Palaeontology

Close kin of the first flying vertebrates identified

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Dinosaur relatives called pterosaurs are the earliest known flying vertebrates. The branch of the evolutionary tree from which pterosaurs evolved has been unclear, but new fossil discoveries offer a solution to the mystery. **See p.445**

In 1812, Georges Cuvier, the incomparable anatomist at the Museum of Natural History in Paris, produced the first comprehensive book to be published on the history of fossil tetrapods (animals with backbones, excluding fishes)[1]. Cuvier surveyed all that was known of the palaeontology of these animals, exploring the wonders of their great variation and strange fossil forms. Some were clear relatives of familiar living animals; others were strange and difficult to classify. But none was quite as odd as a small, long-beaked, long-limbed creature from the Jurassic period (around 150 million years ago) that was excavated in Bavaria, Germany. On page 445, Ezcurra *et al.*[2] shed first light on the origin of this striking group.

In 1800, Cuvier had received a letter from his friend Jean Hermann, professor and curator of natural history at Strasbourg in France[3]. Hermann told Cuvier of a fossil he had read about, in the collections in Mannheim, Germany, that was unlike anything he had ever encountered. On the basis of the original[3] and classically philosophical description by Cosimo Collini in 1784, Hermann described some of its features and enclosed sketches he had made (Fig. 1a). He realized that the animal had a very long finger that he correctly thought would support a wing membrane. This could not be a bird, but bats have wings supported by finger bones, so maybe the animal was something like that. Hermann drew the creature as a kind of mammal, complete with soft ear pinnae, fur (also prescient) and genitalia.

Cuvier was fascinated and frustrated. He wanted a cast of the fossil, but Hermann died before he could help. In the following years, naturalists who saw the specimen sent drawings to Cuvier (Fig. 1b), but he could not get his hands on a fossil cast until 1818, after his book had been published. Worse still, all the drawings were notably different. Yet, thanks to his anatomical expertise, Cuvier could reconcile the discrepancies, and he realized that the animal's features made it a reptile, not a mammal.

But it was no ordinary reptile. Cuvier inferred that it flew, was warm-blooded, had a hairy covering, walked on its back legs and folded its wings. He wrote[4]: "of all the organisms whose ancient existence is revealed in this book, these are incontestably the most extraordinary, and if we saw them alive, would seem the strangest as compared to all living beings." And he concluded: "[it] would seem, to those who have not followed this entire discussion, the product of a sick imagination rather than the ordinary forces of nature."

Welcome to the world of pterosaurs, or, as Cuvier named the first ones, ptéro-dactyles, which means wing-fingers (a typo in his original title rendered them pétro-dactyles, or rock-fingers). More than two centuries later, pterosaurs remain among the most controversial animals in the fossil record. In the 1980s, it was established that pterosaurs actively flapped their wings (instead of merely gliding), and walked on hindlimbs organized like those of birds and other dinosaurs[5], and that they were much more bird-like than bat-like.

Well over 100 probably valid kinds of pterosaur are currently known from all over the world, from the Triassic through to the Cretaceous periods (approximately 235 million to 66 million years ago). Some (Fig. 2) are extremely bizarre[6]; but their origins and relationships to other archosaurs (crocodiles and birds, including dinosaurs) have not been well established.

In the 1980s, it was suggested that the closest relatives of pterosaurs were small bipedal reptiles closely aligned with dinosaurs[7], and this theory was supported by even the earliest phylogenetic analyses of how these groups fit on the evolutionary tree[8]. But the fossil evidence that was needed to confirm this was elusive: pterosaurs are so strangely

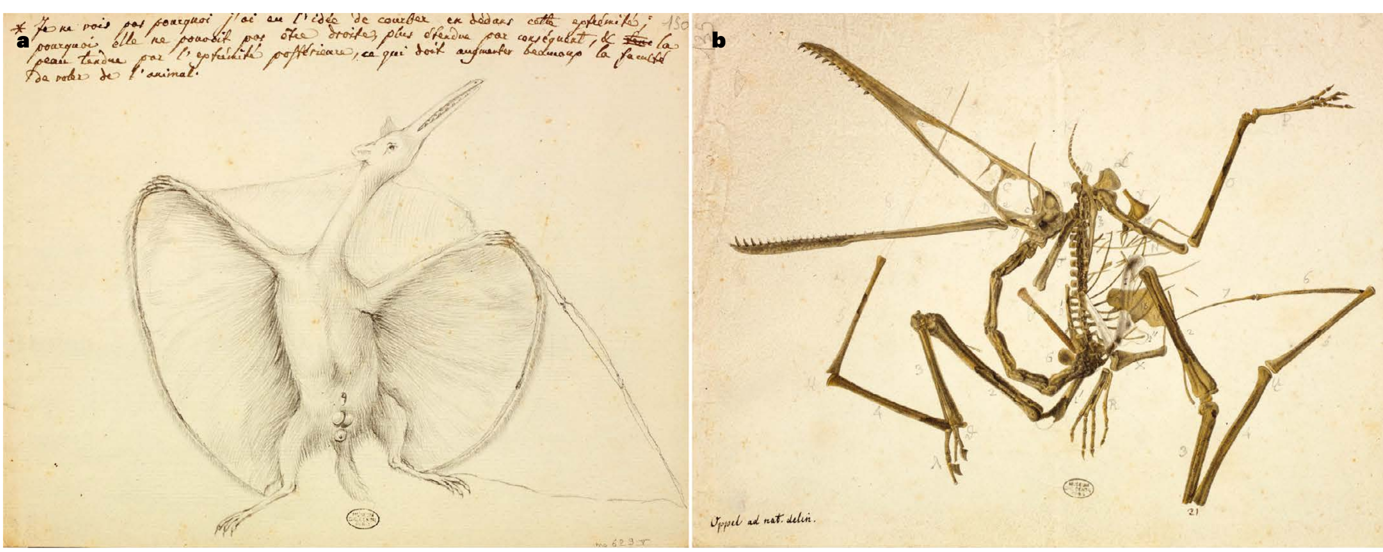

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Figure 1 | Ptéro-dactyle sketches. a, A sketch made by Jean Hermann based on a fossil description that he sent in a letter to Georges Cuvier at the Museum of Natural History in Paris, who was preparing a book about fossils of tetrapods (animals with backbones, not including fishes). **b**, A drawing by Michael Oppel of the original fossil specimen corresponding to the creature shown in **a**. Cuvier named the creature a ptéro-dactyle, and it was the earliest known member of the group called pterosaurs, the first vertebrates to evolve the ability to fly.

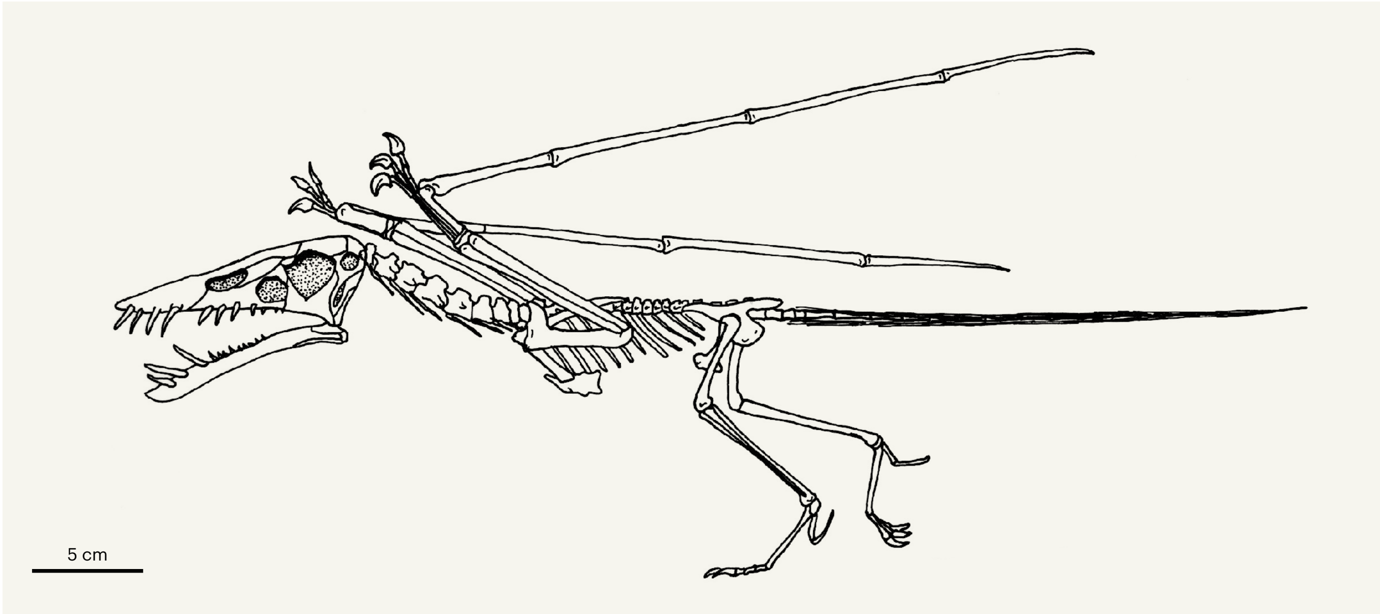

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Figure 2 | *Dorygnathus*. Reconstruction of an early pterosaur. Ezcurra *et al.*[2] have identified dinosaur relatives called lagerpetids as being the long-sought probable closest relatives of pterosaurs.

constructed that their extreme adaptations for flight actually mask many of the features that might otherwise reveal their relationships to other animals.

Ezcurra and colleagues provide this long-sought evidence, which points to a specific group of dinosaur-line archosaurs. The authors examined all the remains of the likely candidate groups known worldwide, some of which were specimens they had collected themselves. These small animals are called lagerpetids, a name that means rabbit-reptiles. They had long legs, a bipedal stance and the ability to run fast. Lagerpetids lived in the Middle and Late Triassic (some 235 million to 205 million years ago) and are known mostly from the Americas; however, deposits of this age are not well distributed worldwide. Lagerpetids form a constellation of bird-line archosaurs that would include creatures such as lagosuchids, silesaurids, *Scleromochlus* and the first pterosaurs and dinosaurs.

So what makes lagerpetids the best candidates for pterosaur kinfolk? It has been clear for several decades that pterosaurs evolved from small bipedal archosaurs whose hindlimbs were organized like those of birds and other dinosaurs, rather than like the more sprawling hindlimbs of crocodiles[5,9]. The proportions of their slender limbs, as well as the shape of their back, are fully consistent with a bird-like body plan[9].

Lagerpetids fit this profile, and, unlike other candidate relatives, they share some features with pterosaurs that other archosaurs do not. The authors made this finding through the use of an approach called phylogenetic systematics, which has been applied to uncover relationships between every group of organisms, including dinosaurs[10]. It searches out newly evolved features that link different organisms, the reasoning for this being that the most recently evolved traits must have appeared in forms most recently diverged from each other, and hence must be the closest genetically. These features, which often seem trivial even to experienced observers, provide the key to relationships, and sometimes to the evolution of adaptations, because one divergent group, the flying pterosaurs in this case, might have unusual features that reflect functions its sister divergent group lacks.

Ezcurra *et al.* realized that, although lagerpetids didn't fly, they share specific features with pterosaurs, such as complex characteristics of their braincase and inner ear, that might relate to the increased agility they had evolved. Their elongated hand (palm) bones (hyperelongated in pterosaurs, along with the fourth finger) suggest a good starting point for animals to evolve flight. Other shared features of the skull, jaws, pelvis, fore- and hindlimbs and vertebrae make a compelling case for the relationship.

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The results presented by Ezcurra *et al.* don't lay out the complete evolutionary path from a small, Earth-bound reptile to the first flying vertebrates. But one day a pterosaurian ancestor might emerge from Triassic rocks to fill in some of the blanks, in much the same way that the discovery of *Archaeopteryx* provided key clues to the early stages of bird flight.

Meanwhile, Ezcurra and colleagues' study underscores the view that pterosaurs are the closest major group to dinosaurs, that another group (lagerpetids) formerly thought close to dinosaurs are now shown to be even closer to pterosaurs than previously thought, and that the common ancestor of all of these groups was probably a small, long-limbed, short-bodied, slender biped with a large head, peg-like teeth, considerable agility and an acute awareness of its surroundings. So, ground-dwelling pterosaur precursors already had forelimbs that were free to evolve flapping flight. Cuvier, although he did not accept evolutionary transmutation to explain the transitions between major forms of life, would otherwise have felt vindicated regarding his original inferences about the anatomy and ecology of pterosaurs.

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