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Fossil Focus: Pterosaurs

by David W.E. Hone [*1]

Introduction:

Pterosaurs are often mistakenly called flying dinosaurs, but they are a distinct, although related, lineage. They are an extinct group of reptiles from the Mesozoic era (251 million to 66 million years ago) and were the first vertebrates to evolve powered flight (Figs 1 and 2). Pterosaurs were first described as early as 1783 and recognized as flying reptiles shortly afterwards, and more than 150 species are now known. Fossil pterosaurs have been found around the world, with every continent except Antarctica (so far) yielding specimens.

FIGURE 1 — THE HOLOTYPE SPECIMEN OF PTERODACTYLUS, THE FIRST PTEROSAUR KNOWN, DESCRIBED IN 1783. PERMISSION TO USE THIS PHOTO WAS KINDLY GRANTED BY THE BAVARIAN STATE COLLECTION OF MUNICH, GERMANY. PHOTOGRAPH TAKEN BY GEORG JANSSEN.

Adult pterosaurs ranged in size from around 1 metre in wingspan to more than 10 metres; the largest species were the biggest flying animals of all time. They occupied the skies for much of the Mesozoic era and had the air to themselves until the birds first appeared in the middle to late Jurassic period (176 million to 146 million years ago). Pterosaurs died out along with the non-avian dinosaurs and many other groups 65 million years ago, in the great extinction at the end of the Cretaceous period.

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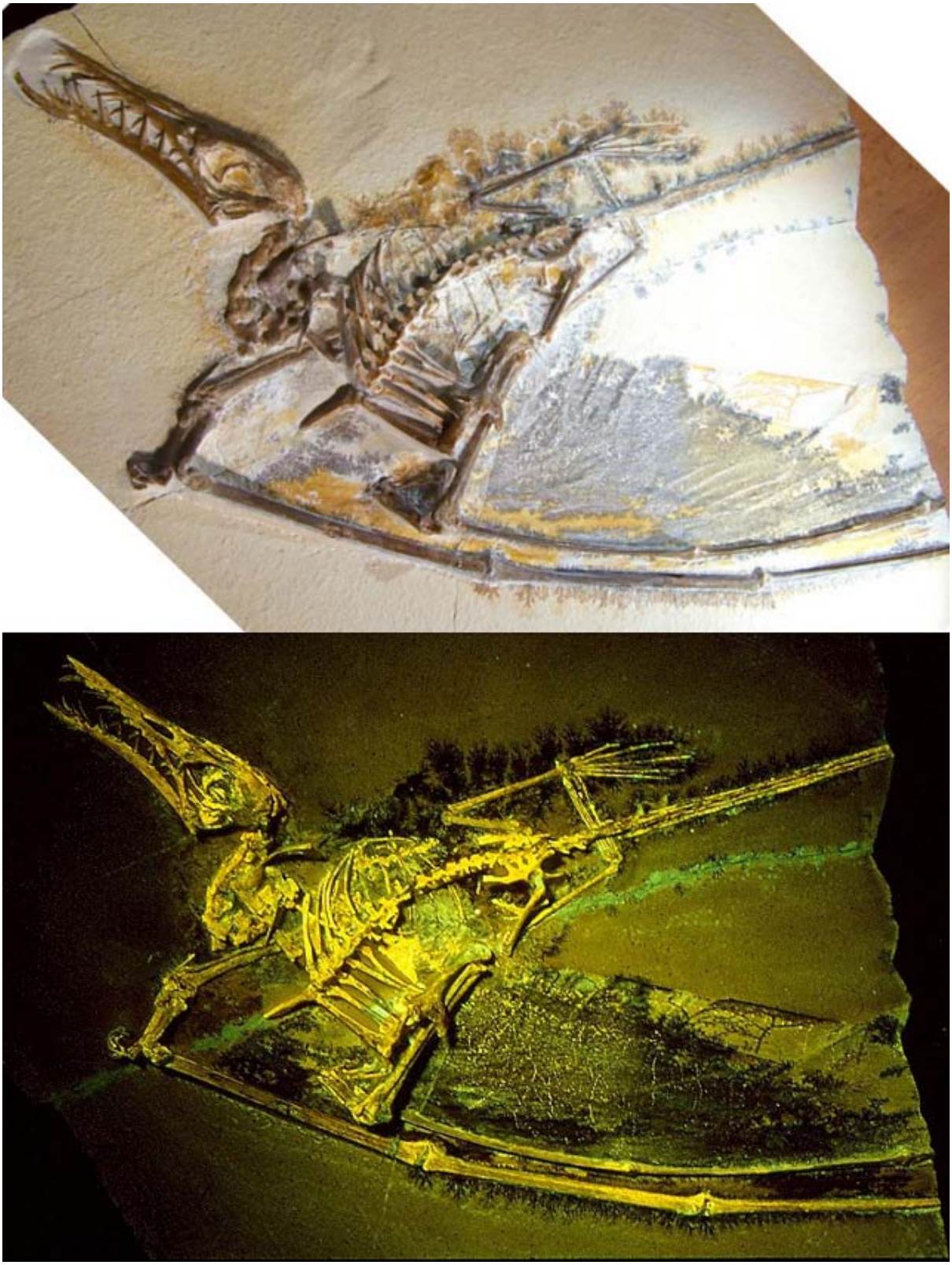

FIGURE 2 — THE 'DARK WING' SPECIMEN OF RHAMPHORHYNCHUS. THIS BEAUTIFUL SPECIMEN IS PARTIALLY PRESERVED IN THREE DIMENSIONS AND ALSO HAS SPECTACULARLY DETAILED WING MEMBRANES. TOP: THE SPECIMEN UNDER NATURAL LIGHT. BOTTOM: UNDER ULTRAVIOLET LIGHT, WHERE EXTRA DETAILS CAN BE SEEN. NATURAL-LIGHT IMAGE BY D. HONE, ULTRAVIOLET PHOTOGRAPH KINDLY SENT BY HELMUT TISCHLINGER.

The fossil record for pterosaurs is poor compared to that for many Mesozoic reptile groups, because their bones were fragile and so were not readily preserved. Until the past few years, there was little research dedicated to pterosaurs, and as a result many things relating to their biology are still either contentious or poorly understood. However, a recent resurgence in interest in this group and a raft of new finds are helping palaeontologists to get to grips with this important group, or clade.

Phylogeny:

The origins and the relationships of the pterosaurs have long been contentious, although a consensus is forming on both issues. Often confused with dinosaurs, pterosaurs are members of their own clade, but are close relatives of their more famous cousins.

Over the years, palaeontologists have hypothesized that pterosaurs originated from various parts of the reptile evolutionary tree. Very early researchers considered them to be the ancestors of birds or even bats, and for a long time it seemed that they were probably basal archosaurs (the clade that contains dinosaurs, birds, crocodilians and some other groups). More recently evidence has begun to stack up that they are a separate group to the dinosauromorphs (dinosaurs and their closest relatives) but that the two groups evolved from a common ancestor. Most researchers now support this position. This makes pterosaurs reasonably close relatives to birds, but they are not bird ancestors as is sometimes wrongly reported.

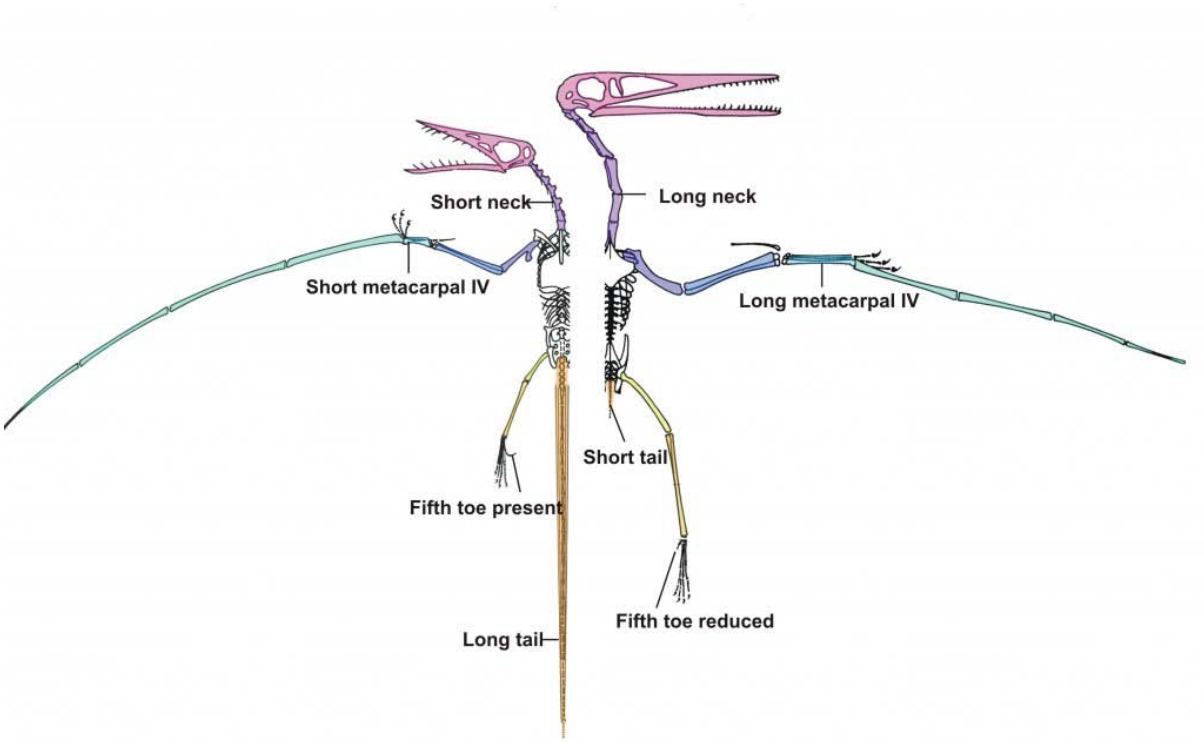

FIGURE 3 — SKELETAL OUTLINES OF RHAMPHORHYNCHUS (LEFT) AND PTERODACTYLUS (RIGHT) SHOWING OFF THE BASIC BODY PLANS OF THE RHAMPHORHYNCHOIDS AND PTERODACTYLOIDS RESPECTIVELY. NOTE THE DIFFERENT SIZES OF THE HEADS AND BODIES, AND THE DIFFERENT PROPORTIONS OF THE WINGS. IMAGE BY EDINA PRONDVAI, BASED ON AN ORIGINAL BY PETER WELLNHOFER.

Pterosaurs are divided into two broad groups. The basal pterosaurs are called the rhamphorhynchoids and are characterized by a number of features of the skeleton, including: relatively small heads with a separate nostril and antorbital fenestra (an opening in the front of the skull between the eye and the nostril, also present in dinosaurs); short necks and large bodies; a

short first bone in the fourth finger; a short pteroid bone (see below); a long fifth toe; and a long tail. The more derived pterosaurs have been grouped into the pterodactyloids and had the opposite set of characters: a long head with a combined (and often very large) nostril and antorbital fenestra forming one large opening in the skull; a long neck and short body; long fourth finger and pteroid bones; a short fifth toe; and a short tail (Fig. 3). (As an aside, the name pterodactyloid obviously derives from *Pterodactylus*, the genus of a type of pterosaur, although neither of these really means the same as the term pterodactyl, which is often misused in place of 'pterosaur').

The rhamphorhynchoids and pterodactyloids remained really rather separate with a large anatomical gap between them, until the discovery of *Darwinopterus* in 2010. This animal is from the Middle Jurassic of China and has a mixture of traits: the large head, combined nasoantorbital fenestra and long neck of the pterodactyloids, but the long tail, short fourth finger bone, long fifth toe and other features otherwise seen only in the basal forms (Fig. 4). *Darwinopterus* (and several close relatives that have since been discovered) is a wonderful example of a transitional fossil showing in part how one group of animals evolved into another.

FIGURE 4 — SKELETON OF DARWINOPTERUS. NOTE THE PTERODACTYLOID-LIKE HEAD AND LONG NECK, BUT THE RHAMPHORHYNCHOID BODY, WINGS AND TAIL (COMPARE WITH FIG. 3). IMAGE KINDLY PROVIDED BY LÜ JUNCHANG.

Anatomy:

Pterosaurs can be identified instantly by their highly modified arms. The first three fingers of the hand are small and would be used to move around when not in flight. The fifth finger of the hand is absent, but the fourth is both robust and massively elongated, and would have provided the main support for the wing membrane. Many of the bones of pterosaurs were thin-walled and hollow like those of birds and some dinosaurs, making the skeleton light overall.

Running from the tip of each wing finger to each ankle was the main wing membrane. This was not leathery, as is often stated, but in fact was a skin-like structure with layers of stiffening fibres, blood vessels and a sheet of muscle (Fig. 2). A smaller membrane sat in the crook of the elbow, supported by a modified wrist bone called the pteroid that was unique to pterosaurs. Finally, a membrane

spanned the space between the legs. In rhamphorhynchoids, this was a single broad sheet and was anchored to the long fifth toe on each foot. In pterodactyloids, it was split into two smaller parts, with each half running from the ankle to the base of the tail. This arrangement freed the legs and allowed the reptiles to walk more easily on the ground. In addition to all this flight apparatus, the rhamphorhynchoids also had a vane, on the end of their long tails.

Pterosaurs were also 'furry'. Their bodies were covered in thin, hair-like fibres termed pycnofibres. This was neither true fur as in mammals nor the simple feathers seen in early dinosaurs and baby birds, but probably evolved independently. It may have been linked to their ability to fly and there is a strong suggestion that pterosaurs were homeothermic ('warm blooded').

As might be expected of flying animals, in general the pterosaurs had rather conservative anatomy; that is to say that the restrictions on body shape imposed by flight meant that their overall shape was relatively similar between taxa. Over time there was a general trend for increasing size, with the earliest pterosaurs being rather small and the later ones being especially large. Early forms had lots of — often large — teeth, whereas the most derived forms from the late Cretaceous period were toothless. The most obvious deviation from conservatism was in the remarkable array of head crests that many members of the group sported. These had many different sizes and shapes and could be made of bone, soft tissues or a combination of both (Fig. 5).

Lifestyle:

Despite occasional reports, there is currently no evidence that any pterosaurs were flightless. Pterosaurs were not clumsy flappers or gliders as they have occasionally been portrayed, but were excellent fliers. It is likely that most pterosaurs hunted on the wing, and many lineages seem to have been well adapted to catching fish: some specimens have fish preserved in the stomach. However, other lineages were filter feeders, insect eaters, shellfish specialists or predators who hunted on land. Some species have been suggested to have fed mostly on fruits or seeds.

Pterosaurs laid thin-shelled eggs, which were probably buried in soil with vegetation to keep them moist. Several fossil eggs are known, including some preserved with intact embryos. Both the embryos and very young pterosaurs have remarkably well-formed bones, and it seems likely that even very young pterosaurs could fly.

Rhamphorhynchoids are generally thought to have had difficulty walking on the ground: no footprints have been found for them, and they would probably have stuck to the trees when not flying. The pterodactyloids were better adapted for life on the ground and numerous tracks are known for them (Fig. 6).

At least some species lived in large colonies, and many may have been social animals. The head crests were probably some form of sexual adornment or signalling structure.

Fossil Record:

Pterosaur specimens are found spanning most of the Mesozoic era. Their fossil record is rather mixed — they are generally rare and often known only from fragments, but areas of exceptional preservation can produce superb specimens and some species are known from large numbers of fossils. The famous ***Pteranodon*** is known from more than 1,000 individuals, although most are fragmentary and in poor condition. ***Rhamphorhynchus*** is known from more than 100 specimens,

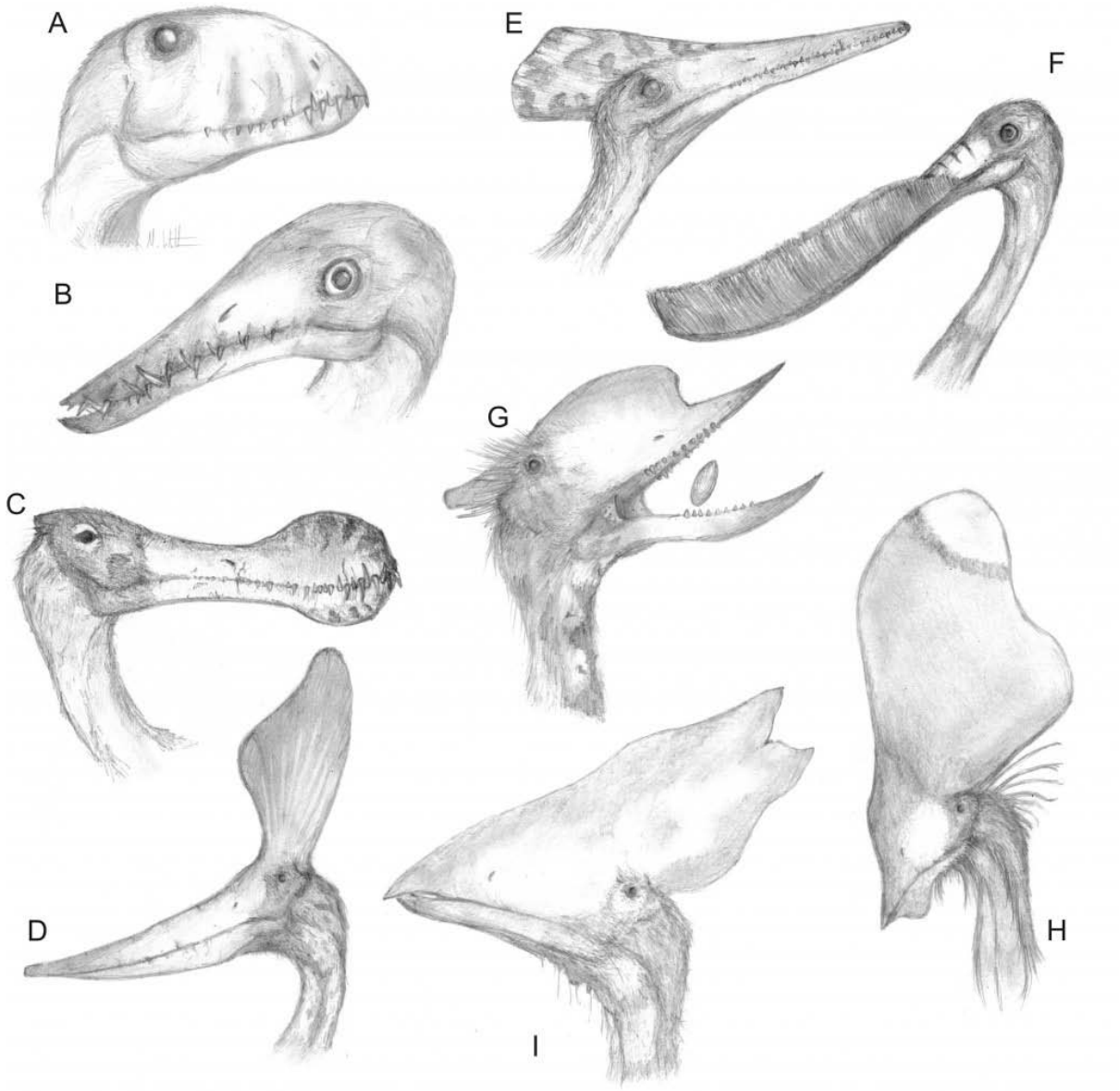

FIGURE 5 — A WIDE VARIETY OF PTEROSAUR HEADS SHOWING OFF THE DIFFERENT SHAPES AND TEETH, BUT ESPECIALLY THE RANGE OF UNUSUAL HEAD CRESTS. (A) DIMORPHODON, (B) RHAMPHORHYNCHUS, (C) ORNITHOCHEIRUS, (D) PTERANODON, (E) PTERODACTYLUS, (F) PTERODAUSTRO, (G) DSUNGARIPTERUS, (H) TUPANADACTYLUS, AND (G) THALASSODROMEUS. ARTWORK KINDLY PROVIDED BY MARK WITTON.

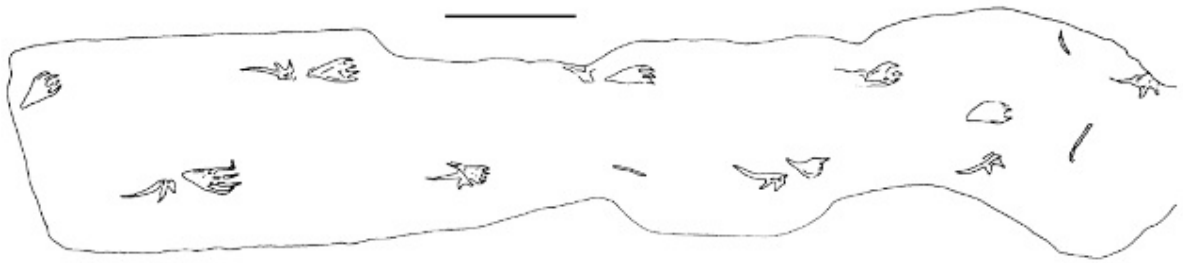

FIGURE 6 — DRAWING OF A PTERODACTYLOID FOSSIL TRACKWAY SHOWING THE LARGE FOUR-TOED FEET AND THE SPLAYED THREE-FINGERED HANDS (THE WING FINGER DOES NOT NORMALLY LEAVE A MARK; IT IS HELD UP OUT OF THE WAY, AS SEEN IN FIG. 7). DRAWING BY MARK WITTON.

most of which are more or less complete. Pterosaurs from areas of exceptional preservation are often preserved with soft tissues including wing membranes and head crests, but the bones are typically crushed flat.

The rhamphorhynchoids arose in the late Triassic period (around 200 million years ago) and go at end of Jurassic period. There are records of some in the early Cretaceous of China, but more recent studies suggest that these are the result of errors in fossil dating and the specimens are in fact older. Intermediate forms such as ***Darwinopterus*** date from the middle Jurassic; shortly afterwards, in the late Jurassic, the first pterodactyloids appear. Pterosaur footprints first appear in the late Jurassic alongside the origin of the pterodactyloids, and are found in many locations around the world.

Summary:

Pterosaurs were an important component of Mesozoic land and sea ecosystems. This group lived for more than 150 million years alongside the dinosaurs; they filled numerous ecological niches and included the largest flying animals of all time (Fig. 7). Well adapted for flight, these were not clumsy gliders as they are often unfairly portrayed, but were probably every bit as good as birds in the sky. In some ways they even may have been more agile. Pterosaur research and discoveries are currently booming, and palaeontologists are rapidly gaining a better understanding of the evolution and biology of these fascinating creatures.

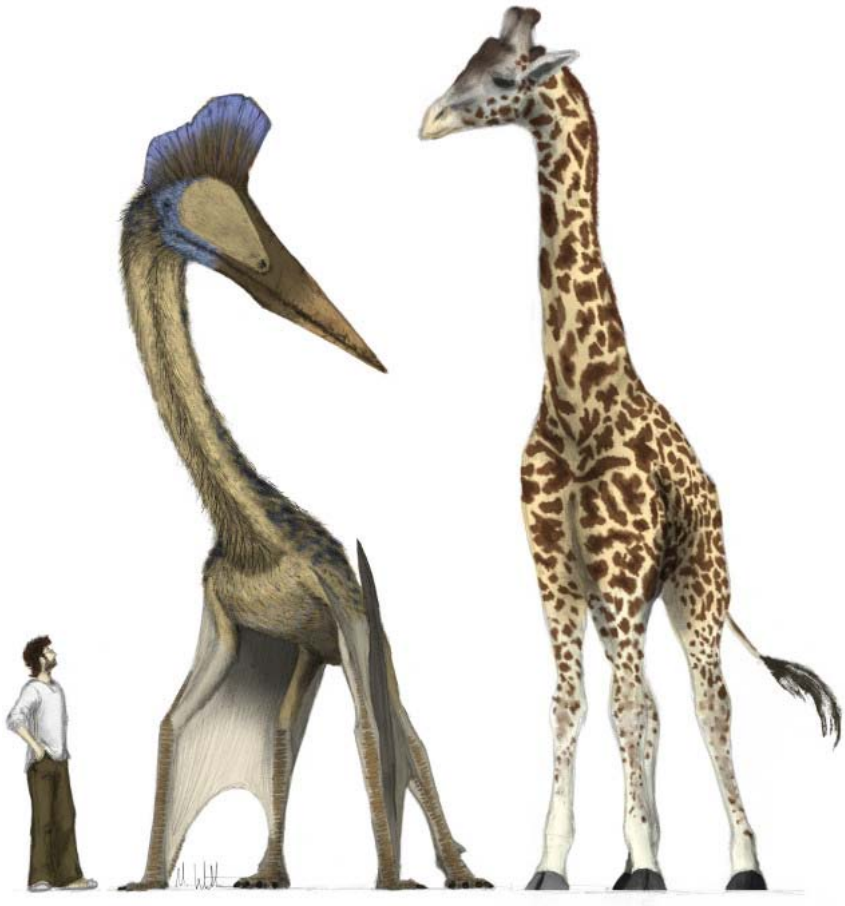

FIGURE 7 — A FULL-SIZED AZHDARCHID PTEROSAUR OF AROUND 10-METRE IN WINGSPAN, STANDING NEXT TO A MODERN GIRAFFE FOR SCALE. THE GIANT AZHDARCHOIDS WERE THE LARGEST FLYING ANIMALS OF ALL TIME. IMAGE KINDLY PROVIDED BY MARK WITTON.

Suggestions for further reading:

http://www.pterosaur.net

http://www.pterosaur-net.blogspot.com.

Unwin, D.M. 2005. ***The Pterosaurs: From Deep Time***. Pi Press. ISBN: 9780131463080.

Wellnhofer, P. 1991. ***The Illustrated Encyclopedia of Pterosaurs***. Salamander Books. ISBN: 9780517037010. ***— Now out of print and a little dated, but still available***.

Witton, M.P. 2012. ***Pterosaurs***. Princeton University Press. ***— Not yet published***.

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