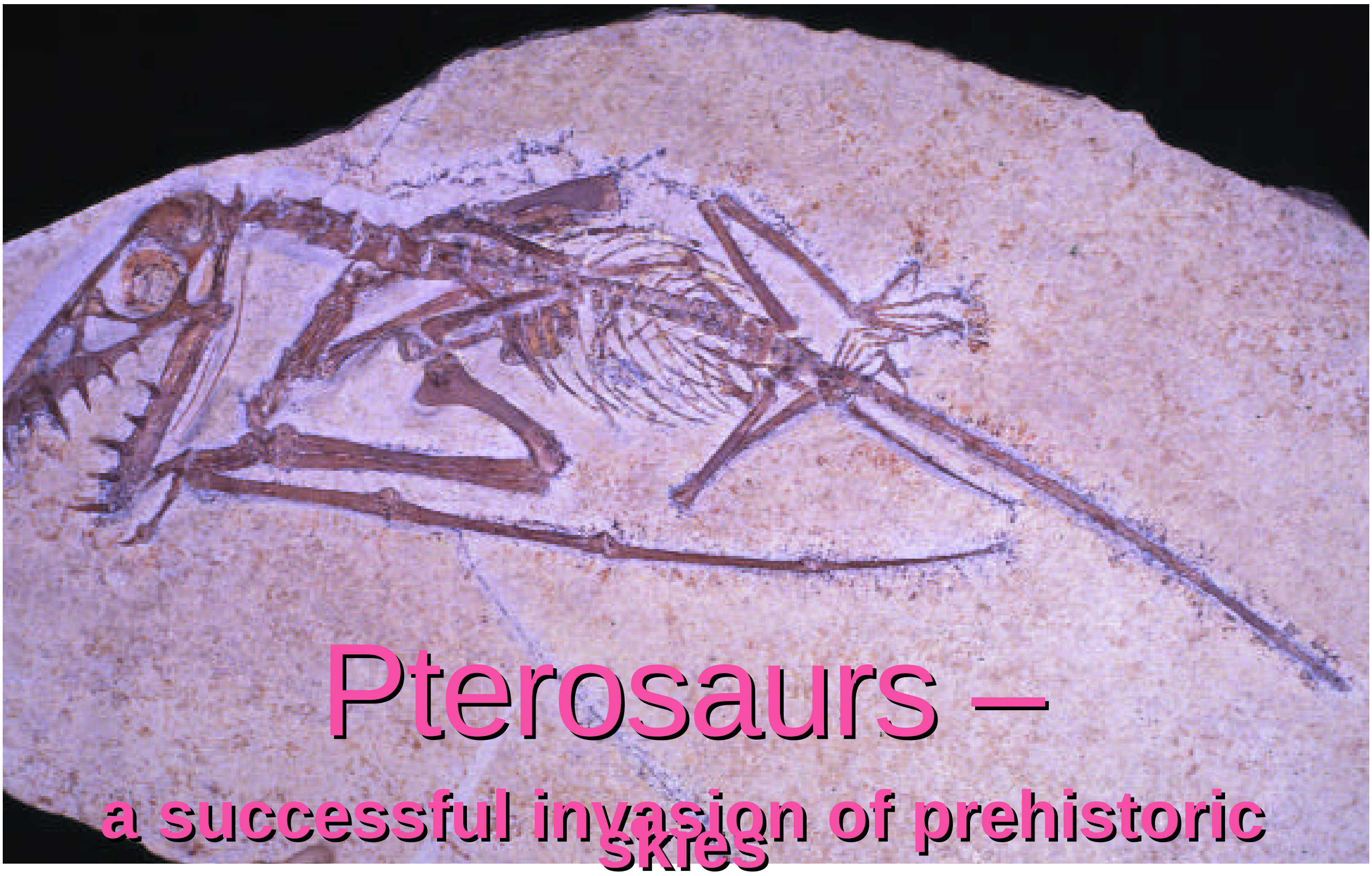

Title image. Skeleton of Scaphognathus*, a basal long-tailed pterosaur from the Upper Jurassic Solnhofen Limestone of Germany. It shows the characteristic pterosaurian hallmarks of hyper-elongate digits to which were attached the flight membranes. Photo courtesy of Dr Dino Frey.*

Pterosaurs – a successful invasion of prehistoric skies

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Inhabiting the skies from the Triassic to the end of the Cretaceous, pterosaurs were actively flying reptiles with a unique wing configuration. Recent discoveries have revealed hitherto unsuspected diversity in pterosaur skeletal and soft-tissue morphology, and shed light on their origins, evolution and palaeobiology.

While the 'dinosaur renaissance' of the late 1960s is relatively well known, less appreciated is that a similar surge of interest has occurred in the study of pterosaurs, the flying reptiles of the Mesozoic Era. Spectacular new discoveries, combined with the application of computer modelling, aerodynamic studies and ultra-violet and x-ray investigation, have shed new light on pterosaur palaeobiology. While little agreement had been achieved previously, the main outcome of the 2001 meeting, 'Two Hundred Years of Pterosaurs' (held in Toulouse, France), was a general consensus on their palaeobiology (Unwin and Henderson, 2002; Buffetaut and Mazin, 2003).

Stereotyped for most of the 20th century as weak fliers, unable to flap and with wings inferior to those of birds and bats, pterosaurs are today recognised as a group whose evolutionary success was at least equal to that of other power-flying vertebrates. Uniquely, the main wing spar in pterosaurs was formed by a hypertrophied digit. Attached to this were both the main flight membrane (the brachiopatagium) and the accessory, leading-edge propatagium (Figure 1). Prominent muscle attachment sites on the arm, shoulder and chest bones show that pterosaurs were active 'flappers'. Foramina on their bones show that most pterosaurs had pneumatic skeletons, and thus they probably possessed an air sac system like that of birds. Notably, there is little indication that pterosaurs radiated as small forms of terrestrial environments, as both birds and bats did. In fact, pterosaurs seem to have been analogues of seabirds.

Paradigm shifts

Pterosaurs were first recognised as a group of flying reptiles in 1801. By 1901, when Harry Seeley wrote *Dragons of the air*, the first book devoted to pterosaurs, a diverse assortment of types were known. During the 1970s, great strides were made in anatomical studies by Peter Wellnhofer of the State Museum for Natural History, Munich, but he emphasised that there was still much to be learnt about pterosaur morphology, diversity and palaeobiology. Describing Jurassic pterosaurs with preserved evidence of body hair and wing membranes, Wellnhofer regarded pterosaurs as being neither like bats nor birds, but as combining features of both, with unique attributes. Wellnhofer is almost single-handedly responsible for the present surge in interest in pterosaurs (see Wellnhofer, 1991; Buffetaut and Mazin, 2003). Significantly, Wellnhofer's impetus coincided with new discoveries made in China, Kazakhstan, South America and elsewhere, many of which provided the data needed to fill some of the gaps in our knowl-

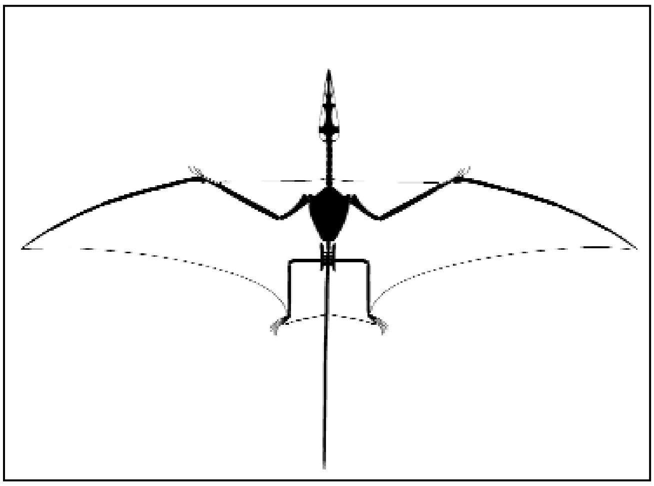

Figure 1. Schematic skeletal reconstruction of the small Jurassic pterosaur Sordes pilosus *showing the distribution of the wing membranes. After Unwin and Bakhurina.*

edge of pterosaur diversity.

A paradigm shift in pterosaur palaeobiology, instigated during the 1980s by Kevin Padian of the University of California, also played a major part in renewing interest in pterosaurs. Based on perceived similarities of the pterosaur hindlimb and pelvis with that of cursorial (ground-running) dinosaurs and birds, Padian proposed that pterosaurs were capable bipeds; that they were close kin of dinosaurs; and that pterosaur wing membranes were narrow and did not incorporate the hindlimb (Padian, 1983).

The return of 'the traditional model'

Recent analyses of evidence for these claims, combined with new data, better support claims for quadrupedality and extensive wing membranes. Pterosaur hindlimbs are not suited for bipedality or cursoriality; new, articulated specimens and abundant trackways reveal that pterosaurs were plantigrade quadrupeds, ill suited for fast running; and wing membranes, preserved under exceptional conditions, reveal attachment of the brachiopatagia to the shin or ankle. Plots of pterosaur hindlimb dimensions onto ternary diagrams reveal that pterosaurs were comparatively conservative in terms of hindlimb diversity. Pterosaur hindlimb lengths also correlate with forelimb lengths and, so far as we know, pterosaurs never lost the ability to fly. These observations are in agreement with evidence for quadrupedality and broad wing membranes. They all indicate a forelimb-hindlimb linkage that constrained pterosaur evolution.

New phylogenetic studies indicate that pterosaurs did not descend from dinosaur-like cursorial bipeds, but from more basal quadrupedal, climbing reptiles, though the exact ancestry of pterosaurs still remains controversial. Basal pterosaurs exhibit: a dorsoventrally shallow body; sharply curved hand and foot claws; feet in which the penultimate phalanges are longest; and sesamoids on the extensor surfaces of either the hand or foot. These features, all indicative of tree climbing, mimic those seen in climbing primates and other living climbers, and strongly indicate that pterosaurs had arboreal origins. Consequently, a recent review of the evidence for pterosaur life appearance implied that the current view might be regarded as an updated, fine-tuned version of 'the traditional model' envisioned by Wellnhofer (Unwin, 1999).

Astounding dimensions, surprising diversity

Recent pterosaur discoveries have revealed some surprises in diversity and dimensions. The 1971 discovery of *Quetzalcoatlus northropi,* a Late Cretaceous azhdarchid from Texas, showed that there were pterosaurs with 10–11 m wingspans. A new genus from Spain was perhaps bigger; and *Hatzegopteryx* from Romania was bigger still, having an estimated wingspan in excess of 12 m and a skull at least 2.5 m long. *Hatzegopteryx* is particularly noteworthy in that its skull bones have an internal architecture resembling that of expanded polystyrene, unlike those of most other pterosaurs. Indeed, its skull was misidentified as that of a predatory dinosaur, prior to 2002.

Among the most bizarre of pterosaurs were the tapejarids, a group unknown until 1988. While tapejarid postcranial skeletons were not substantially different from those of other Cretaceous short-tailed pterosaurs, the toothless skull of one of the best known genera, *Tapejara*, was unusually short and deep with pointed, tweezer-like jaw tips. An intriguing, but highly speculative, interpretation of *Tapejara* is that it was a frugivore (fruit eater), a notion that has appealed to workers searching for Mesozoic taxa that were able to disperse Cretaceous diaspores (Fleming and Lipps, 1991). Unfortunately, corroboration for this idea is lacking.

Ctenochasmatoids include *Pterodactylus* and an array of Late Jurassic and Cretaceous forms with needle-like meshes of teeth, presumably employed in filter-feeding. Surprisingly, recent studies indicate that *Cearadactylus*, a large predatory ctenochasmatoid, named in 1985, is nested within this clade of filter-feeders (Unwin, 2002). This implies both the evolution of giant size within the clade and of a cranial morphology and dentition equipped to deal with bigger prey than those favoured by other ctenochasmatoids: something akin to a sea eagle evolving from a spoonbill (Figure 2).

A new way to fly

Several recent discoveries hint at previously unsuspected aspects of pterosaur flight mechanics. Azhdarchids have long been known to differ from most other advanced pterosaurs in the cross-sectional shape of their wing bones and in possessing an abbreviated, distal-most wing phalanx. The implication that these features are correlated with a distinctive flight style has recently been confirmed by new work on the pterosaur shoulder girdle. Unlike ornithocheiroids, another group of large

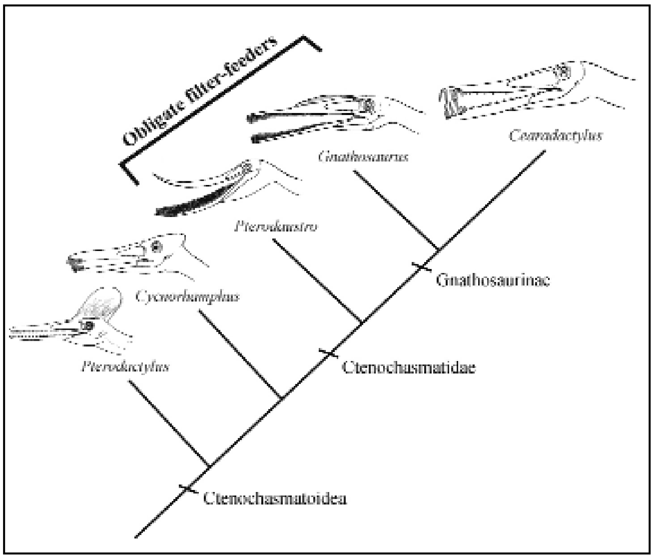

Figure 2. Simplified cladogram (only select taxa depicted) showing the proposed phylogeny of the Ctenochasmatoidea (based on Unwin, 2002). Surprisingly, the large predatory Cearadactylus *(wingspan 5.5 m) is nested within a clade of small obligate filter-feeders (the biggest of which had a maximum wingspan of 1.7 m).*

pterosaurs (in which the glenoid fossa for the head of the humerus is located high up on the shoulder girdle), in azhdarchids the fossa is located low down, level with the sternum. By comparing the resulting wing attitudes of these pterosaurs with those of aircraft, Frey *et al.* (2001) found that the ornithocheiroid condition is a 'stable' wing configuration, well suited for soaring, while the azhdarchid condition is 'unstable', permitting more manoeuvrability. Cretaceous pterosaurs are otherwise conservative in postcranial morphology, so the discovery of these different flight styles was unexpected.

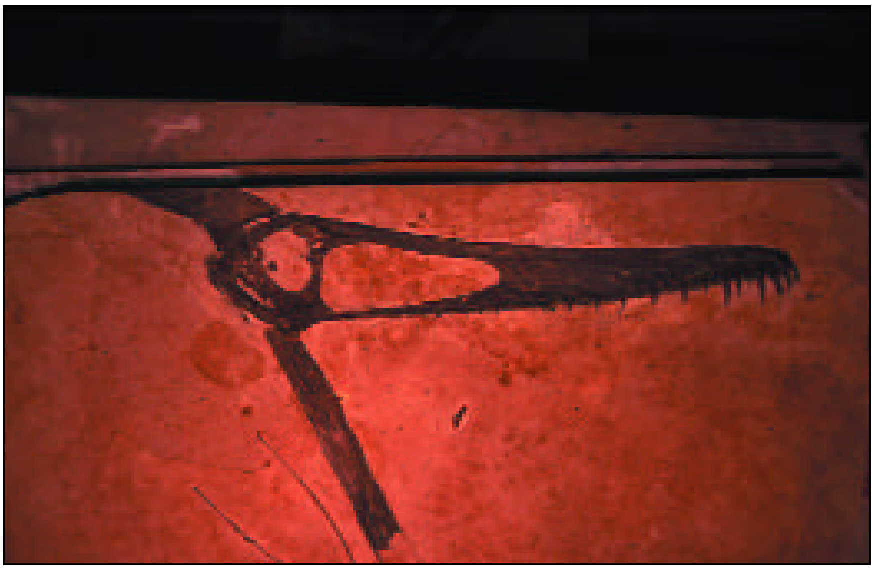

Figure 3. Skull of newly discovered pterosaur from the Early Cretaceous Crato Formation of north east Brazil. This specimen has a Pteranodon-like crest and fang-like teeth, thus confirming the observations of Messrs Fred Flintstone and Barney Rubble.

Head crests aplenty

Even since *Pteranodon* was described in 1876, pterosaurs have been famous for sporting head crests. Amusingly, two recently discovered pterosaurs, one from Brazil and one from the Isle of Wight, match the imaginary pterosaurs that cartoonists and toy manufacturers have been depicting for years: both combine *Pteranodon*-like crests with fang-like teeth (Figure 3).

Three recent discoveries have revolutionised our perception of pterosaur crest diversity. The first is that a primitive pterosaur from the Triassic of Austria, *Austriadactylus cristatus,* was crested (Dalla Vecchia *et al.,* 2002). This shows that even basal groups included crested species. The occurrence of a crest so near the base of the pterosaur family tree implies a strong genetic tendency for evolution of these 'luxury' organs.

The second discovery is that some pterosaur lineages evolved radically strange crests, far more striking than the familiar, posteriorly directed blade of *Pteranodon. Tapejara imperator,* described in 1997, exhibits a posteriorly-directed spike at the rear of the skull, and a long sub-vertical rod growing upwards from a crest at its beak tip. Soft tissue spanned the space between the two spikes, providing the creature with a surreal crest, shaped like a triangular sail, substantially larger than the rest of the skull. Even more surprising are specimens of *Nyctosaurus* with rod-like crests, easily longer than the combined length of the rest of the skull and entire body (Bennett, 2003). Near its base the rod bifurcates to give rise to a short, posteriorly-directed branch: the result is an absurd pseudo-antler. These must surely be among the most incredible of all recently discovered vertebrate fossils.

The third discovery is that soft tissue crests were widespread, and that the crests seen in fossils from several pterosaur groups only represent the bony cores of what were, in life, larger soft-tissue structures. The discovery of a soft-tissue crest in *Pterodactylus,* a genus that lacks a bony crest entirely, makes it possible that other pterosaurs lacking bony crests were more flamboyant than previously thought. The functions of pterosaur crests remain uncertain but it is probable that many played a role in sexual attraction and species recognition. At least some pterosaur crests presumably had an aerodynamic effect, but whether this was positive or negative remains untested.

Wing membranes and other soft tissues

Contrary to the old idea that pterosaur wing membranes were flimsy and ineffectual, recent discoveries show that they were surprisingly complex. Embedded within the membranes were a series of parallel stiffening fibres, termed actinofibrils, a thin layer of muscles, a meshwork of fibrous tissue and a complex, looping blood vessel system (Figures 4, 5). The latter, first discovered in 2001, hints at an important thermoregulatory role for the wing membranes.

In some recent reviews of fossil reptile physiology, some authors have argued that pterosaurs lacked body hair. However, such views are misinformed and pterosaur hair is

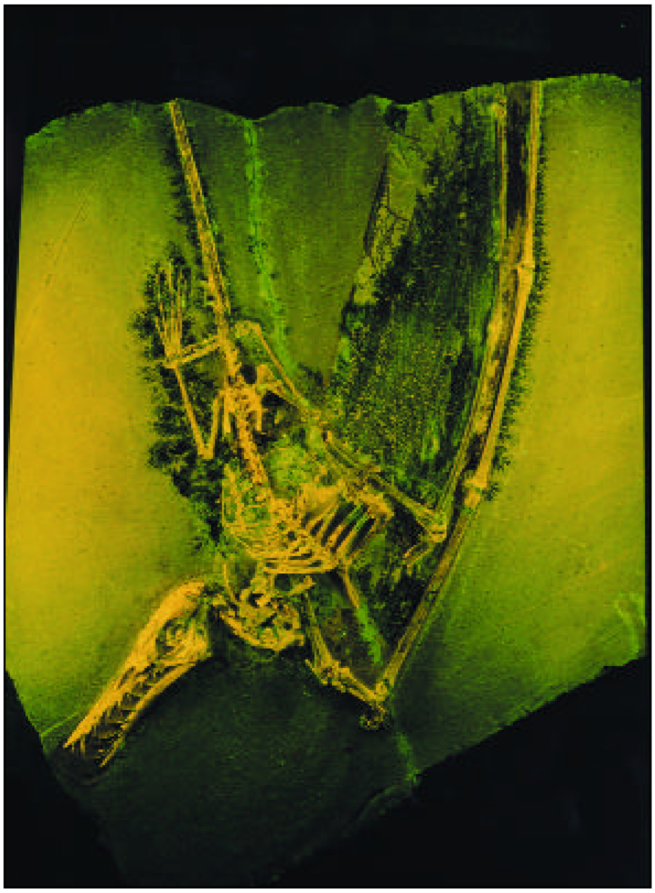

Figure 4. Spectacularly preserved skeleton of Rhamphorhynchus sp. *in which the wing membrane is preserved. This specimen is from the Upper Jurassic Solnhofen Limestone of Germany. Skull length 90 mm. Photo courtesy Helmut Tischlinger.*

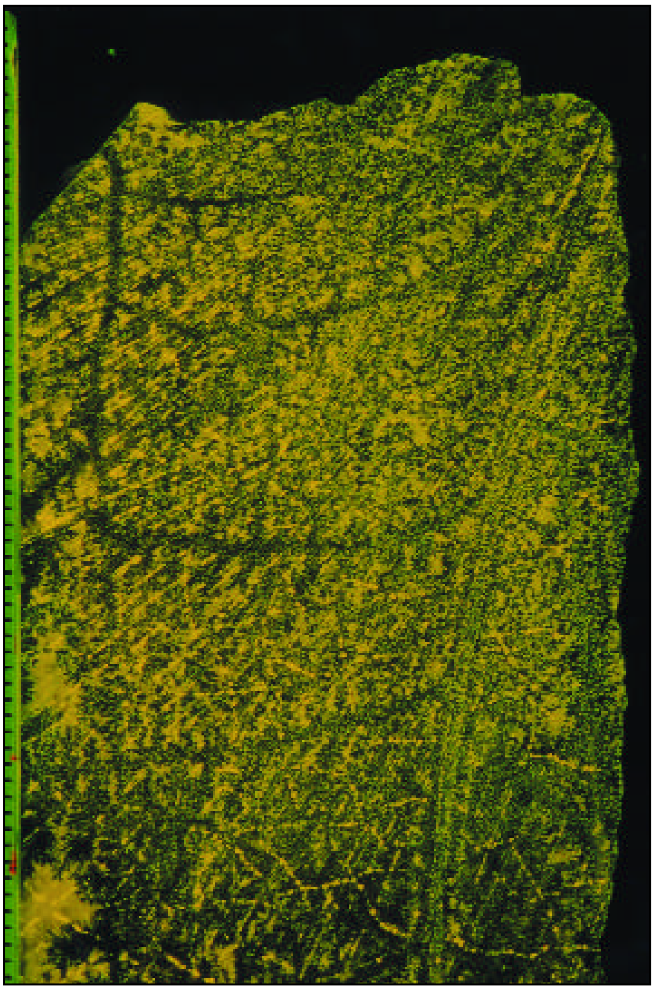

Figure 5. Detail of the wing membrane of specimen shown in figure 4, showing fan-like supports called actinofibrils, a meshwork of unknown function, and a looping blood vessel system. Such soft tissue specimens are incredibly rare, and are only preserved when fossilisation processes are sufficiently rapid to beat the decay processes. Photo courtesy Helmut Tischlinger.

certainly present in forms both large and small (Wellnhofer, 1991). While definitive evidence allowing determination of pterosaur physiology will probably never be found, this furry pelt at least implies an elevated metabolism, as does the presence in the group of skeletal pneumaticity and active flapping flight.

At least some pterosaur fossils reveal the presence of webbing between the three free fingers of the hand. This confirms a controversial reconstruction of the pterosaur wing, where the free fingers support a propatagium, more extensive than that depicted conventionally (Frey and Riess, 1981). Webbing between the toes (implying use of the feet as paddles or air-brakes), scales and pads on the soles of the feet, throat sacs, beaks and claw sheaths are also known for some genera. While virtually nothing is known about pterosaur reproduction and little direct data are available on their ecology, the wealth of new soft tissue information has allowed palaeontologists to reconstruct pterosaurs to a high degree of detail. Seeing as the last pterosaur died 65 million years ago, this really isn't bad going.

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Go here to see the fabulous new *Nyctosaurus* specimens described by Bennett (2003)

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