermal columns because their wings were too narrow; you need broad wings for this.

Being able to fly and soar does not mean by definition that you never come to land to search for food. Some present-day birds that are extremely well adapted to gliding, such as albatrosses and fulmars – do not eat during their flights but have no hesitation in landing on water or on land. They are perfectly capable of taking off once again, and it seems not unlikely that *Anhanguera* and its companions may have done this too.

But some species display an adaptation that indicates feeding without landing. *Anhanguera* and its fellows have teeth of varying size that protrude from the jaw at every conceivable angle. The front teeth are long, curved teeth that dovetail together and are thus extremely suited to grab and hold a moving, slippery prey, such as a writhing fish. The teeth toward the back of the jaw are much smaller and there are bigger gaps between them (see figure 40). These teeth have a different function: they ensure that the food is transported further toward the throat. The lack of large teeth at the back of the jaw to grab the prey indicates that only the front teeth were used for that purpose. This is quite logical for an animal that attempts to keep the distance between its body and the water surface as large as possible in order to minimize the chance of crashing down into the water. The extension of the jaw is a good way of realizing this.

An animal in flight will always go faster than its prey underwater, so its jaws will be thrust downward and backward when it inserts its snout into the water to grab its prey. A strong flexible neck such as that of *Anhanguera* is a precondition for this type of fishing. Pterosaurs that dip their jaws into the water while in flight must neutralize the forces that are exerted upon their skull when they withdraw their jaws from the water. And that takes a lot of strength. Therefore they must have had very strong neck muscles to suddenly extract their jaws, and their prey, against the thrust of all acting forces. In fossils, it is only possible to determine the presence of such muscles by looking for relatively swollen and complex front neck vertebrae. In contrast to most pterosaurs, *Anhanguera* do exhibit this feature. Some animals related to *Anhanguera* have smaller front neck vertebrae, which means that they did not catch fish in the same way as *Anhanguera* did, despite the fact that their life was primarily spent in the air.

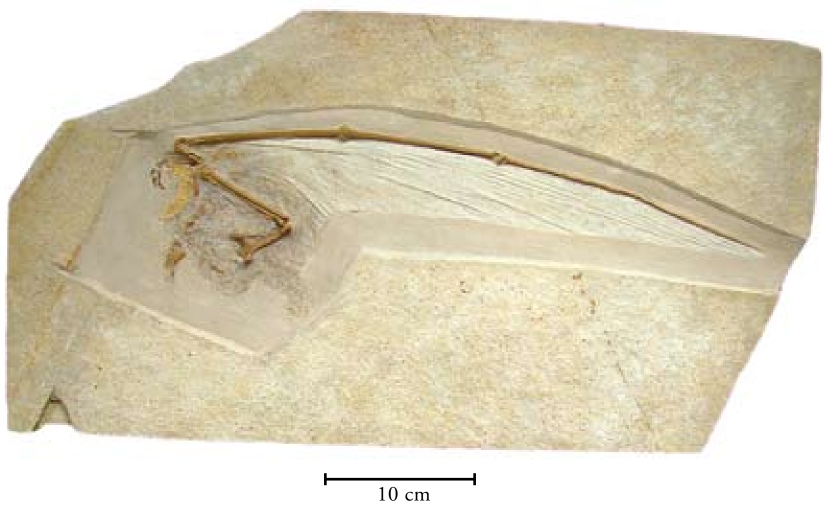
Soft parts

Muscles

The attachment of muscles by ligaments leaves scars on the bones. Here, the surface of the bone is rough, or has ridges or still bigger protrusions and from these palaeontologists gain an impression of the muscles and how strong they were. The upper arm bone is a good example (figure 58): here the big process is meant for the attachment of the powerful flight muscles (see figure 51). Other clear scars can be seen on the skull and lower jaw. These give an idea of the power with which the animal could close its jaws and gives indirect evidence of the creature's way of life. In pterosaurs that could catch fish whilst flying, the muscles to close the lower jaw are extremely strongly developed (see also 'Mark explains: *Anhanguer*', pp. 81-83).

Brains

Remarkably we know quite a lot about the pterosaur brain, despite the fact that they cannot fossilise. The brain consists for the most part of water and is, therefore, almost the first element of a body to decay when an organism dies. Sometimes, however, the brain cavity fills with sediments that fossilise, yielding a perfect impression of the cavity: a brain cast (*endocast*). There are also other means by which palaeontologists can examine the shape and capacity of the brain, notably by scanning using Computed Tomography (see figure 11). An object, in this case the skull, is digitally cut into slices from which the shape of the brain (and the skull) can be reconstructed with computer software and, if desired, be physically reproduced in three-dimensions by rapid prototyping or similar means. The brains of the advanced pterosaurs of the Cretaceous looked much like those of modern birds. The



► *Figure 68. The flight membrane of this* Rhamphorhynchus muensteri *is so perfectly preserved that the internal reinforcement of fibrous tissue (*actinofibrils*) still could be mapped. This fossil is known as the 'Zittel wing', named after the scientist Karl Alfred von Zittel (1839-1904) who described the fossil in 1882.*

FOCUS

Flight membranes and skin

The most important part of the flight membrane was that of the wing (*cheiropatagium*; figures 6 and 68), but such membranes were fairly small. In contrast to the wings of bats which are supported by the elongated fingers of the entire hand (see figure 37) the flight membranes of pterosaurs were internally reinforced by thick fibres of tissue (*actinofibrillen*) that ran parallel to the wingfinger. At the front of the wing was another membrane (*propatagium*), which was supported by a bone unique to pterosaurs, the *pteroïd* (see page 77). There is much discussion as to the shape of the flight membranes, but despite perfect skin impressions, we still do not know exactly how they looked. The membrane that forms the wing almost certainly extended in a large curve to the ankles (figure 69). It is clear, however, that the shape of the flight membrane differed among the various species. For example, that in *Quetzalcoatlus* was very small compared to *Coloborhynchus*. In the early forms, a membrane is also visible between the hind legs (*cruropatagium*) but in the later forms this membrane is split. In addition, feet have been found with skin between the toes and we also have impressions of three short fingers with skin. Throat pouches (figure 70), cushions on the feet (figure 71) and webbed feet are also known.

Figure 69. The flight membrane between the front and hind limbs is clearly visible in this fossil.

▲ *Figure 70. Throat pouches are attested in some pterosaurs, as seen here in a specimen from Solnhofen, Germany.*

► *Figure 71. The foot of an Azhdarchidea-species (Early Cretaceous, Brazil). Clearly visible are the soles under the heel.*

areas that are responsible for sight are well-developed, but not those for smell. It has been known for some time that the areas responsible for reflexes (such as balance and posture) were well-developed, but recent research has shown that the organ that was responsible for balance was extraordinarily large. The shape of the brains seems, however, to exclude complex social behaviour.

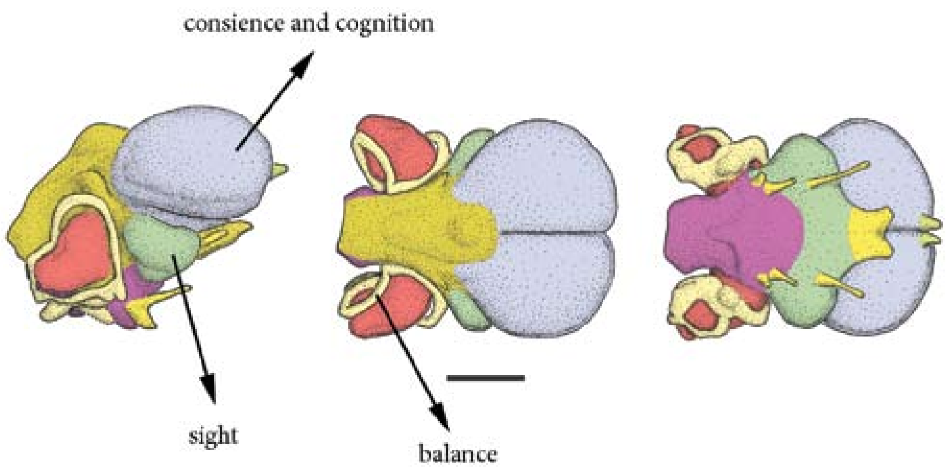


Figure 72. The brain of the Cretaceous pterosaur Anhanguera santanae *(seen from the side, from above and from below). They are clearly reptilian but also compare well with the brains in birds - these are indicated in the illustration. Areas that are responsible for smell are badly developed, but those for sight are well-developed. That the parts of the brain responsible for reflexes was well-developed has been long known but recent research shows that the part responsible for balance was exceptionally large.*

FOCUS

Body cover

The skin of a pterosaur looked a bit like human skin and sported a remarkable feature for reptiles, namely hair. This hair did not have a same origin as ours or that of other mammals and is not comparable. It does, however, compare with the covering seen in some dinosaurs although the latter might be better compared with feathers. The 'hairs' of a pterosaur do not originate from deep in the skin, but from its surface. Along with a practical function such as the regulation of body temperature or of decreasing friction between air and skin during flight, it is not unreasonable to assume that the 'fur' or 'fuzz' differed in texture and colour for better recognition and/or to impress potential mates.

Locomotion

Terrestrial

Ongoing discussions about terrestrial locomotion focus on how exactly pterosaurs walked on all fours. Palaeontologists have long known that pterosaurs walked on the sole of their feet (plantigrade) rather than on their toes (digitigrade) but in recent years additional evidence has come to light about exactly how they did this. It was thought that pterosaurs were bipedal, thus more or less upright, but nowadays it is generally accepted that they were in fact quadrupedal. On land the wing pointed upwards and backwards along the body. They must have been rather adept, although the basal pterosaurs far less so because of the membrane between their legs and the long, rigid tail (see 'Mark explains: *Dimorphodon*', pp. 19-21). Moreover, the body of these early pterosaurs were much closer to the ground because of the different ratio and position of the bones of the limbs, which meant that the body was orientated much more horizontally rather than vertically.

Flying

The origin of pterosaurs and also of active flight is largely a matter of theory. There are no fossils found (or at least recognised) of their ancestors. As suggested above pterosaur's ancestors were most probably tree-dwellers who in the course of evolution developed a flight membrane as an adaptation toward their habit of jumping between trees. This gradually increased so permitting soaring for which a large surface area is needed (see figure 33).

The different shapes of the wings and flight membranes, and indeed the range of size of the animals, must have resulted in a wide variety of flying behaviours. It is generally assumed that the smaller species were active flappers whereas the bigger species, with wingspans of six metres or more, specialised in soaring and so were able to cover long distances. Taking off from the ground does not seem to have been a problem because the velocity needed was very low and even the biggest pterosaurs, albeit less easily, must have been able to take to the air after a short sprint.

Diversity

Over 200 years of collecting pterosaur fossils has resulted in over 60 different genera amounting to well over 100 species. Exact numbers differ, as is usual in palaeontology, as the validity of different species is sometimes unclear due to the fragmentary nature of many of the remains provoking difference of insight among scholars. About half of the species have been described over the last 30 years. This sudden increase is partially due to the strong increase in palaeontological research, as mentioned, but also due to the discovery of new sites, such as those in Brazil and China.

Lifestyle

The manner of living adopted by pterosaurs differed according to species, just as the lives and habits of different species of bird differ. It was long believed that the majority of the known species were fish-eaters (piscivorous), but modern research has repeatedly shown that not all of these species ate fish and different species evidently occupied their own particular niches. Nonetheless, most fossils are found in layers that are either marine in nature or closely related to it and many pterosaurs did have a fish diet. However, this bias toward marine environments seems to be because the chance of fossilisation in a watery environment is much greater since a corpse could be covered quickly by sediment and so protected it from scavenging. Moreover, many of these marine environments were extremely toxic, prohibiting any form of life in the deeper water. Whilst fossils tend to come from these marine locations this does not mean that there were no pterosaurs living on land.

Reproduction

As discussed, many pterosaurs had crests, which were probably related to courtship and/or mating: used to impress females and to scare off other males. More information on this topic can be found in the 'Mark explains' text about *Pteranodon* (pp. 92-95).

From the very beginning, scientists assumed that pterosaurs laid eggs (figure 73). The reasoning was that they were reptiles and all reptiles were egg-bearing. However, although dinosaur eggs were known, none were discovered that could be attributed to pterosaurs. This led palaeontologists to theorise that perhaps they were ovoviviparous – retaining the eggs in the body until they are ready to hatch – in the same way as do present-day snakes. The first pterosaur eggs were discovered only in the 21st century and, ironically, three at almost the same time: two from China and one from Argentina. Recently, a further, extremely rare find was reported: a fossilised pterosaur with an egg still inside its body. The eggs had a soft shell, perhaps comparable to the leathery covering of the eggs of modern snakes. Study of the bones of the embryos suggests that the baby-pterosaurs were nidifugous, that is: as soon as they hatched they were able to fly, though this may not have been the case for all species. Despite the rarity of eggs we do have a relatively large numbers of fossils of immature animals and even of animals that were newly hatched. These mostly belong to the Jurassic period (see figures 6 and 17).

Food

Most pterosaurs were piscivorous, and although this picture has been nuanced in recent years, it remains true, as explained, that most known species ate fish or other marine/aquatic animals. There are, however, many species that had other dietary requirements (figure 74), such as the early pterosaur *Anurognathus* (see figure 26),

Figure 73. Fossilised pterosaur eggs have been found only recently in Argentina and China.

Mark explains

Pteranodon

For years, the size of some pterosaurs has been rather overestimated. For instance, the wingspan of *Quetzalcoatlus* was estimated at more than 20 metres, and a few years ago there were even rumours about a pterosaur with a wingspan of 25 metres! But the wingspan of *Quetzalcoatlus* was probably no more than 10 metres (which is still pretty big!), and the traces on which a calculated wingspan of 25 metres was based have turned out to be false. Even the wingspan of everyone's favourite pterosaur, *Pteranodon*, was overestimated at a given moment. A robust skull that belonged to an older type of *Pteranodon*, the one with the tapering crest, was regarded as belonging to a *Pteranodon* with a wingspan of approximately 10 metres. However, this species, *Pteranodon sternbergi,* with a wingspan of around six or seven metres, was probably similar in size to the other species of *Pteranodon*. The point is, *Pteranodon* was not so very large … On the contrary, most of them were actually considerably smaller than people thought, and the outline reveals a surprising amount of details about the lifestyle of the long-extinct animal …

We know of *Pteranodon* for more than a century. The first fossils were found in the chalk sediments of Kansas, USA, in 1870 by expeditions under the leadership of the renowned American palaeontologist Othniel Marsh (see figure 29). Down to the present-day, more than 1000 individuals of this animal have been found and we thus have sufficient material to study and to obtain a reasonably good picture of its anatomy and proportions. And that occurred through a manner of fossilisation that was very different from that of some Cretaceous pterosaurs from Brazil: *Pteranodon* fossils are as flat as a pancake! Besides the enormous toothless jaws and the striking crest, *Pteranodon* gained fame as the first true giant of the skies – an animal that could compete with the wingspans of the newly developed aeroplanes (we are talking of more than 100 years ago). In terms of size, they caused the famous pterosaurs from the English Wealden sediments to pale in comparison. *Pteranodon*'s size has received much attention from many researchers engaged in aviation, in order to find out how such an oversized animal was able to fly. *Pteranodon* was an ultra-efficient, dynamic glider that cruised the airways above the *Western Interior Seaway* – the sea, hundreds of kilometres in length that divided North America in two at the time. Due to the discovery of a well-preserved food pellet, we know that it lived from relatively small fish; therefore, this one time, we have a legitimate mirroring of lifestyle between pterosaurs and seabirds (see also 'Mark explains: *Anhanguera*', pp. 81-83). At last!

All right, let's get back to the size. The so-called 'fact' that *Pteranodon* was a giant with a wingspan of seven metres has permeated more or less every popular book (and even some scientific ones!), so why has doubt now arisen? Chris Bennett is the person who can help us: he is responsible for the situation that we can now draw a picture based on the most recent research. Chris has roamed all over the world to study, measure and identify every *Pteranodon* fossil he could find. His unique, exhaustive analysis revealed a surprising result: all examples of *Pteranodon* could be divided into two groups. The distinction between these two groups is primarily based on difference

in size. The largest group, containing 66% of all examples, consists of the smallest individuals with a wingspan of approximately four metres maximum. Although this is larger than any modern bird, for a pterosaur, and certainly a pterosaur from the Late Cretaceous era – where the size of the largest pterosaurs went right through the roof – four metres is hardly even average. The other 34% of the fossils have wingspans of between six and seven metres. The difference could possibly be explained by the fact that the animals were in different stages of their lifespan. However, a study of the bone structure shows that almost all the fossils were adult or near adult at the time of death. The evidence is closing…

But the research revealed that there are even more details that distinguish these groups from one another: the smaller animals have a much shorter crest than the larger animals, where these crests could grow just as long as the jaw itself. The tip of the jaw follows a similar pattern. The true big shots developed upper jaws that terminate in blunt points, with an overbite of the upper jaw. But with the smaller *Pteranodon* the length of the upper and lower jaw is much more equal. There are also differences in the rest of the skeleton: seen relatively, the smaller examples have larger pelvic canals. These differences are less pronounced among immature animals.

With the exception of the differences in headgear and the pelvic canal, the skeletons of the two groups are identical. You could explain this by thinking that these differences involved some kind of specialisation of the animals. But an explanation that is much more plausible is that we are dealing with the difference between males and females – in other words, they are sexually dimorphic, meaning that there are visible differences in appearance between males and females.

I find everything about this pterosaur really cool. It's absolutely great that we have sufficient data to be certain that *Pteranodon* is sexually dimorphic! In order to establish this, we have to examine their reproductive system. Males don't have very much to do in the reproduction process… In fact, our 'tools' only require very little muscle attachment. This means that the male *Pteranodon* only needs a narrow pelvic canal to accommodate the last remnants of its intestines and a few other bits. With the females, this is different: they have to lay eggs and therefore must have a wider pelvic canal in order to be able to expel the egg. In the small fossils we see the relatively wide opening of the pelvic canal and therefore we can assume that the large *Pteranodon* fossils are those of the males and the smaller ones, females. Once we have accepted this we can make a comparison with modern animals and we can perhaps learn more about *Pteranodon*'s urge to mate, based on the 'patterns' of difference between males and females in modern animals.

Let's look at the males first. What makes a *Pteranodon* a male *Pteranodon*? Apparently a large body and striking head ornamentation. It turns out that there is much variation in shape and size of the crest and the points of the jaw: some males have straight crests whereas others have crescent-shaped crests. Some jaws end in a sharp point, while others are blunt to a greater or lesser degree. The fact that immature animals do not have crests indicates that these crests were only important in the lives of adult animals. And it seems evident that they played a role in mating: a type of behaviour only applicable to adults. Males

would be able to show off their crests and jaws in competition for female attention. If we assume that the behaviour of these extinct animals – with regard to reproduction – is comparable to that of modern animals, the enormous size of the headgear demonstrates a short but very intensive period of male rivalry for the favours of the female.

But would we (well, I personally in any case) go as far as to speculate that their relatively robust physical proportions could be an indication of physical competition? In other words, the males probably clashed quite vehemently now and again. This may explain some of the wounds that we find in some of the *Pteranodon* fossils.

The males may have been great philanderers. Animals that are strongly dimorphic have the tendency to be polygamous: they enjoy entering into relationships with different partners. We can imagine our *Pteranodon* males fighting to win harems of females, or continually battling one another until a nice girl comes along with whom they have a fleeting affair, after which the female flies off to generate and lay eggs, leaving the men to fight for the favours of the next female.

In contrast, the females have it relatively easy. With polygamous males, who are constantly fighting for the favours of the females, they only need to wait for the winner and thus for the highest quality sperm. That is why their smaller bodies lack decoration.

Much of this picture borders on speculation, but it is an educated guess and based on reliable observations of modern animals. Of course, we can never be absolutely sure about our interpretation. But the fact that we have actually been able to gather so much information – by means of palaeontology – that we can speculate about the mating habits of animals that became extinct more than 80 million years ago is quite amazing, don't you think?

I hope that my figure of *Pteranodon sternbergi* and his harem will help explain the above-mentioned points. Everything about the males indicates competition with the other males. Not only are they much larger than the more sedate-looking females (including their one-metre-long robust skull) but they also have a large crest in the hope of surpassing their rivals. Please note that, when standing erect, the male would have been much larger than shown here. In the figure, he is engaged in the process of getting to his feet in the same way as mammals with long limbs do – pushing himself upward with the front limbs to balance on the hind legs. I have opted for an older animal because I wished to show that he would be the last individual you might want to challenge for a fight. He is not getting up to run away from the storm approaching from the right, but to demonstrate who is really the boss here.

The females have a smaller skull that is much less robust. They were probably lighter in colour than the males, which harmonizes with the functional restrictions of the seabird-like life. I would like to point out one more detail: there were no cliffs along this part of the coast of the *Western Interior Seaway*. It is often claimed that cliffs were essential to enable pterosaurs to take off and, ironically enough, studies of *Pteranodon* are often quoted to support such claims. But, consider it … there is absolutely no indication that demonstrate the existence of cliffs in this part of the world at that time (at least, not on the eastern shore), so that argument in favour of taking off from cliffs is not particularly strong.

which is evidenced by the broad jaws full with small teeth. *Tapejara wellnhoferi* (figure 75) whose muzzle looked much like the bill of a parrot, was probably vegetarian and lived on fruits and seeds (and occasionally a lost lizard?, see 'Mark explains: *Tapejara*', pp. 114-115). *Sinopterus dongi* (see 'Mark explains: *Sinopterus*', pp. 104-106) might have been fruitivorous. Recent research on the giant *Quetzalcoatlus* suggests that these animals had small land animals as part of their diet, rather like modern storks.

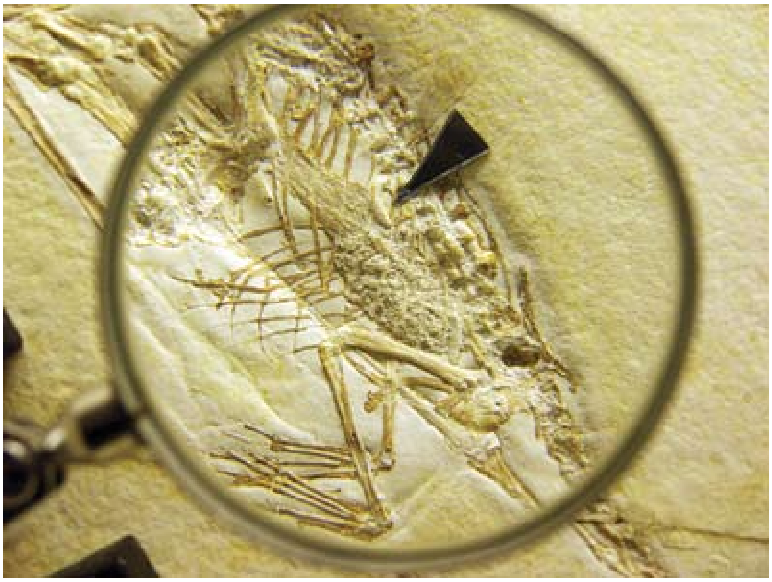


Figure 74. Unidentifed stomach contents of a small pterosaur.

◄ *Figure 75.* Tapejara wellnhoferi *was probably a seed-eater.*

► *Figure 76.* Quetzalcoatlus *has caught a baby-dinosaur.*

Catching fish can be done in several ways. A big group of pterosaurs, referred to by some palaeontologists as *Ornithocheiridea* and by others as *Anhangueridea,* had teeth that were well adapted to catch the slippery, wriggling fish out of the water whilst in flight (see 'Mark explains: *Anhanguera*', pp. 81-83).

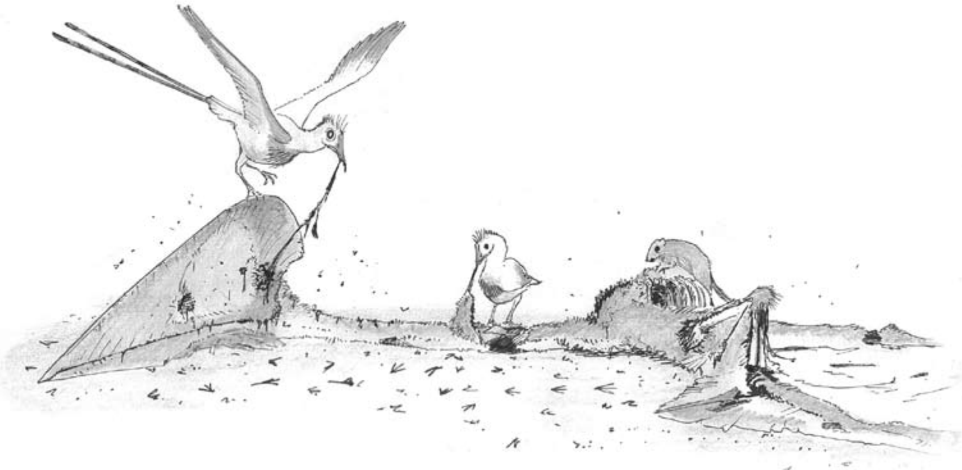
For the edentulous species (*Thalassodromeus*; figure 77), another technique has been suggested, namely ploughing through the water whilst in flight, rather like modern-day skimmers (see 'Mark explains: *Quetzalcoatlus*', pp. 41-45), but there is much debate about this very specialised way of fishing as it is relatively inefficient and requires many special adaptations. Moreover, *Thalassodromeus* was an enormous pterosaur with a huge skull, a major disadvantage for fishing. This manner of fishing has also been suggested for several other, smaller, species such as *Rhamphorhychus* that had both razor sharp jaws (to enable them to easily plough through the water) as well as large teeth.

...and becoming food

Without doubt there were opportunistic scavengers that fed on the carcasses of pterosaurs (figure 78), but this activity is rarely visible in the fossil record. But there are some clues that pterosaurs were eaten by other animals.

A remarkable find from Solnhofen, Germany, shows a pterosaur that has been eaten, digested and the remains spit out. A pellet consists of a partially digested *Rhamphorhynchus,* whose small bones suggest that it was not very old when it was

Figure 77. Thalassodromeus sethi*, erroneously named after the Egyptian god Seth because of the shape of the crest (which looks like the crown of the god Amun rather than that of Seth). See also figure 31.*



▲► *Figure 78. Like all animals pterosaurs eventually died. Doubtless scavengers feasted on their carcasses.*

FOCUS

Steneosaur

Figure 79 shows an ocean dwelling *Steneosaur*-crocodile that lived in the Solnhofen lagoon. Superbly preserved specimens are known of up to four metres long with jaws and teeth that suggest that they were piscivorous. But although fish was their main prey, it is not unreasonable to assume that if the opportunity arose they would seize a bird, mammal or pterosaur. To catch a small, agile pterosaur would not be easy but a quick ambush from the deep, dark waters might catch a pterosaur unawares. The indigestible parts might then be disgorged as a pellet which preserved as a valuable fossil.

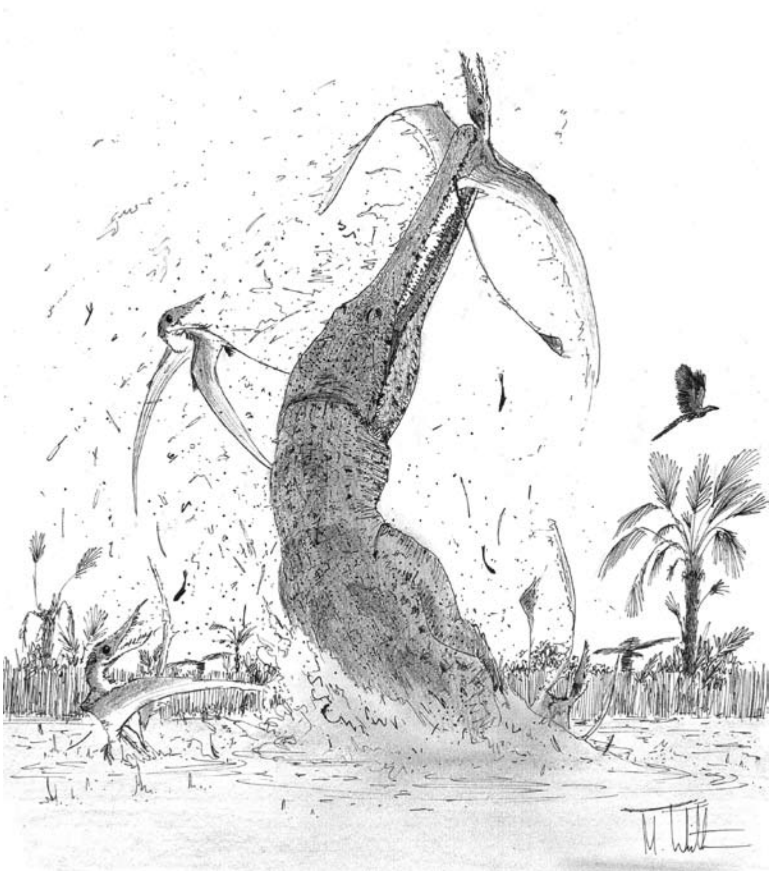


Figure 79. Steneosaurus *seizing a Rhamphorhynchus.*

Irritator

It is a fact that the tooth of *Irritator* is embedded in a pterosaur cervical, but can we say anything about how this happened? There are only two logical possibilities: the *Irritator* caught the living animal and killed it or found the dead animal and ate it. Unfortunately, the single tooth cannot tell us which of the two scenarios is correct, although the scavenging theory is preferred. But modern predators, be they cats or crocodiles, kill flying animals whenever there is an opportunity. So why should this not be equally true of *Irritator*? It may not have been easy because flight is a rapid form of escape but if ambushed or sick, the pterosaur would be easier prey. In figure 80 an *Irritator challengeri* hunts a *Brasileodactylus*, a species closely related to *Anhanguera* (see 'Mark explains: *Anhanguera*', pp. 81-83). The scene is set about 110 million years ago at the edge of a lagoon that we now know as the Santana Formation in northeast Brazil (see above).

Figure 80. Hunting Irritator.

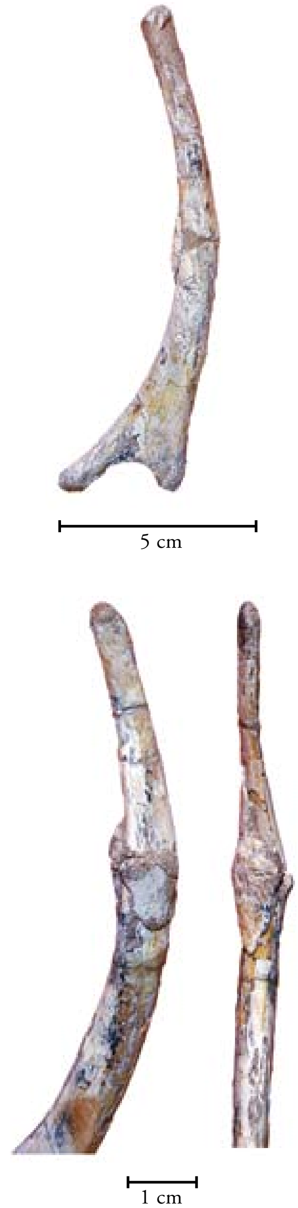
eaten. We do not know whether the animal was already dead when eaten or had been predated. Equally unknown is what kind of animal ate the pterosaur, although it has been suggested hat it may have been a large fish or crocodile (figure 79). In 2012 a publication came out that shows a large fish with a pterosaur as prey: clearly, something went horribly wrong as both died 'in the act'.

There are other clues to suggest that pterosaurs were themselves preyed upon. Three cervicals of a pterosaur still had a tooth of *Irritator,* a predatory dinosaur, embedded in them and prove without a doubt that these dinosaurs occasionally preyed on pterosaurs. The absence of chemical erosion on the cervical tells us that this part of the neck had only been swallowed by the predator before it too met its end, and as a result its stomach acids had had little chance to corrode the bone.

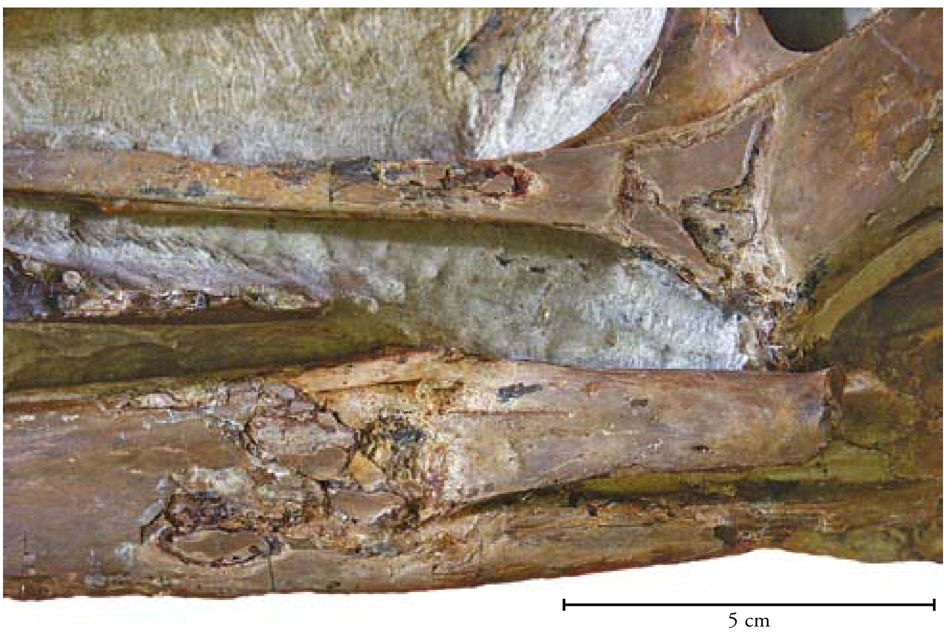
Sick and cured

Like all animals, pterosaurs could become sick or suffer wounds. There are several examples of animals with serious wounds and infections, which they survived. A good example is the Tokyo-specimen of *Coloborhynchus* that survived a broken rib (figure 81), but which also had two severe infections of the lower jaw and skull (figure 82), as evidenced by distortion of the bone. It was suggested that these infections must have caused the death of the creature.

A rather different case is presented by *Ludodactylus* (figure 83). This unfortunate animal caught a sharp tree leaf between the two branches of the lower jaw. The scratch marks at the end of it shows that the animal tried to get rid of it, but without success. The leaf prevented the creature from feeding and/or the wound became infected. Another example is a pterosaur that made a mis-judged landing, crushing its jaws so seriously that it died from its injuries (figure 84).



▲ *Figure 81. Many fossils show wounds. These broken ribs of* Coloborhynchus piscator *healed.*



◀ *Figure 82. Besides the broken ribs in figure 81, the animal also suffered from infected bones in the lower jaw and skull. Possibly this caused his premature death.*

Figure 83. This special fossil is of Ludodactylus sibbicki. *The animal died because the leaf of a woody plant, comparable to our yucca or agave, became stuck between the two branches of the lower jaw. Because of the leaf, that ran along the tongue, the animal was not able to eat. The frayed end of the leaf sadly indicates that the animal tried to remove the leaf.*

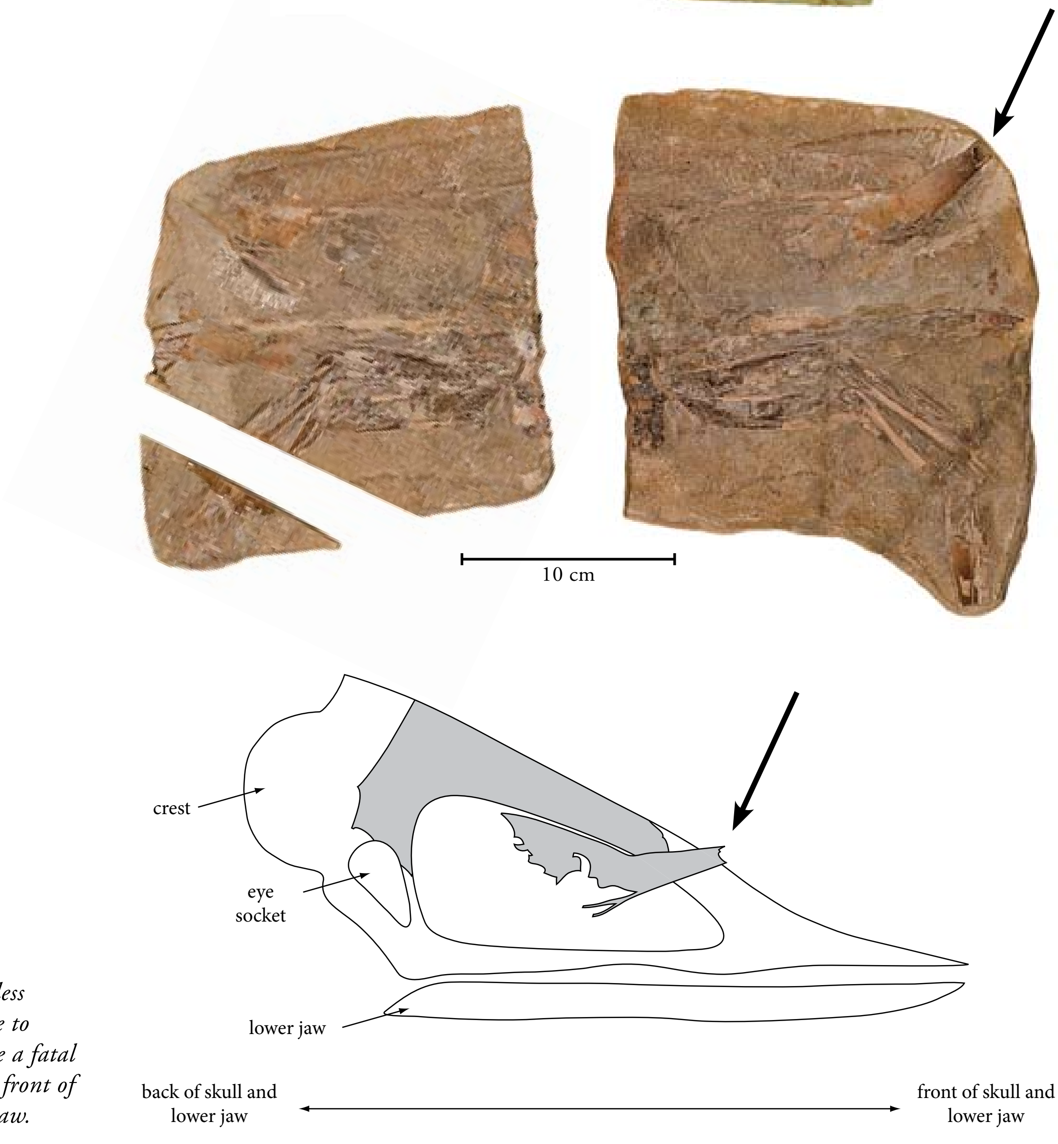


Figure 84. This toothless pterosaur (comparable to Tupandactylus*) made a fatal landing, crushing the front of the upper and lower jaw.*

Mark explains

Sinopterus

Sinopterus dongi is a toothless pterosaur from the Early Cretaceous of China and is akin to *Tapejara wellnhoferi*, for example (see 'Mark explains: *Tapejara*', pp. 114-115). The layers of sediment in which these fossils were found are renowned due to the fossils of 'bird-dinosaurs' and 'dinosaur-birds', as well as a recently unearthed giant gliding lizard. The perfectly fossilised hand and fingers of *Sinopterus* display a series of curved, narrow claws and extended penultimate phalanges. These are characteristics that you might expect to see in animals that are good climbers. Other aspects of the anatomy of these pterosaurs also point to adaptations for climbing. They have shoulder joints that are directed completely outward, instead of a little backward, as is common with other pterosaurs. This ensures greater mobility in the upper arm and, as a consequence, the lower arm can extend further. Pterosaurs walked with the feet flat on the ground, which contrasts with many other animals that walk on their toes, and this has prepared them for a life style of climbing. In addition, the joints of the hind legs ensured much mobility, which is also very handy if you wish to climb trees. Thus, it appears that some groups, such as the Tapejarids to which *Sinopterus* belongs, and some early ptero-

saurs such as *Dimorphodon* (see 'Mark explains: *Dimorphodon*', pp. 19-21) were extremely dexterous in climbing. Palaeontologists believe that *Sinopterus dongi* – and some other similar pterosaurs – ate fruit, and climbing would be very useful, of course, for plucking the fruit hanging in the trees. There are various modern birds, such as the cassowary, that find everything they need on the ground. Perhaps *Sinopterus dongi* did both. But being able to climb well has more advantages. You can find good accommodation for brooding, and it helps to avoid natural enemies. Although some preying dinosaurs could also climb very well, the lightweight pterosaurs could probably move along branches that could not carry the larger and heavier hunters.

In some respects, these ideas are not new. Since the very beginning of research of this group of animals, we have all known about pterosaurs hanging on cliffs and in trees. That they may have climbed from tree trunk to tree trunk is plausible, but they will not have lodged between the small, densely leafed branches, because their claws resemble small climbing hooks and crampons rather than grasping tools. This certainly applies to their feet and, accordingly, illustrations in which you see pterosaurs hanging in trees in a bat-like way are simply imaginary because this is impossible from a morphological point of view (see focus 'Pterosaurs in the media').

So, a climbing pterosaur… But what is that bird doing in the jaws of our *Sinopterus*? Well, this illustration is based on a fossil pellet from the Early Cretaceous in Spain, which indicates that there was a bird-lover that regularly compiled a festive meal of young birds! It is believed that the pellet came from a pterosaur or from a dinosaur, but we cannot go further than that … unfortunately. Because *Sinopterus* has a beak that bears a vague resemblance to that of a toucan, it could easily be a candidate for this Mesozoic nest plunderer.

Three dimensional models

Introduction

Models are based on scientific research, but this does not mean that they all look the same. An example of this variation between scholars is the two differing reconstructions of *Tupandactylus imperator* (figure 85). The differences result from individual palaeo-artists using different techniques (compare the account of Erwin Meerman with the one from the Portsmouth team below). Individual scientists also give varying importance to the same evidence stressing some characteristics over others. Furthermore, research continues and knowledge improves and established views become modified or replaced.

Erwin Meerman

Part of a palaeontologist's work is to reconstruct extinct animals. One can do this digitally with a computer or simply on paper, as seen in many of the images in this book. However, for exhibition, three-dimensional models are of course preferable (figure 87).

Figure 85. Two interpretations of Tupandactylus imperator *(see also figure 44). Left a model made on the basis of scientific knowledge several decades ago, whereas recent research led to the interpretation seen to the right.*

Figure 87. Erwin Meerman's model of Dimorphodon.

FOCUS

Pterosaurs in the media

The way popular media brings extinct animals back to life differs from professionals. Palaeontologists and palaeo-artists try to 're-create' the creatures as authentically as possible, using the results of scientific research. Moviemakers, but also some documentary makers, use a different set of rules that sometimes make the reconstructions look more spectacular but are incorrect. For example, the, otherwise marvellous Jurassic Park movie and its sequels of the late 1990s featured pterosaurs in the third of the films. *Pteranodon* (see 'Mark explains: *Pteranodon*', pp. 92-95), as we have seen earlier, was edentulous but in the movie it was given huge teeth. Moreover, the movie's pterosaurs catch their prey with their hind legs. Real ones were not able to do this because, unlike modern birds, they did not have a *hallux* (reversed toe). In birds, this toe opposes the other toes, allowing them to grasp (figure 86). This lack of a hallux is a well-known pterosaur trait and should not have been overlooked. Even a reputable organisation like the BBC showed *Quetzalcoatlus* with teeth on their website for *Walking with Dinosaurs*, whereas it is well-known that they were edentulous as well (see 'Mark explains: *Quetzalcoatlus*', pp. 41-45).

Figure 86. Some birds of prey are able to catch their prey with their legs because the big toe opposes the other toes. Pterosaurs could not catch their prey as they lacked this opposable toe arrangement.

But how are such models made? Some palaeontologists do this themselves, but more often they collaborate with professional artists. Naturally, there are different ways to do this and the methods largely depends from the individuals themselves. Here we examine the methods of palaeo-artist Erwin Meerman, who made, among others, the life size 'Rotterdam pterosaur' (figure 64).

The first thing is to understand the anatomy of the animal. This means that an artist, like a palaeontologist, has to study the skeleton, muscles, tendons, skin, eyes etc. The bones are measured with great precision, preferably from the original fossils. These measurements are turned into a schematic, life-size drawing and printed, thus creating a blueprint. This immediately gives a good idea of the size of the model.

Next, the main parts of the animal (head, neck and torso) are cut from blocks of polyurethane or 'pur-foam'; this is a chemical substance that is much used as a liquid (for example in paintwork for cars), or as blocks to insulate roofs and floors. It is light but strong and easy to work with. The blocks are secured with iron thread that serves as a frame and substitutes for the spine of the animal. It also forms the basis for the limbs (figure 88).

Muscles are shaped using a lightweight clay ('Artista') that is much used in the world of handycrafts. This material too is light but strong, just like polyurethane-foam, and is easy to work with.

Next the body is finished, except for the skin. But before this is added, the flight membrane has to be created. The frame is put in the required pose and a mould of clay is added in the shape of the membrane and clad with polyester resins

▼ *Figure 88. Left, the first stage of the life size reconstruction of* Dimorphodon*: pur-foam blocks, secured with threads of iron, form the basis. Right, the wings are added.*

and fibre glass, which serves to reinforce the polyester resins. Once the clay is dried it is removed, leaving a thin layer of polyester flight membrane (see figure 88). If the skin is too thin, a layer of epoxy can be added.

Next, the other skin structures are added to the rest of the body and the entire surface is covered with 'epoxy sculpt'. This material is extremely suitable for this task, and it is easy to work with (comparable to clay), relatively light and hardens automatically in one or two hours. This does mean, however, that the sculptor has to work fast to shape it. The eyes are the same as those used in taxidermy for mounting birds or mammals. The model is finished by airbrushing with acrylics.

All in all it is a time consuming process that can take several months, time spent not only in preparing the reconstruction but in dialogue with the palaeontologists. The result is a high quality life-size model of a long extinct creature.

The English models

Typically, dinosaurs, as the most well-known of fossil creatures, are given priority in life-size dioramas, but, in 2008, the Royal Society granted palaeontologists working at the University of Portsmouth an opportunity to create a series of life-size pterosaur reconstructions to be displayed on London's Southbank alongside the River Thames during the summer of 2010. The proposed exhibition would take pride of place at the Royal Society's Summer Science Festival, an annual event celebrating the best of British Science. As 2010 was the Royal Society's 350^{th} anniversary, the Summer Science exhibition was set to be held in and around the Royal Festival Hall. The University of Portsmouth has an established record in the display of pterosaur research stretching back to the late 1980s and of pterosaur modelling dating back to 1997. However, the prestige of the proposed 2010 exhibition meant the pressure was on the team to deliver something grander and more spectacular than anything previously produced. With the majority of the display destined to be installed outside, and so at the mercy of the unpredictable British weather, the engineering of the exhibition had to be more robust that anything attempted by the team to date.

Figure 89. Finally, details are added.

The concept

Both the Royal Society and University of Portsmouth team appreciated that the proposed exhibition had to be large, spectacular and, ideally, a little quirky. Fortunately for them both, pterosaurs deliver all of these attributes through being the largest flying animals ever: they are impressive and certainly very unusual. Initially, the Royal Society were inspired by new artwork of standing giant pterosaurs set alongside modern giraffes and suggested that the team built a three-dimensional rendition of those images: quite literally a giant azhdarchid pterosaur, such as *Quetzalcoatlus,* standing alongside a giraffe. As the scale of the project grew, however, the giraffe was abandoned in favour of building a whole flock of giant azhdarchids, with two standing animals and three 'flying' animals suspended between Royal Festival Hall and the offices of the Southbank Centre next door. Potentially, one of these animals was destined to bridge the gap between the terrestrial and flying animals by appearing as if it were landing. Inspired by this idea the team was determined that at least one of the models should represent the largest pterosaur known, spanning up to 12 metres across the wings and standing over six metres tall.

In addition to demonstrating their size, the team also wanted to demonstrate modern knowledge of pterosaur diversity with additional life-size models. The number of pterosaur species known has increased markedly in the last few decades and the Royal Society exhibition provided a great opportunity to showcase many animals that would be new to virtually everyone who saw the exhibition. To demonstrate this diversity, an additional space inside Royal Festival Hall was allotted for a smaller exhibition that would accompany the outdoor display. There was clearly no shortage of work for the team as they began work on the project towards the end of winter in 2009.

Figure 90. The initial idea of the exhibition in London was to put Quetzalcoatlus *next to a giraffe.*

Realising the concept

Design work for the project began in February 2009 and designs for the giant models were prioritised over all else. It may be imagined that designing the pterosaur models would be a relatively straightforward exercise: all the team had to do was pick an appropriate species of giant pterosaur, use its fossilised skeleton to determine its proportions and size and make the models. But it is not that simple. Although the team knew that they wanted to showcase giant azhdarchids, these pterosaurs are known only from extremely scrappy remains and have a very muddled taxonomy. Hence, before their manufacture could start, the team had to work out exactly what their giant pterosaurs should look like and which azhdarchid species they would be making.

When starting in the winter of 2009, the largest azhdarchids – and indeed the largest pterosaurs known – were *Quetzalcoatlus* (10 – 11 metre span), *Hatzegopteryx* (10 – 12 metre span) and *Arambourgiania* (11 – 13 metre span). With the goal of building the largest flying animal replica the team would have to work with one of the latter taxa. However, when investigating the fossil material for these forms, problems with their size estimates became very apparent. While the claims for a 10 – 11 metre span *Quetzalcoatlus* are reasonably sound, the team found that the methods employed to estimate the size of *Hatzegopteryx* and *Arambourgiania* were less reliable. The fossils of *Hatzegopteryx* are somewhat distorted and look larger than they actually are, leading to over-inflated size estimates. Similarly, over-simplified scaling of *Arambourgiania* has led to overestimates of its size. As with modern animals, pterosaur bodies do not grow consistently; their necks and heads, for instance, become disproportionately longer as they become larger. As such, estimating the size of any pterosaur has to take such growth regimes into account or risk erroneously estimating the animal's size. The estimates for *Arambourgiania* did not do this and so probably overestimated the wingspan of the species. Reassessment

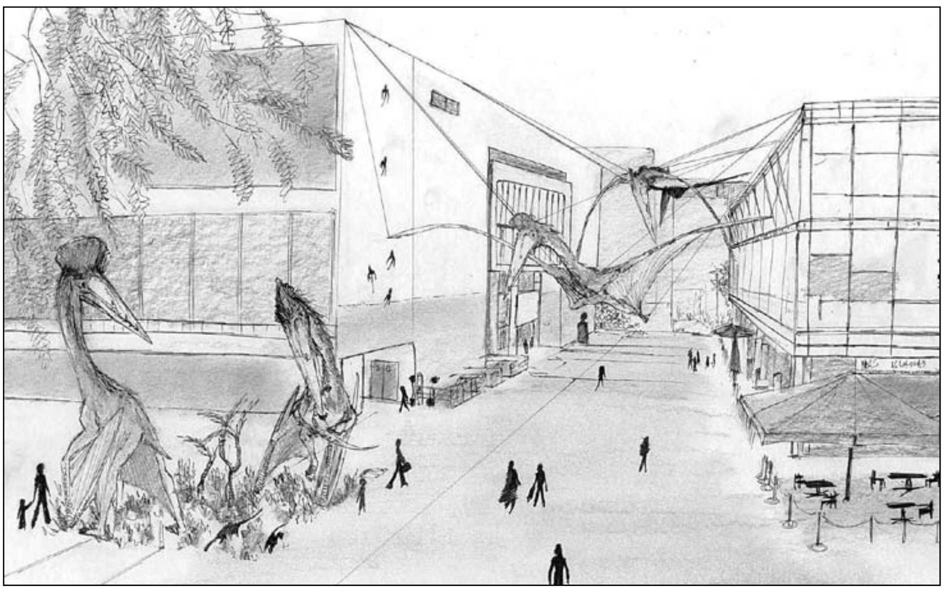


Figure 91. Design sketch of the exhibition in London, where it was part of the bigger Summer Science Exhibition, celebrating the 350th anniversary of the British Royal Society.

suggested to the team that both *Hatzegopteryx* and *Arambourgiania* were comparable in size to *Quetzalcoatlus*, still very big, but perhaps not as enormous as originally thought. As a result, the largest models would not span more than 10.5 metres. It was decided that both the grounded animals would be represented at this size, along with at least one of those in flight. To add some diversity to the ground pterosaur scene, an element of sexual dimorphism would be included in the design of both ground animals. The inclusion of this is well-founded: at least one pterosaur species has been convincingly demonstrated to show sexual dimorphism and, although not an azhdarchid, it is reasonable to assume that other pterosaurs were dimorphic too. Attributes such as head crest development and jaw robustness have been identified as pterosaurian sexual traits, and these would be used, along with other details such as colour, to distinguish the sexes.

Not all the models would be so large, however. The two other flying models would be scaled to eight and six metres across the wings, respectively, the plan being to create an illusion of perspective and variation amongst the flying group.

Wingspans are just one dimension of many, of course, and other data was needed to establish the proportions of different body elements. Since giant azhdarchid material is so poorly represented the lengths of individual body elements – skulls, necks, limb bones and the like – were mostly scaled from smaller, more complete azhdarchids, with the dimensions of the giant form used when available. Ideally, only one giant azhdarchid species would have been used in their reconstruction but, with so little material available (and virtually no overlapping material to demonstrate differences between different giant taxa), all the available data from *Quetzalcoatlus*, *Hatzegopteryx* and *Arambourgiania* was used. In this respect, the finished models represent 'generic' giant azhdarchids, rather than a specific species. While the team decided too that the models would represent the North American form *Quetzalcoatlus*, the decision to allocate the models to this genus was quite arbitrary: *Arambourgiania* or *Hatzegopteryx* would have been equally suitable.

With the scaling done, it became clear that the largest models would be absolutely huge, so large that when stood upright, a man could walk under them and, when in flight, would eclipse the sun as they passed overhead. One aspect of the models was deliberately left shorter than it probably was in life – the necks. Azhdarchids have unusually long necks even compared to other long-necked pterosaurs and, on azhdarchids spanning ten metres or so across the wings, neck lengths of over three metres are predicted. Although constructing the full neck lengths would have made the models more spectacular, the models had their neck lengths capped at 2.5 metres to facilitate ease of construction and transportation and to improve stability. As a result whilest the reconstructions of the azhdarchids are impressive they should actually be still taller.

Postures

With the basic proportions in place, the stature and postures of the models could be realised. Whereas the poses for the flying animals followed pretty typical conventions of previous pterosaur restorations, the grounded models provided scope

Mark explains

Tapejara

A small lizard attempts to save its skin from the jaws of the hungry *Tapejara wellnhoferi*. The snack's panic is clearly evident: just as modern lizards in great haste, the animal stands up and runs on its hind legs only.

You hadn't expected that, a pterosaur that could sprint… After all, pterosaurs are rather clumsy on land – or perhaps not? Traces of pterosaurs (see figure 3) indicate that they could walk easily with straight or almost straight limbs, without there being any hint of them waggling with legs splayed or crawling over the ground as was thought in the early days of pterosaurology. But some of the traces consist of footprints that are so far from one another that the only way they could have been made was by running – yes, even with the soft tissue between the front and hind limbs and all other specific pterosaur characteristics. In fact, the first descriptions of pterosaur traces actually refer to a running animal, but that was only realised later. Perhaps they could run fast, but they did so in an unusual way.

Generally, when animals run, they draw their gait inwards, so that the tracks tend to be in a single line. In the case of pterosaurs, the opposite is true: when the animals were walking, the feet tended to shift to the middle and, when they ran, the lines of the feet were more tangential. The idea behind this is that the body then leans forward. In that way you can take longer steps and advance faster. As a consequence, the relatively long front limbs are directed outward.

Oh, just one more fact. Believe it or not, there is an idea that pterosaurs were very active only in the early morning and late evening, when the sun's rays were at a certain angle to the earth. The theory behind this is that the animals flew laterally in relation to the sun and they used the crests on their heads as solar panels to absorb heat. This early solar energy theory has never been very popular because it is full of holes through which a whole flock of *Quetzalcoatlus* could fly.

A glimpse at the variation in crests shows us that there were pterosaurs with very small crests and that a reasonably large group had no crest at all. Some have crests that are large but have little surface area (see 'Mark explains: *Nyctosaurus*', pp. 72-73) whereas others, including those with the largest crests, have crests made of tissue that had no heat-conducting properties at all. Yes, you might say, but hasn't *Thalassodromeus* clearly proven this to be the case? Didn't this pterosaur have an enormously rich blood flow to its crest, ensuring good heat conduction? Well, let me help you dismiss that illusion: I recently charted the structure of the blood vessels of *Tupandactylus*, *Thalassodromeus* and various skulls of birds. The result suggests that the flow of blood to the crest of *Thalassodromeus* was nothing special. In fact: the beaks of birds have a better blood flow than many pterosaur crests, and – as far as I know – there is no bird that uses its beak to regulate its body temperature.

With another rejected theory, you can rightly wonder if these animals were so special after all. I mean, they had their own individual flying mechanism and occasionally a very strange skull, but does this mean that they did everything differently from other animals? To adhere to the current example, if they wanted to warm themselves up why didn't they stand in the sunshine with outstretched wings, as many modern birds do, such as the cormorant? If they wished to cool down, isn't it far more plausible that they would retreat into the shade or perhaps allow the cool breeze to sweep over them, or simply stand gasping or panting like modern birds also do?

◀ *Figure 92. The male and female* Quetzalcoatlus *as exhibited in London.*

▲ *Figure 93. The enormous animals make terrifying shadows.*

for the team to demonstrate new ideas on pterosaur terrestrial locomotion. Recent research indicates that rather than walking with the slightly sprawled gait of other pterosaurs, azhdarchids walked with their limbs held straight beneath the body in a mammalian or avian-like fashion. The ground models were designed to reflect this. As a result the bodies of the grounded pterosaurs stand 2.5 metres off the ground and, depending on the posture of the neck, up to five metres tall. One model – the 'male' – was designed to achieve the maximum height possible, demonstrating just how big azhdarchids were. His head is raised to near its maximum extension, allowing him to cast his gaze toward the flying animals. His accomplice, the 'female', was designed to appear as if in motion, apparently moving swiftly whilst grabbing a small animal in her jaws. This reflected recent research on azhdarchid lifestyles that indicates they foraged on the ground in a stork- or ground hornbill-like manner.

Turning engineers into palaeo-artists

Such enormous models would obviously require some rigorous engineering at their cores not only to carry their own weight, but to withstand the unpredictable British weather. Welded metal frames were designed to run throughout the bulkier parts of the models, producing metal skeletons that approximated the appearance of giant pterosaur skeletons. Professional engineers and welders were approached to help design and produce sound, robust frames for all the models, with in-house University of Portsmouth engineers asked to provide the frames for the two grounded sculptures. The frames for these models were comprised of steel that was coated in red oxide paint to resist rusting. The large size of the models and their relatively narrow gaits proved problematic, however, when attempting to make the frames stable. Since the body and neck were held so far off the ground on relatively spindly limbs, these ground models proved rather top heavy. The risks that twisting and bending forces posed to these frames were nullified with metal straps that were welded across the limbs and later hidden within the wing membranes. The frames of the

*Figure 94. A wood stork (*Mycteria americana*).*

grounded models, as with all the fully reconstructed animals, were made to have detachable head and neck components to ease their transportation and installation. The heads and necks were anchored into the main frames with extensions of their frames that were continuous for the entire body lengths of each model. Hence, although the necks of each model had been deliberately stunted, the steel neck frames of the largest models still attained lengths exceeding three metres.

The flying models presented very different challenges to the ground models. Whereas the weight of the grounded sculptures was of secondary consideration, the aerial animals needed to be relatively light so as to put as little strain on their supporting cables as possible. In addition, their frames had to be strong enough to support the entire model from a few cable attachment points and be entirely resistant to the high winds to which they would be exposed when suspended between two buildings. The team asked *Griffon Hoverworks*, a company that specialises in manufacturing hovercraft for commercial and military contracts, to design, test and assemble the frames. Digital frames were constructed and their strain performance tested in virtual wind tunnels before the actual assembly from light weight aluminium. Each was armed with numerous cable attachment points across the bodies and distal limb- and neck regions that would be used to suspend the models. Though it later proved unnecessary, each was also provided with the facility to also attach it to a ground anchor that would prevent the models lifting off if the weather proved too windy.

Flesh on bone

If the frames of the models mimicked the skeletons of the animals, styrofoam, represented the muscle, viscera and other tissues that would give the models their general shape. In contrast to the majority of other pterosaur reconstructions, the team were keen to demonstrate that pterosaurs were not delicately-built animals with stick-thin limbs and neck that looked like atrophied, anorexic living skeletons. Using muscle scars from the complex, sculpted surfaces that adorn many pterosaur bones, the pterosaurs were designed to have relatively muscular proximal limb segments, thereby making them comparable with the powerfully muscled bodies we see in modern flying vertebrates. What little is known of giant azhdarchid heads, too, indicate that their neck soft-tissues were thicker than has often been reconstructed, prompting the team to generate much thicker, jowlier necks for their reconstructions.

To create these shapes, blocks of styrofoam were carved into appropriate shapes using scrapers, saws and files and attached to the frames with expanding foam. The latter not only filled any gaps between carved body segments and acted as a fantastic, fully water-resistant adhesive to attach the foam to the frames. Indeed, the bonding agents in the expanding foam are so strong that the rigidity of the frames was noticeably improved once the frames had been clad (unfortunately, the expanding foam was equally good at sticking to skin or hair and could, even with adequate precautions, prove a nightmarish material to work with). After attachment to the frames, the foam sculptures were coated in several layers of epoxy resin embedded with powdered glass to give each model a rigid, damage resistant skin. Unfortunately, the dried resin often had an irregular pitted texture that then had to be sanded smooth – with a minimum of 20 m^2 of resin on the largest models, this was a huge task that took dozens of man hours for each model.

Wings

The wings of the pterosaur models represented one of the greatest challenges to the modelling team. This was particularly true for the flying animals whose wings had to be fully extended. Birds and bats support their flight surfaces through the feathers or bones of their fingers, but pterosaur wings lack obvious structural supports to hold their wings rigid. Instead, their wings were embedded with a series of seemingly rigid fibres that were probably individually weak but, when acting in an entire sheet, held the wing strong and taut. This arrangement worked well for

◄ *Figure 95. The body of a standing* Quetzalcoatlus *at its full size: the neck with the head can easily be inserted in the body.*

▼ *Figure 96. The pur-phase of one of the flying animals (compare with figure 88).*

real pterosaurs, but meant that the pterosaur model membranes could not bear any obvious supporting members. In the grounded models, this problem was overcome by attaching heavy steel mesh in areas where membranes were needed, which then acted as a base for adhering fibreglass sheets. Weight was of little concern for these models and heavy materials such as steel and fibreglass could be used in their construction. The postures of the grounded models were also more compliant with anchoring heavy metal meshes where membranes were required.

Quite the opposite was true for the flying models. Weight was of prime concern and their limbs were positioned far apart, meaning heavy wings would add too much mass, and were likely to sag or droop with so little anchorage to the model frames. Hence, aluminium mesh and epoxy resin-embedded canvas sheeting were used to construct the wings of the aerial models, making the wings of the aerial models a lightweight version of those on the ground. While their construction makes their wings somewhat more delicate than those of the ground models, they still remain more than capable of withstanding heavy weather conditions and, in being so light, have minimal effects on the stability and security of the models when suspended.

Detailing

While the metal frames, styrofoam bulk and resin wings comprised the majority of the models, the details that would bring them to life – eyes, scars, pycnofibres, scales and colour – needed to be added before the models could really look vital. The portrayal of the integument was of particular importance as this provided an excellent opportunity to demonstrate that pterosaurs possessed a hair-like covering over much of their bodies. While this fact is well-known to pterosaurologists and supported by numerous fossil specimens, it was undoubtedly a surprising sight for members of the public used to thinking of reptiles as being exclusively scaly. Typically, sculptures of animals designed for external exhibitions use carved or stamped fur-like impressions across their bodies to give the impression of fuzzy integument, but the team decided that nothing looked quite so much like real fuzz

Figure 97. The light, but strong aluminium construction of the flying models.

as fuzz itself! Hence, a durable synthetic fur-fabric was sourced and glued to the faces, necks, bodies and upper limbs of each pterosaur model. Acknowledging that the fur or feathers of modern animals have distinctive directional tracts, the synthetic pterosaur fuzz was orientated along hypothesised fur tracts to make it look more convincing. Elsewhere, the skin was left 'naked' and merely painted but, on the hands and feet of the models, scales akin to those seen on some lizard, crocodile and bird feet were added to reaffirm the reptilian affinities of pterosaurs.

With no eye sockets known from any giant azhdarchid fossil, the team estimated the eyeball sizes of the giant pterosaurs using a dataset of eye socket sizes from a range of smaller pterosaurs. In the largest pterosaurs the predicted eyeball diameter measured about 70 millimetres, large compared to our own eyes (about 25 millimetres) but a tiny fraction of the 2.5 metres length of the skull. The eyes were mounted in the models with acrylic-embedded fabric 'skin' used to create eyelids and wrinkles around them. Sculpted acrylic was also used to add nostrils to each pterosaur model.

Colour

As explained previously, there are some constraints in colouring prehistoric animals. For the giant pterosaur models, the size of the animals suggested that drab colours would be more appropriate than bright ones. Because the team wanted to show both pterosaur sexes, the male was painted an imposing dark grey and black (complete with gorilla-like silver colouring across the back) and given more prominent blue flashes along his leading wing edges. His crest was also made a striking black, recognition of the fact that, despite it being very fashionable amongst

Figure 98. The models are equipped with synthetic fur.

palaeo-artists to paint *every* crest, spike or frill some luminous colour, some large display structures in modern animals are not especially strikingly coloured (see, for instance, the cassowaries and ground hornbills).

Additional details, such as scars, cuts and chipped bills were added to the models to give the illusion that they represented real animals that were interacting with their world and with other animals. Many pterosaur fossils show signs of *en vivo* damage and, far from being delicate, many individuals appear to have endured and survived quite nasty injuries. The male model was made to look particularly scarred in line with suggestions that some pterosaurs may have had mating strate-

FOCUS

Colour: the scientific evidence…at last

Probably one of the most frequently asked questions about prehistoric animals is their colour. Until recently, palaeontologists could not answer this question with any certainty. Some aspects of colour and patterns have been known for a long time for a very select group of fossils, but most details of the patterns and colours remained unknown. However, new techniques allow colour-producing cells in fossil feathers and hair to be detected and have been trialled on extremely well-preserved dinosaurs from China and with great success. It is hoped that in the near future these techniques can be used on a large scale to determine the colour of many extinct animals, including pterosaurs.

Currently, however, the techniques only work for extremely well-preserved fossils and it is therefore unlikely that we can determine colours more widely. As a result it seems that palaeontologists still have to make educated guesses based on evidence from living creatures and their habitats. The ecology of an extinct animal often determines its colour. For example, an ambush predator will not be brightly coloured. Palaeontologists examine the animals that inhabit our world and are related to extinct animals in order to predict which wave-lengths of light their ancestors could see since it is improbable that an extinct animal would put energy into producing a coloured fur or feathers, if these colours were not visible to them. Moreover, we learn from modern-day animals that some colours are much less common than others, but also that large animals tend to have rather dull colours when compared to small ones. The type of skin also influences colour: feathers and scales break light in a different way than does bare skin. Although these are general indications, they give a framework within which the palaeo-artist works to achieve the most scientifically accurate result.

gies in which single males hold and defend harems of females from other males. The male pterosaur is, therefore, depicted as having been in his share of skirmishes with rival suitors. Folds in the skin and jowly throat pouches were added in an additional effort to add vitality to the models.

'Dinner' and other embellishments

Along with showing the grounded giants in their new postures, the team wanted to show how ideas of pterosaur diets have changed in recent years. To do this, they needed to feed their pterosaur models with something and, in line with recent research into azhdarchid palaeoecology, a small dinosaur was chosen. The team could have selected almost any of the most famous dinosaur groups to be 'Dinner' (the pet name for the pterosaur prey model) as many major groups coexisted with giant azhdarchids. In the end, 'Dinner' became a baby *Alamosaurus*, a common type of sauropod dinosaur from the Late Cretaceous that is known to coexist alongside some species of giant pterosaurs. Dinner's identity factored two major considerations into account. Firstly, sauropods are iconic, easily recognised dinosaurs that would leave visitors in no doubt as to the dietary habits of the giant pterosaurs. Moreover, embryonic and adult sauropod skin impressions indicate that most forms had lightly scaled skin, meaning that the team would not have to worry about applying feathers or fuzz to the animal. 'Dinner' is meant to be a freshly hatched individual, perhaps no more than a few weeks old and measuring 1.3 metres in length. Dinner's colouring reflects early abandonment by its parents, being a stripy brown across his back and lighter on his underbelly.

Of course, 'Dinner' and the two ground models would look somewhat out of place acting out their parts on paving slabs, so the team designed an enclosure defined by educational display boards to home them and filled the inside with a more convincing Mesozoic setting. A plethora of representative Mesozoic plants – including ginkgos, Wollemi pines and cycads, were added along with bark to recreate a sparsely vegetated Mesozoic scene. A subtle feature, a pterosaur nest with a single, precocial baby azhdarchid hatchling, was also manufactured and added to the scene to reflect the recent discovery of pterosaur eggs.

The heads

Thirteen life-size busts of different pterosaur species were also produced along with the giant models. Most of these were made by University of Portsmouth students under direction from other members of the team. An attempt was made to reflect the vast majority of pterosaur phylogenetic and ecological diversity, though the tiny size of some pterosaurs (such as the insect-eating anurognathids) meant models of these forms were not suitable for the exhibition. Most major pterosaur groups were represented, though: the climbing-pitbull pterosaur, *Dimorphodon*; the gull-like *Rhamphorhynchus* and albatross-like *Coloborhynchus*, *Pteranodon* (male and female) and *Nyctosaurus* were all reconstructed. The filter feeding *Pterodaustro* made an appearance, as did the closely related spoonbill-like form *Gnathosaurus*. A robustly-skulled shellfish-crushing pterosaur, *Dsungaripterus,* along with a possible

FOCUS

Alamosaurus

A full-grown *Alamosaurus* dinosaur could reach 20 metres in length, perhaps even more, and was born from eggs not much bigger than a football. A hatchling, however, would have been only about a metre in length and could therefore have been a suitable prey for the large pterosaur *Quetzalcoatlus.* Fossils suggest that baby-sauropods, like present-day turtles, were left to hatch without any parental protection. They must have relied on protective coloration to avoid predation by other dinosaurs and pterosaurs.

pterosaurian vulture, *Istiodactylus* were also exhibited. Different types of the flamboyantly-crested tapejarids – nicknamed 'Hell's cassowaries' by the team thanks to their short faces and crests – were built, as were two types of equally extroverted thalassodromids. These heads were constructed using the same materials as the external models but without internal metal frames supporting them. As with the fully restored animals, details were added to the busts to give the impression of individual histories and conflicts. The *Thalassodromeus*, for instance, was given a prominent scar across its face and a cataract in its left eye, while the *Rhamphorhynchus* bears some partially emerged teeth. The fuzz of some forms was enhanced with longer quills and manes or cut to produce different effects. These heads were not as robust or weather-resistant as the fully-restored models, however, as they only needed to be sound enough for indoor display.

Moving it all about

Constructing so many models, many of them of huge size, dictated that several workshops and large rooms be used to build and house them before they were finally sent to London. Transporting the replicas took three separate vehicles: two cavernous covered trucks took the ground-based pterosaurs, smaller flying models and other exhibition components, while an articulated flatbed transported the largest, ten metres span flying model. Despite the size of this trailer, the model was still too large to fit within its boundaries and a timber frame was constructed to tilt the model up 60º from the trailer base, sending its feet skyward.

Because of the potential hazards involved with installing several large, heavy models on the Southbank (particularly for those models being suspended in midair), the exhibition had to be installed overnight, a marathon job that kept a combined University of Portsmouth, Royal Society and Southbank team up all night. The flying models were suspended from cables attached to numerous points on their frames and specially installed rigs on the surrounding buildings. These cables held the models taut in several directions and, in virtually all wind conditions, they remained eerily stable. Although the ground models had the capacity for similar stabilising cables, weighing their bases down with sandbags proved to be more than sufficient at keeping their top-heavy structures upright.

The finished product

The exhibition officially ran from the 25th of June to the 4th of July, 2010, and attracted thousands of visitors in this short time. The reaction was overwhelmingly positive with the public intrigued and amazed by the scale, bizarre nature and fuzziness of the pterosaur sculptures. The team, including the many students that had contributed to the building of the models, were on hand to answer the many questions the public had about the bizarre-looking animals suddenly thrown alongside their commuter path, school trips or drinking venues. Numerous journalists and film teams arrived to film and document the models, including one team that asked to feature the models in a forthcoming pterosaur documentary. The interior exhibition even had a quick visit from Royalty. The exhibition was considered a huge success by all involved and, happily, the short-lived career of the models in London was set to extend with the pterosaurs set to be on display in Europe in the Autumn of 2010 in the Natural History Museum in Rotterdam (The Netherlands).

Figure 99. The transport of the biggest of the three flying models was only possible on a trailer.

Figure 100. Overview of the exhibtion 'Ptero's boven Rotterdam' *in the Natural History Museum Rotterdam, The Netherlands (22 September 2010 - 6 March 2011).*

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Names of the animals

(in alphabetical order)

Alamosaurus (Lizard from the Alamo)
Anchiornis (Almost a bird)
Anhanguera (From the city of Anhangüera)
Anhangueridae (Old devils)
Anurognathus (Without tail or jaw)
Apatosaurus (Different lizard)
Arambourgiania (After the scholar Camille Arambourg)
Archaeopteryx (Ancient wing)
Austriadactylus (Southern finger)
Azhdarchidae (After the dragon Ashdaar from Persian mythology)
Brasileodactylus (Finger from Brasil)
Brontosaurus (Thunder lizard)
Camarosaurus (Lizard from Camara)
Coloborhynchus (Maimed beak)
Criorhynchus (Battering-ram snout)
Darwinopterus (Darwin's wing)
Dimorphodon (Two forms of teeth)
Diplodocus (Two beams)
Dsungaripterus (Wing from the Junggar Basin)
Eudimorphodon (Before the two forms of teeth - i.e., Dimorphodon)
Giganotosaurus (Large lizard from the south)
Gnathosaurus (Jaw lizard)
Hatzegopteryx (Hațeg basin wing)
Ichtyosaurus (Fish lizard)
Iguanodon (Iguana tooth)
Irritator (From the 'irritation' the authors felt when they realised they had been confronted with a doctored specimen)
Istiodactyloidae (Broad wing)
Lacusovagus (Lake wanderer)
Leedsichthys (Fish from Leeds)
Liopleurodon (Smooth-sided teeth)
Ludodactylus (Game finger)
Megalosaurus (Great lizard)
Nyctosaurus (Night lizard)
Ornithocheiridae (Bird hands)
Plesiosaurus (Almost a lizard)
Pteranodon (Wing without teeth)
Pterodactylus (Winged finger)
Pterodaustro (Wing from the south)
Pterosaur (Winged lizard)
Quetzalcoatlus ('Winged serpent', after the Aztec god Quetzalcoatl)

Rhamphorhynchus (Beaked snout)
Sinopterus (Chinese wing)
Sordes (Scum)
Spinosaurus (Spined lizard)
Stegosaurus (Roofed lizard)
Steneosaurus (Narrow lizard)
Tapejara ('The old being', from a Tupi word)
Thalassodromeus (Sea runner)
Tupandactylus (Tupan finger, in reference to the thunder god of the Tupi)
Tupuxuara (After the Tupi word for 'familiar ghost')
Tyrannosaurus (Tyrant lizard)

Note: the Greek word 'sauros' (σαυρος) is here translated as 'lizard'; in its original meaning it might just as well be interpreted as 'reptile' or even 'salamander'. We have here used 'lizard' for no other reason than that it is usually translated that way. However, it is important to realise that dinosaurs ('terrible lizards') are only distantly related to modern-day iguanas and monitors.

Further reading

There are not many books on pterosaurs for the general public, but nonetheless the few that are available are most certainly worthwhile.

Although 20 years old and so prepared before many significant recent developments is Peter Wellnhofer's *Illustrated Encyclopedia of Pterosaurs* (1991) which is one of the primary works on these extinct animals. The book, elaborately illustrated with photographs and beautiful palaeo-art by the legendary John Sibbick, is a very good introduction to the subject. Peter Wellnhofer, the 'father of pterosaurology', has published extensively on pterosaurs, among which are several scientific monographs.

A more recent, general book is Dave Unwin's *The Pterosaurs: From Deep Time* (2006). The content is very up-to-date.

Mark Witton is currently working on an overview that will present a fresh view in word and image of these flying pioneers.

Many scientific publications have appeared over the last 20 to 30 years. Eric Buffetaut and Jean-Michel Mazin edited the book *Evolution and Palaeobiology of Pterosaurs* (2003), which is the result of the first international congress on pterosaurs and deals with a large variety of topics. The Zitteliana volume *Flugsaurier: Pterosaur Papers in Honour of Peter Wellnhofer* was published in 2008 and is edited by Dave Hone and Eric Buffetaut and is the result of the second international congress on pterosaurs in Munich. The book by Sankar Chatterjee and R.J. Templin (*Posture, Locomotion, and Paleoecology of Pterosaurs,* 2004) focusses on morphology.

Much information can be found on the internet. First and foremost is http://www.pterosaur.net/, a website that focusses on these extinct animals and is managed by pterosaurologists and palaeo-artists.

Chris Bennet's website http://bigcat.fhsu.edu/biology/cbennett/research.html is important because it includes a fairly complete bibliography.

Much information can also be found on Dave Hone's blog http://archosaurmusings.wordpress.com/.

Finally, many pterosaur species are discussed at Wikipedia. Although much information, especially the basics, is reasonable well presented, this source should be viewed critically.